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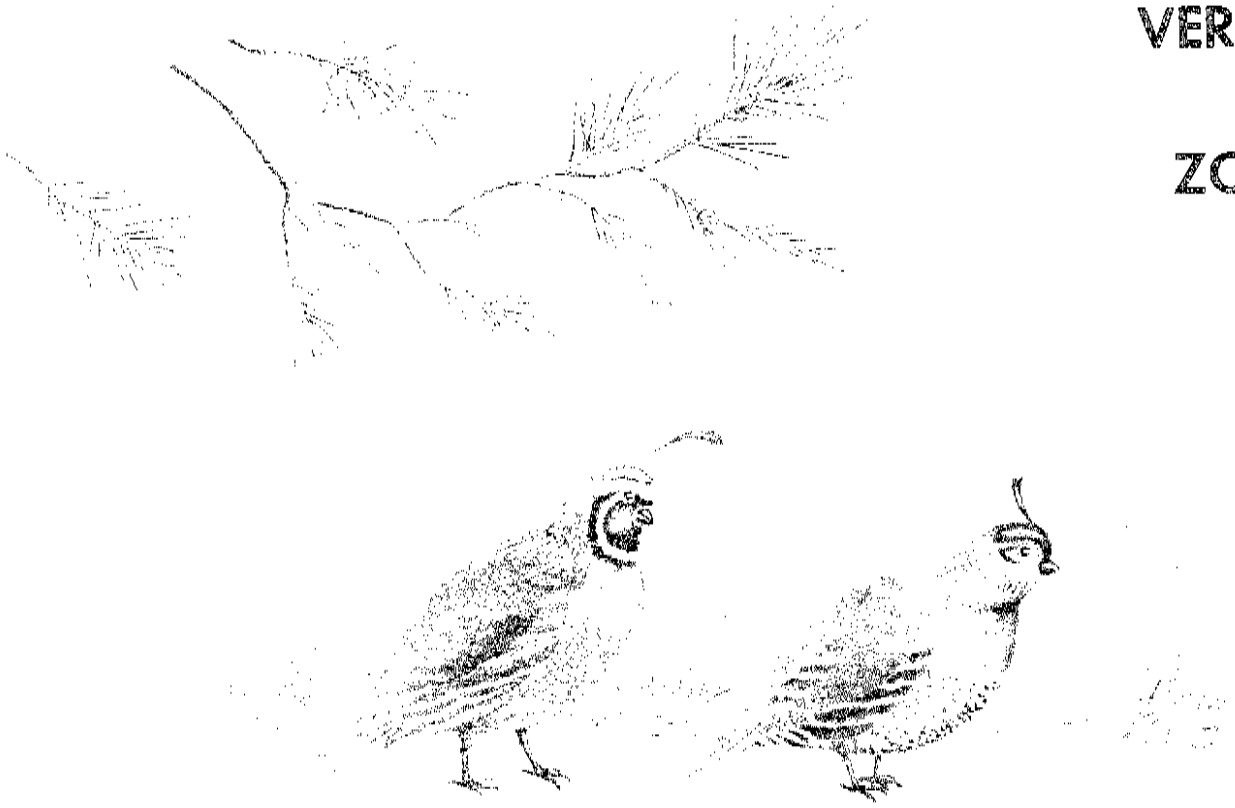

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BY JOE T. MARSHALL, JR.

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A NON-PROFIT CORPORATION DEDICATED TO THE STUDY OF ORNITHOLGY, OOLOGY, AND MAMMALOGY

Date of Publication: 10 August 1967

Joe T. Marshall, Jr.

Male *Otus asio aikeni* in its natural setting of velvet mesquite (*Prosopis velutina*). The compressed plumage and fierce expression are due to belligerence aroused from hearing his own song played on a tape recorder in his own territory. Photographed in the field in Arizona.

PARALLEL VARIATION IN NORTH AND MIDDLE AMERICAN SCREECH-OWLS

JOE T. MARSHALL, JR.

My objective in this paper is to provide for the first time a delineation of species of North and Middle American *Otus* based on acquaintance with their biological traits in the field. Next I wish to show their racial convergence in concealing color patterns. Finally, I attempt to portray the dramatic geographic variation in those evanescent colors and patterns of fresh autumn plumage, in recently collected specimens (largely taken by myself). These colors alone are relevant to concealment against the bark and foliage. Worn and faded specimens teach us nothing about nature except that the birds can afford such degradation of pattern in the nesting season. To me, this proves that selection pressure from predators is relaxed in summer. If not, there would be a prealternate molt to restore the details of cryptic coloration! The facts of racial variation that emerge from fresh fall birds are so different from any other treatment in the literature of the genus that you will doubt I speak of the same creatures! Only the writings of William Brewster and some of the other describers who happened to select fall type specimens correspond to what will unfold here. It is a shame that we cannot devise means of saving specimens of gray species from turning brown in the museum. The chemical means is surely hinted by the non-fading of those feathers still partly ensheathed on specimens taken during the annual molt.

The genus *Otus* consists of small arboreal horned owls that fly from a branch to catch mostly invertebrate prey on the ground or in foliage. Their wings are long and rounded, tail short, ear openings symmetrical and of moderate size, and their large eyes are set in conspicuous black-rimmed facial discs. Screech-owls live on small territories in woodlands and open forests, where they are the most abundant birds of prey. Mellow hoots and trills, characteristic for each species, secure the territory against intrusion by the same kind and unite the pair through duetting. *Otus asio* and *Otus trichopsis* divide these functions between two different tunes called respectively the primary song, which introduces a period of singing, and the secondary song, delivered later during the sequence. Among those species which have but a single commonly used song, I have heard duetting of the pair in *Otus guatemalae, bakkamoena* of Singapore, *whiteheadi* of Luzon, and *"Otus" podarginus* of Palau. The last two have long and involved duets during which the female chimes in to become synchronized with the male so that their songs end together. This sometimes happens in longer duets of Pacific coastal *O. asio*. In all these duetting species the female's song is of the same pattern as the male's but differs in being a fourth or fifth higher in pitch (except in *whiteheadi*) and of less mellow quality. I have not heard prolonged or regular duetting by the pair in *Otus flammeolus,* or in *O. spilocephalus* of Thailand. In these species the male sings his single note incessantly at regular intervals, generally in response to males on adjacent territories. They do not actually sing antiphonally, note for note, but each individual maintains his own interval between songs. The same appears to be true of *Otus scops* in Europe, as recorded by Dr. K. H. Voous, and of *Otus choliba* in Venezuela, recorded by Paul Schwartz. I regret that I have not heard these last in the field, nor do I yet have field acquaintance with *O. barbarus* and *O. clarkii*. I use the word "trill" for a rapid succession of pure musical tones at the same pitch. Though contrary to its dictionary definition, it is so used by ornithologists because there is no acoustic term for this song.

CONCEALING COLORATION AND PREDATION

Screech-owls are colored in soft gray, brown, buff or rufous above, white below, with a pattern of black pencillings. The white outer webs of the lateral row of scapulars are rimmed narrowly with black and there are some characteristic white marks on the distal secondary coverts. The sides of the forehead and inner side of the ear tufts are usually frosted with white, in some forms extended as a coronal band. This complex coloration is more interesting artistically than the blurry patterns of other owls. There are two styles in North and Middle America: spotted and barred in *Otus barbarus* and *O. clarkii;* normal style in the other five species. Normal *Otus* dorsal color is made up of little dots, wavy lines, and light interspaces. When telescoped together these produce a homogeneous effect, a fine texture; when less compact, the same marks are magnified into a heterogeneous background, of coarse texture. A black shaft streak, flared laterally at intervals, adorns each back feather. On the white underparts, shaft streaks crossed by several wavy bars look like large black ants marching in rows up the flanks. Several feathers on the upper chest have streaks three times as wide as those of the belly and flanks. In life these line up into two straight rows which I call the black cravats, one on either side of the chest, as seen in the frontispiece. The juvenile is narrowly barred all over except for the flight feathers, which are colored as in the adult.

Most screech-owls are dimorphic; the other plumage called the "red phase" is apparently caused by a dominant autosomal gene. Its black markings are often reduced and replaced ventrally by red anchors; the back is a gorgeous rufous like the red fox. D. F. Owen points out that "phase" is a poor word because it implies a transitory condition; remember that the red phase of *Otus* is fixed genetically for the lifetime of the individual. Dimorphic red and gray types occur in other arboreal nocturnal birds but are sex-linked. Females of *Otophanes mcleodi, Batrachostomus hodgsoni* and *B. javensis* are red whereas the male is red in *B. stellatus*.

By "artistic interest" I mean absence of monotony, contrast between sharply defined black designs and their soft-hued background, graded shades of the same color, and repetition of pencilled figures in a regular way with augmentation and diminution. Other birds rival or excel *Otus* in this, such as the wry-neck, *Jynx torquilla;* the poor-wills, *Phalaenoptilus* and *Otophanes;* frogmouths, such as *Batrachostomus javensis;* and some buttonquails and snipes. *Phalaenoptilus* spends the day beneath a bush, prone on rocky ground which it resembles so closely as to be invisible. It is perhaps the most beautiful of all birds and the best example of cryptic coloration in the animal kingdom. *Batrachostomus* and *Otus* sit in trees, whose bark they match beautifully.

Superb cryptic design is attended in *Otus* by appropriate immobility when surprised in the daytime. Roosting birds "play possum" and seem to be in a mesmerized state. I once weighed the live, unfettered owl by hooking its bill over the loop of a spring balance; I hauled one down from its roost merely by poking a stick under its toes whereupon it transferred its grip. I have caught *Otus asio* and *Otus trichopsis* by hand at night. They rely on their concealing coloration and shape of a broken branch to escape predation, rather than on ferocity or flight. Movement is imperceptible. While walking around the roost tree of an *Otus bakkamoena* I noticed that he was always looking straight at me, yet I could never perceive the slightest motion of his head. One shape of the roosting owl is normal posture, feathers fluffed out, and ear tufts elevated at about a 45 degree angle. With eyes open it resembles an ill-humored cat; with eyes shut it resembles the bark. A second roosting shape mimics a broken-off branch. It is elongate, with feathers compressed, head held high, ear tufts shot straight up, and loral feathers folded laterally to screen the eyes. Even at night while they are hunting, screech-owls often perch at the base of the branch, where it joins the trunk, and this is the special trait of the flammulated owl that makes it so difficult to see. Predators on *Otus* are probably carnivorous tree-climbing mammals and hawks by day, larger owls by night. The hawk would be attracted by mobs of small birds putting the owl to flight. Horned owls feed on *Otus asio* and W. C. Russell took a fresh *Otus flammeolus* from a horned owl stomach (along with an entire *Neotoma*). I found *O. asio* bones in pellets of the spotted owl (Condor, 1942, **44**:66-67).

PARALLELISM AND NATURAL SELECTION

The exquisite adaptiveness of coloration in *Otus* gains precision through racial variation fitting the birds to their local environment. Species after species accomplishes the same trends even on different continents. Where two or more occur in the same region, their coloration is almost identical. They are responding to the same forces of natural selection in the same way with comparable sets of genes. Most similar are *Otus asio* and *Otus trichopsis* where they occur together, such that they can scarcely be distinguished by coloration alone. In southern Arizona, both are grayest of their species; on the Mexican Plateau both are the blackest. Near the east edge of the plateau. *Otus guatemalae* joins in similarity to *O. trichopsis,* where both are the darkest and most coarsely patterned of their respective species. In general, *Otus asio, O. trichopsis, O. flammeolus* and *O. guatemalae* change from bold, coarse pattern in the north to fine and blended in the tropics, from rich dark brown in humid areas of the north to gray in deserts and to rufous in the tropics, and they all have their blackest form at or near arid country of high altitude (high mountains of the Great Basin for *flammeolus,* near the south end of the Mexican Plateau for the others). All have the red phase appearing in the southeastern tropics (where there actually are red-barked trees, and some with very smooth trunks) and additionally, for *Otus asio,* in the broad-leaved deciduous woods of the eastern United States. It seems to me inescapable that these parallels are caused by natural selection for cryptic coloration against the prevailing local color and texture of bark, leaves, and twigs.

By such reasoning Hasbrouck (Amer. Nat., 1893, **27**:521-533, 638-649) explained the virtual restriction of the red phase of *Otus asio* to the east, where deciduous broad-leaved woodlands prevail. Miller and Miller (Condor, 1951, **53**:161-177) accounted for the fine pattern and gray color of desert races of this species as enhancing concealment in the prevailing microphyll desert vegetation, where the bark is gray and leaves are dull. I would like to propose the following hypotheses to explain parallelism, cryptic coloration, and uneven distribution of the red phase, as a logical extension of the views of Hasbrouck and the Millers:

1. There is predation upon *Otus* by carnivores in the daytime and large owls at night; these predators are color-blind and cannot separate the color of the red phase from green leaves. They tend to eliminate individuals which do not match the background of their roost in the daytime, or of their perch while hunting or announcing territory at night. The color pattern reconstituted by the fall molt is completed at the crucial time when the population is densest, when the leaves have fallen, and when predation is most severe.

2. Different climatic areas have different prevailing color and texture of bark and foliage; for instance somber in the western United States, bright and varied in the east. Through natural selection by predation screech-owl races tend to match the prevailing color and texture. Where this is dull and monotonous, the owls are monomorphic and dull-colored. Where the vegetation is varied with contrasting textures and colors including bright, shiny ones as in Florida, there the owls run the gamut of colors between normal and red phases. Continuous variability over a broad spectrum is thus an advantage, where the varied trees are not deciduous.

3. In the eastern United States the red phase persists side-by-side with normal plumage because it is cryptic against the summer green and fall red leaves as far as the color-blind predators are concerned, whereas the normal gray phase is cryptic against the bark and twigs of the naked woods of winter. In deciduous forest, dimorphism is advantageous —two plumages for the two states of vegetation. (But this does not explain the red phase of *Otus trichopsis*).

4. There is something about the bark or foliage of tropical woods which puts a fine pattern and buffy or vinaceous tints at selective advantage.

5. Screech-owls must individually choose their roosts to match their own colors and pattern. We should notice whether the red birds tend to roost in foliage and the gray ones against bark.

These propositions, which I think are necessitated by what we know about geographic variation of screech-owls, all require testing by appropriate experiment and observation. I have found this difficult enough with unpatterned colors matching the soil (*Rattus exulans,* with *Asio flammeus* the predator, Bull. Bishop Mus., 1962, **225**:177-189). Evidence for predation on the basis of arboreal gray-brown and red morphs will be harder to obtain, in view of the complex floras which constitute the background.

THE SPECIES QUESTION

We taxonomists are so engrossed with subspecies that we have ignored a species problem existing in the United States, involving one of our most familiar birds, the common screech-owl, *Otus asio.* Western and eastern forms have different vocalizations; clines of geographically variable traits are interrupted between them; and they are almost wholly isolated from each other geographically. I found overlap with limited hybridizing in the Big Bend region of Texas, and regard them as incipient species well on the way to achieving full specific rank. My guess is that they cannot attain this rank without first diverging in ecology.

Why have the interrelations of western and eastern screech-owls been misunderstood? Principally because of the recovery of a pale red phase at Colorado Springs, Colorado, the type locality of the race *Otus asio aikeni.* Since the red phase is a characteristic of the eastern screech-owl, *aikeni* was thought to be an eastern form; for instance, Grinnell felt secure in describing its closest relative, *inyoensis,* without comparing it with *aikeni* (Auk, 1928, **45**:213). Actually the red specimens, together with a few more of normal phase in the Colorado Springs series, are *Otus asio maxwelliae*—an undoubted eastern race to the north. O. A. Knorr set the matter straight (Univ. Colo. Studies Series in Biology, 1959, **5**:22) when he stated that *aikeni* is the common resident about Colorado Springs and that *maxwelliae* is a rare winter visitor from north of the Arkansas divide. It remained only to determine whether *aikeni* was a western or eastern screech-owl.

My efforts to call up eastern screech-owls at Fountain Creek, Colorado Springs, in September, 1961, by playing taped songs, were rewarded with near trampling by a loudly answering horse. But western "bouncing ball" songs attracted topotypical examples of *aikeni;* I recorded their western style songs on tape, and preserved four as specimens for the University of Arizona collection. Their black bills and longitudinally arranged pattern, in addition to voice and clear gray dorsal ground color, settle *aikeni* as belonging to the western screech-owl, which may also be known as the incipient species, *Otus kennicottii,* or the Kennicottii Group. Two additional groups, more similar to the western screech-owl than is the eastern screech-owl, enlarge the same species question to include populations south to Costa Rica!

Method.—By now it should be obvious that the species question in *Otus* can be solved only by recourse to the combined evidence from morphology and biology. Biological traits are from my own field observations, in notebooks deposited at the Museum of Vertebrate Zoology and the Western Foundation of Vertebrate Zoology. These are very detailed as to habitat, spacing and voice. Sites of these observations are listed in the accounts that follow under the habitat of each form; also are mentioned whether or not specimens were collected by myself and tape recordings made. I must dwell on field notation of screech-owl songs because some persons will contest every vocal comparison not made with sonagrams. I have not been using recorders long enough to gather on tape the quantitative data represented in my field notes. These simple songs are amenable to written description and rendering by diagrams, easily understood by others. My notes are full of them and thus I am confidently able to present the *usual* vocalizations. Because of field experience with hundreds of individuals I can avoid comparing non-homologous songs, which would produce bizarre splitting of species. For instance, you cannot split *Otus asio seductus* as a species distinct from *Otus asio aikeni* by contrasting the only preserved tape of it, which happens to be the nest alarm call of the female, with the double trill of the male *aikeni,* unless you ignore all data of the field observers who know that both give the same primary and secondary songs, and that females excited at the nest are capable of quite varied sounds.

Using all possible criteria of structure, especially the foot and its feathering, ecology, distribution, and voice, the following key can be set up, which clarifies species limits.

KEY TO SPECIES AND INCIPIENT SPECIES OF NORTH AND MIDDLE AMERICAN *OTUS*

I. Toes and tarsus feathered (those of toes bristle-like in south); medium to large size wing chord (130-190 mm.); normal *Otus* pattern of shaft marks on back and shaft streaks with crossbars on venter; iris yellow (except brown in *seductus*); two territorial songs.

A. Large size (wing 135-190 mm.); bill and feet large; inner web of outer remex with light bands; red phase in east; secondary song a steady trill or two trills; generally non-migratory; southeastern Alaska and Maine to Costa Rica ..... *Otus asio*

1. Usual dorsal pattern is of linear black streaks; ventral pattern is of prominent shaft streaks with thinner, perpendicular crossbars (or rows of dots in south); secondary song a short trill followed by a long one; monomorphic (except a rare red phase in British Columbia).

a. Primary song is of notes speeded-up (bouncing ball) on same pitch. (*Xantusi* in addition uses the 13-note song of the Cooperi Group.)

1) iris yellow; bill black with tip minutely whitish (except interior northwestern population, northern *bendirei,* which is greenish gray); voice soft and mellow; tame except Baja California and Sinaloa races (*xantusi, vinaceus*); southeastern Alaska to western United States, around the Gulf of California, and Mexican Plateau ..... incipient species, Kennicottii Group

2) iris brown, bill greenish; voice loud and gruff; wild; Colima and Río Balsas basin of México ..... incipient species, Seductus Group

b. Primary song is of 13 or 15 even gruff notes rising in pitch during the middle of the series; iris yellow, bill pale greenish; wild; Pacific Coast from Isthmus of Tehuantepec to Costa Rica ..... incipient species, Cooperi Group

2. Dorsal shaft streaks tend to be flared transversely; ventral pattern has crossbars equally wide as shaft streaks, and crossbars are in anchor pattern, not perpendicular to the shaft; secondary song is a long trill; dimorphic, with red phase (except along Río Grande); bill green or yellow or turquoise; eastern United States and coastal plain of eastern México ..... incipient species, Asio Group

B. Medium size (wing 130-150 mm.); bill and feet small; inner web of outer remex unmarked; pattern always coarser than other species at the same latitude; red phase in south; iris yellow; secondary song in a syncopated rhythm; non-migratory; Arizona to Nicaragua ..... *Otus trichopsis*

II. Toes naked; small to large size (wing 120-180 mm.); only one known territorial song.

A. Tarsus feathered for entire length (sparse and tending to rub off distally in southern form of *guatemalae*); normal *Otus* pattern of shaft marks above and streaks with crossbars below (or rows of dots comparable to the crossbars), this pattern degraded to vermiculations in most individuals in southern range of *guatemalae;* no light spots.

1. Iris brown; size small (wing 120-140 mm.); base of toes hidden in dense tarsal feathers: feathers of erectile ear tufts no longer than other feathers of crown; coloration varies from dark gray to reddish without two distinct phases; territorial song a low-pitched single mellow hoot with or without preceding grace-notes; migratory; summers in western North America from southern British Columbia to south end of Mexican Plateau; winters in México and Guatemala ..... *Otus flammeolus*

2. Iris yellow; size medium to large (wing 143-173 mm.); base of toes not hidden; feathers of ear tufts longer than those of crown; territorial song not a single hoot; non-migratory.

a. Toes of normal proportions; black marks are longitudinal sharply-defined streaks; those of the venter are narrow, distinct shaft-streaks with precisely perpendicular black crossbars; plumage everywhere with golden undercoat (the feather bases); plumage normally varying from gray to buff, but a rare red phase occurs; wing about 160-173 mm.; song a series of notes rising in pitch with several final ones accented; Costa Rica to South America ..... *Otus choliba*

b. Toes extraordinarily long; black marks on back are transverse, in the shape of little pagodas; ventral crossbars not exactly perpendicular to the shaft streaks; bases of feathers not golden; dimorphic, commonly with a red phase; wing 143-170 mm.; bill pale greenish; song a prolonged trill at one pitch as in Asio Group but longer and increasing in loudness; México to South America ..... *Otus guatemalae*

B. Tarsus naked at distal end; plumage pattern of paired buff or white spots with black bars or chevrons (not of normal *Otus* style); song unknown; non-migratory.

1. Small (wing 131-139 mm.); tarsus bare for about 3 mm. distally; ear tufts bear a continuation of a bold white bridle and collar on the head; iris yellow; high mountain forests of Chiapas and Guatemala, where evidently an ecological counterpart of *Otus flammeolus*.....*Otus barbarus*
2. Large (wing 180 mm.); distal third of tarsus naked; ear tufts colored like rest of upperparts; no white lines on head; iris yellow, bill blue-gray; mountains of Costa Rica and Panamá.....*Otus clarkii*

GEOGRAPHIC VARIATION

Methods.—Geographic variation in screech-owls is so extreme, and their coloration so complicated, that it is a real problem to describe and tabulate them. R. T. Moore was understandably a victim of the great number of traits that could be used, including artificial differences due to wear and fading. His bizarre racial distributions in standard works like Peters' *Checklist of Birds of the World,* vol. IV, 1940: Moore and Peters, The Genus *Otus* of Mexico and Central America (Auk, 1939, **56**:38-56); and Friedmann, Griscom and Moore, *Distributional Check-list of the Birds of Mexico* (Pac. Coast Avifauna no. 29, 1950) made it appear that nature had created an excess of screech-owl races in blind, senseless caprice. At the opposite pole, D. F. Owen (Systematic Zoology, 1963, **12**:8-14 and Wilson Bull., 1963, **75**:183-190) through oversimplification suppressed all the biological facts not concerned with the red phase in the eastern United States—which he dealt with competently. Normal plumages were merely "dark" or "light" which failed to resolve rich fuscous birds of the humid coast of British Columbia and Florida from the black ones of the arid Mexican Plateau and Baja California Norte.

We can hope to make biological sense by confining our attention to a few features of cryptic coloration involved in parallelism—hence of evolutionary importance—and following them through the whole genus. These features are the dorsal ground color and dorsal black shaft marks as seen on the middle of the interscapulars and the ventral pattern as observed on the middle of the flanks. Other parts concerned with protective mimicry of bark (crown, face, wings, tail) are correlated with these, or at least do not clash (legs), and they are not described here. Fall specimens are grouped by populations from the largest geographic areas within which there seems to be no further subdivision into color races. There are about 32 such populations for the four geographically variable species in our area. The prevailing coloration of a population is given a name, and a typical specimen is picked as a standard against which each museum specimen can be compared and given the two names that stand for its dorsal and ventral coloration. The result is plotted on a graph, as I have done for the song sparrow (Condor, 1948, **50**:193-215, 233-256) and for the whiskered screech-owl in this paper, showing the proportion of specimens from one population that have coloration identical with that of a neighboring population.

Implementation of this method is incomplete, particularly for *Otus asio.* It has taken me years to discover what colorations actually characterize certain localities; meanwhile my own September and October specimens from critical areas have turned brown. I have not yet compared the various collections against the same set of standards. This will be a rewarding task for the future, if the quantitative data thus obtained will correlate irregularities of intergrading with ecologic and geographic features.

Recent fresh fall ground colors are cold, clear gray above and pure white below, as contrasted with recent spring or old fall specimens. Even the red phase is a colder tone when fresh. The red of *Otus flammeolus* is underlaid by gray, so is the buff of *Otus asio cooperi.* The back of *Otus asio yumanensis,* described by the Millers variously as "light tawny," "light warm gray," and "yellowish" in their spring specimens, is really clear gray overlaid with pink in the fall. This formidable amount of differential fading and wear, especially severe on the desert, makes it misleading and useless to examine skins taken after December (except in the far north). Individuals will differ according to how much sunlight hits them on the roost and populations will differ in amount of fading due to local climate, and amount of wear according to how active they are in winter and how early they nest. By the time of nesting, weird colors and stains from the tree hole begin to show, and the tips of all feathers wear off. I have limited my color examinations to those specimens showing new feathers during the prebasic molt in August, and from then through December. I include unworn birds from Middle America at any time of year, for the molt seems to be less circumscribed seasonally there. Postmortem fading in the museum is also severe; grays inevitably turn to brown; the white belly becomes sullied; and the first stages can be noticed in three years. The resulting taxonomic confusion can be appreciated in *Otus guatemalae,* in which it is possible every decade or so to describe from recent skins a "new, blacker" race, *fuscus* Moore and Peters, for example!

Crude as they are, wing chord and weight are still the most valuable measurements. Unworn wings only were measured, on the side that seemed to preserve the most natural curvature. Even a little spring balance or postal scales are useful in the field, to show us for one thing that tropical forms of *Otus asio* are large bodied in proportion to their wing-length; their weights are in keeping with their large feet. Graphs of measurements and weights are planned for a future paper, when they can accompany refined tabulations of fall phenotypes and distribution maps.

Subspecies.—I shall use the terms subspecies, race, and distinctive population synonymously. The trouble with subspecies, of course, is that they have become loaded with all sorts of false attributes that do not exist in nature, such as discreteness, discontinuity, and sharp boundaries done with zipatone on distribution maps. Actually, most geographic variation on continents is continuous, by way of smooth clines. Nevertheless, the use of subspecific scientific names is the only solution to the staggering problem of bookkeeping involved in studying geographic variation of complex, cryptic color patterns. The old racial names serve the mnemonic need splendidly. I shall use each as a one-word designation of the particular style of coloration predominating in a geographic area. Such a name sums up the following information: the color and texture of the dorsal ground; the distinctness, shape, and width of the dorsal shaft mark; width of the ventral shaft streak; the direction and width of the ventral crossbars; and whether they are wavy, dotted, or linear, distinct or misty.

Formal trinomials will be limited to those populations that are 100% separable in color, which I can now confidently describe. Don't worry; there are plenty of them, as we shall presently see. To me, such geographic races are islands of unique traits developed to an extreme, set about in a vast sea of heterogeneous intergrades and intermediates.

OTUS ASIO, Common Screech-owl

Distinction from **Otus trichopsis.**—*Otus asio* is so similar to its close relative, *Otus trichopsis,* as to be distinguishable afield only by voice. Its duetting song is a rapid succession of short notes at even pitch and interval lasting 2 to 4½ seconds; a short pause sets off an opening burst from the remainder of this song in western races. *Trichopsis,* on the other hand, utters an even series of slower notes, or produces a syncopated rhythm of short and long notes. In the hand, first look for feathers or bristles on the toes, which set *asio* and *trichopsis* apart from all other American *Otus*. Second, find that the feet are large and powerful and that the inner web of the outermost primary is banded or blotched with a regular series of light patches. These traits determine the specimen as *Otus asio.* Its pattern of black marks is always finer than that of *Otus trichopsis* of the same region or latitude.

Separation from **Otus bakkamoena.**—The common screech-owl's ecologic counterpart in Asia is the collared scops-owl, *Otus bakkamoena,* which has from time to time been synonymized. Herbert Deignan renounced this disposition upon learning that their Mallophaga are different species, at opposite poles within the two genera *Strigiphilus* and *Kurodaia. Otus bakkamoena* harbors *S. heterogenitalis* Emerson and Elbel and *K. deignani* Elbel and Emerson, whereas *Otus asio* is host to *S. otus* Emerson and *K. painei* (McGregor). *Strigiphilus otus* has been found in the races *kennicottii, aikeni, seductus, hasbroucki* and *asio;* it is more similar to a species on the burrowing owl than to the one from the collared scops-owl. These Mallophaga are pictured in the following publications by K. C. Emerson and R. E. Elbel: Proc. Ent. Soc. Wash., 1955, **57**:241-242; Proc. Biol. Soc. Wash, 1957, **70**:198-200; *ibid,* 1960, **73**:119-122. They give the taxonomic implications for *Otus* in Proc. Okla. Acad. Sci., 1959, **39**:76-78.

Otus bakkamoena has the same broad ecologic tolerance as *Otus asio,* preferring lowlands but occupying all sorts of woodlands and even forests. It enjoys the same enormous latitudinal spread, over which it shows profound geographic variation including reduction in size southward; also it is of the same size and proportions as *Otus asio.* There the resemblance ends, for *Otus bakkamoena* is a buffy bird, with long ear tufts, diminished pattern of black marks, and with brown eyes. It varies geographically in amount of toe feathering, all but the northernmost races being bare-toed. The specialized papery feathers of the facial disc continue around the throat to encircle the mouth. The toe feathers, when they occur, are in a definite strip on top of the toes, sharply marked off from the naked lower half or two-thirds of the circumference. All these traits are distinct from *Otus asio.* Finally, the voice of *Otus bakkamoena* is entirely different, as the sonagrams show. The ordinary call is a single, muffled, short, descending "bew," uttered at regular intervals. I have heard only one other rare vocalization, and must consider its author a bird of limited and monotonous repertoire.

Size.—Of the species of *Otus* which I have weighed and measured, *Otus asio* shows the greatest differences between populations. It is the only one of the four North American species (*asio, trichopsis, flammeolus* and *guatemalae*) with pronounced sexual difference in size. Females average 15% heavier and 3% longer winged than males (using male values as 100%).

Some details of plumage.—The black cravats, generally decorated with buff or rufous, are more prominent than in other species having the standard pattern. The underwing of fresh fall birds is suffused with a transitory salmon-pink color. Ear tufts are present. Juveniles often have narrower and more pointed primaries than adults but cannot be aged after the complete prebasic molt. Several early September specimens have unworn wing-tips noticeably browner than the rest of the plumage; their primaries are doubtless from the recent juvenile plumage. These are the last to go in all ages, for through the remainder of the month practically all United States specimens are replacing the outer primaries to complete the molt.

Voice.—The common screech-owl has by far the most varied calls of any owl known to me. Besides the primary (territorial) and secondary (duetting) songs there are calls given at dawn different from those at dusk; special calls by the female from inside the nest hole and when bringing food to the young; barks, yips, excitement calls around the nest; alarm notes at horned owl hoots; and various food calls of the young, different for different stages of growth. Finally there is a dramatic outburst of explosive barks uttered in flight to the accompaniment of loud bill-snapping.

Distribution and gaps in range.—This owl occurs from southeastern Alaska, southern Canada and southern Maine south to Costa Rica, with important gaps. The species is absent along the Pacific slope from central Sinaloa to Colima and again from the Río Balsas basin in Guerrero to south-central Oaxaca. It is absent from the Atlantic side of Middle America south of the southern tip of Tamaulipas. From central Sonora southward there is a narrow gap along the west edge of the Sierra Madre Occidental and south base of the Mexican Plateau. The Rocky Mountains apparently constitute a gap from British Columbia to central Colorado which continues southward in treeless plains of southeastern Colorado, eastern New Mexico, and western Texas and thence to the whole length of the Sierra Madre Oriental and treeless plains at its west base in Coahuila, Nuevo León, and San Luís Potosí. With the sole exception of the Río Grande, my efforts to fill these gaps and to find intergrading between the populations thus sundered, have met with repeated failure.

I have not been to the northern Rockies, but I could not find the species in southern Colorado and northern New Mexico along the forested mountain passes, in willow thickets, valleys, and piñon woodlands. Although two forms, a resident and a winter visitor, are known from Colorado Springs, Colorado, I could call up no birds in or around that critical area, even using a tape recorder! The splendid cottonwood forest of Fountain Creek, in September 1961, was barren of screech-owls for fifteen miles south of the city; possibly the use of insecticides had eliminated them from this dairy pasturing area. Past this point the resident form (*aikeni*) was abundant, but that is already too far south of the important overlapping of eastern and western floras which might bring the forms into juxtaposition on the Arkansas Divide, just north of Colorado Springs. In Coahuila I have not found the species in giant yucca woods, nor in mesquites and various riparian trees around Cuatrociénegas. Other areas of México, where most of my vain efforts were directed, have yielded no *Otus asio* as follows: central and southern Veracruz in a variety of habitats; environs of Tehuacán, Puebla, in mesquite woodlands, giant yucca with brush (where, however, Robert Dickerman found a good winter specimen killed in the road), and open tropical woods with giant candelabra cacti; Acatlán, Puebla, again in giant cacti; and valleys and mountains in all directions around Mitla, Oaxaca, in all types of woodland from cacti upward through oaks to pine-oak woodland. Consolation was afforded by turning up the ubiquitous *Micrathene whitneyi* in some of these lowlands, and *Otus trichopsis* with it in the mountains.

Turning again to the Pacific drainage, along the west escarpment of the Sierra Madre Occidental, I have noted its absence in sycamores, oaks, and pine-oak woodlands at middle elevations in central eastern Sonora, and southeastern Sonora at the Chihuahua boundary. The type specimen of *Otus asio vinaceus* comes from between these points, but at a lower elevation. This hiatus divides a Mexican Plateau population in open pine forests of the summit from that of tropical woods along the Pacific coastal base of the Sierra Madre Occidental. There were none along the road between Durango and Mazatlán. I spent two weeks in southern Sinaloa chasing after elusive birds calling like *Otus asio cooperi,* only to find through the skillful assistance of a boy from Elota that they were *Ciccaba virgata.* The farthest south in Sinaloa that I have met *Otus asio* is in short tropical deciduous woodlands with giant cacti at Culiacán, where it was too wild for me to collect the southernmost example. From there on down the coast to Colima is a humid region with tropical tree growth too tall and dense for this owl. I have worked the likely-looking palm savannahs, oaks, mesquites, and pine-oak woods in Nayarit to no avail.

In Oaxaca, suitable arid tropical deciduous woods with giant cacti reappear along the Río Tehuantepec, where Chester Lamb discovered an abundant small race. But I could find the species nowhere else across the Isthmus of Tehuantepec or in Chiapas, except right at the edge of the Pacific coastal mangroves.

Ecology.—Evidence for migration is presented in the discussion of Colorado Springs. Almost all *Otus asio* are sedentary, on small territories, and are found in pairs. Prey is apparently caught in the feet. Large invertebrates such as orthopterans, scorpions and centipedes are the usual food, with an occasional mouse, bird, snake, or lizard for "dessert." Foraging by a short flight from a tree to capture the prey on the ground is facilitated by open woodland growth, where there is bare ground under the trees and around the edges of groves. The various altitudinal and geographic limits of populations coincide with unsuitably dense tall forests in mountains and in humid districts of the tropics. The coloration of *Otus asio,* simulating as it does the texture and color of bark, further proclaims its close association with trees and tree-holes for nesting and roosting. Yet paucity of trees does not invariably limit distribution. Along the banks of the Río Grande from the Big Bend region to Langtry, Texas, are few trees large enough to furnish holes for the scattered owls that exist there, and I assume that they nest in the plentiful holes in rocks and cliffs overlooking the river. Apparently the trees are periodically swept away by floods.

Habitats occupied by *Otus asio* are so varied over its enormous range that they are best described in the accounts of subspecies. An overall species designation can be "any open woods." Oaks, cottonwoods, and mesquites are especially favored. With only two exceptions (Providence Mountains, California, and Seligman, Arizona) I have never found the bird in piñon-juniper woodland. Further points to be remembered about habitat are: (1) absence of the species from the areas listed in México where seemingly ideal giant candelabra cacti with woodpecker holes abound, and (2) the rejection of riparian woodland—even of cottonwoods and willows—by all the populations of the Pacific coastal plain south of Guaymas, Sonora.

Response to man-made changes.—In the United States, the common screech-owl finds a congenial home in suburban trees including exotics, and it uses artificial nest boxes. Even in agricultural areas, shade trees are prized, and they remain to attract birds. There is a move afoot to control cottonwoods in central Arizona for more efficient watershed management, inasmuch as they use a good deal of water. This is a way of removing the owl and other wild creatures which make life interesting in the desert! In México, except for Colima, trees are removed by slash-and-burn from the entire landscape, with disastrous effects on the native avifauna. The burgeoning vegetable growing areas on the coastal plain of Sonora and Sinaloa, made possible by miracles of irrigation, are indicative of the eventual disappearance of the owl from all level terrain; and in this part of its range it does not enter suburbs or riparian woodland, its main refuges in the north. In areas where cattle are raised by running them wild through the natural woods and deserts, it fares much better. In fact, most of its occurrence coincides with such land use both in the United States and in México. In Colima the species is actually abundant in arid woods opened up by grazing and scattered cornfields. Some trees are left even in the largest milpas, and these the owls use for singing and hunting.

Two exotic riparian trees are hospitable to the common screech-owl. I was surprised to find it in normal abundance in tamarisk-choked willow groves along the lower Colorado River. It also is common in pepper-trees which line arroyos on the Mexican Plateau.

Otus asio, *a composite.*—Actually this species is a composite of four geographically-isolated sections which approach the level of full species. Their primary songs are different. Clines of geographically variable traits terminate at their boundaries; none continues on into the next section. And there is one area of overlap! Why not consider them all as full species? Because there are no really good morphological characters to distinguish them, because there are some astonishing similarities in their vocalizations and colorations, and because I have found a mixed pair with grown young and other evidence of interbreeding between the two that differ most in voice. This perplexing state of affairs makes *Otis asio* and its subgroups, for me, the most fascinating of all birds. Each field effort has turned up new excitement and surprises, usually necessitating a complete overhaul of my views. Although I regard them as conspecific, I must present them separately so that you can judge for yourself.

Reference to the key, map, and foregoing account of the distributional gaps which set them apart will serve to introduce these four sections. If they are indeed full species, their names will be *Otus kennicottii* (Elliot), *Otus seductus* Moore, *Otus cooperi* (Ridgway), *Otus asio* (Linnaeus). I shall refer to them as four incipient species: the Kennicottii Group, Seductus Group, Cooperi Group, and Asio Group.

THE KENNICOTTII GROUP

(OTUS KENNICOTTII, Western Screech-owl)

Diagnosis.—Dorsal pattern of dark streaks; ventral pattern of prominent shaft streaks, with much thinner crossbars or corresponding rows of dots. Coloration somber, in plain browns or cold grays; so much less colorful than the Asio Group that the intermediate red phase looks just like the gray phase of the latter. Territorial and duetting songs of mellow pure tone and constant pitch: primary song of notes at decreasing intervals "like a ball bounding more and more rapidly over a frozen surface" (Hoffmann, *Birds of the Pacific States,* 1927:166); secondary song a short burst of rapid notes followed by a longer series of the same—the "double trill." Iris yellow; bill usually black. Monomorphic, except for a red phase in British Columbia and scattered intermediates.

Distribution.—Pacific coastal slope from Juneau, Alaska, south to the Cape of Baja California and Culiacán, Sinaloa. Extends continuously inland to the west base of the Rocky Mountain region from Okanagan Landing, British Columbia, through Idaho and central Utah to New Mexico, where is crosses the Continental Divide to swing northward into southeastern Colorado. It continues southward to include the whole Mexican Plateau with easternmost points at Boise City, Oklahoma; Langtry and Juno, Texas; mountains above Saltillo, Coahuila; and México, D. F. Again notice the uninhabited west escarpment of the mighty Sierra Madre Occidental massif, which separates temperate and tropical zone populations.

Red phase.—This gorgeous coloration, a subdued cinnamon-buff type of red, is shown by one juvenal male and eight adults of both sexes from Alaska and coastal British Columbia. They comprise 7% of their racial population. Almost as distinctive is the intermediate or half-red phase represented by 7 specimens (5%) of the above northwest coastal population, 7 from the interior Northwest (11% of their race), one from Baja California Norte, and one from México, D. F. These have a semi-rufous dorsal ground, and rufous splashed upon the ventral pattern. The black dorsal pattern is reduced; anchor marks similar to the Asio Group are usually developed on the underparts. Rufous overlying the normal bluish gray produces a curious purplish tint above, especially on the wings. All these specimens are listed in the appendix.

The interior Northwest specimens of intermediate phase closely resemble the normal phase of the Asio Group from New England! But on their upper or lower surface they show tell-tale agreement with their local race. For example, Major Bendire's specimen with "testes large and heavy" perfectly matches New England birds above, thus contrasting with the uniform remainder of his series from Fort Walla Walla. Below, however, it is densely cross-barred like its western fellows.

INTERRELATIONS WITH ASIO GROUP

The preceding paragraph confronts us with color similarities between the Kennicottii and Asio Groups. Bill color in the interior Northwest approaches the Asio Group even in normal specimens! From southern California come a few buffy-brown specimens with narrowed ventral streaks and broad, recurved or irregular cross-bars. They also are similar to grayest examples of the Asio Group from the northeastern states. All this suggests close relationship and genes in common. The secondary songs of the two groups are identical in pitch and quality; there are no known ecologic differences. What is the evidence from distribution? This has to be looked for along rivers crossing the Great Plains, where cottonwood timber large enough to have holes or magpie nests may connect eastern and western race groups.

North of the Arkansas divide, the two are apparently separated by the Rocky Mountains. Southward from there, Colonel Wolfe and I have viewed the treeless plains and have found the only cottonwoods, and the only possibilities of contact, to be on the Arkansas, Cimarron, Canadian, Pecos, and Río Grande rivers. On all these except the last, our investigations were in March and April, 1966, when the females were incubating and the pairs were too busy for territorial defense. They would respond to taped songs only briefly at dusk. This precluded tracing them into the scattered cottonwood patches of the gap. This could be done better in the fall. We found no sign of gene exchange between western and eastern common screech-owls in song, coloration, or bill color. Eastern bills were pale grayish-green; western, black. Ecologically they were identical, for the cottonwood groves (stunted by western standards) seemed the same everywhere.

On the Arkansas River, we took a specimen of the eastern screech-owl on the Kansas-Colorado boundary near Coolidge, Hamilton County, Kansas, and made recordings of eastern songs. The specimen is no. JTM 6309 in the U. S. National Museum; the University of Kansas has another from the same place, no. 20886. They are of the *swenki* phenotype. West of Holly, Prowers County, Colorado, the cottonwoods thin out. The next known specimen is pure *aikeni,* the western screech-owl, from Rocky Ford, Otero County, Colorado, American Museum no. 476823. *Aikeni* is the common form on up the Arkansas River from there to Fountain Creek below Colorado Springs.

On the Cimarron River, G. M. Sutton, L. R. Wolfe and I made tape recordings and took specimens of pure *aikeni* near Kenton and Boise City, Cimarron County, Oklahoma. The specimens are nos. JTM 6306 and 6307, U. S. National Museum; and GMS 14940 and 14942, University of Oklahoma. At the Carnegie Museum is another typical fall *aikeni* from Kenton, no. 113344. The closest downstream locality that we visited in the evening was north of Elkhart, Morton County, Kansas. Here tape recordings were made of several eastern birds and a pure eastern specimen, of the phenotype *swenki,* was collected, no. JTM 6308 in the U. S. National Museum. There is a similar fall bird from the same place at the University of Oklahoma, no. RRG 1815. There are other eastern specimens down the Cimarron River, and I recorded more eastern songs and saw two pairs including my first living red phase—an astonishing sight as seen at close range by flashlight—12 miles north of Liberal, Seward County, Kansas. Thus on the Cimarron, the gap is at most 40 miles, with no sign of interbreeding or overlap.

On the Canadian River I saw and made tape recordings of an eastern screech-owl three miles northwest of Tascosa, Oldham County, Texas. Farther upstream we found no suitable riparian timber, just saltcedar brush, around Logan, New Mexico, so there can be no connection of screech-owls there. Similarily on the Pecos River, there was only saltcedar brush from the mouth of Delaware Creek at the New Mexico-Texas boundary to the town of Pecos. There are said to be small patches of cottonwoods at long intervals. Delaware Creek, with its willows, looks like possible habitat for the western screech-owl, which would narrow the gap only slightly between the remote outposts of the Guadalupe Mountains and Sheffield, as documented in figure 7.

Summarizing, it appears that there is a gap between western and eastern screech-owls of as little as 40 miles along rivers crossing the plains and that more could be learned at a season when the birds are responsive to taped calls. At present there is no sign of interbreeding or overlap on these northern rivers. Our only knowledge of bridging the gap comes from Colorado Springs, Colorado, and the Río Grande, Texas.

Colorado Springs.—At Colorado Springs, the resident *aikeni,* palest gray race of the Kennicottii Group comes close to the palest race of the whole species, *maxwelliae,* which is whitish with reduced and inconspicuous pattern. They are enough alike so that an occasional dark *maxwelliae* will look like *aikeni* except for its yellow bill and buffy wash decorating the ventral pattern. This race lives as close as Denver, 60 miles to the north, and occasionally turns up at Colorado Springs in winter. The entire series from this area (El Paso County and Fountain Creek) may be categorized as follows:

aikeni, black bill:	juveniles	3	
	breeding adults, including the type	7	
	fall and winter adults	9	
maxwelliae, yellow bill:	winter red phase	1	January
	winter normal phase	2	(Feb. for one)
	winter exceptionally dark	2	Jan., Dec.

The last two birds, Colorado College numbers 477 and 479, could be hybrids. That of January has only the bill tip yellow. The December bird, still darker and like *aikeni* on the back, has a yellowish-olive bill. Unfortunately, it is a hand-raised pet nine months old and cannot be seriously considered, but one wonders where its nest was and who were its parents. (The above specimens are in the University of Arizona, Colorado College, Denver Museum, and Museum of Comparative Zoology.)

Contact at Big Bend.—Overlap along the Río Grande of Texas is shown in the figure. (The store-bought specimens of *mccallii* in the American Museum of National History labelled "El Paso" are unacceptable; only the Kennicottii Group occurs that far up the Río Grande.)

All the 1961-62 birds were called up very close with a tape recorder. In each area I played songs of both the Asio and Kennicottii groups. I personally listened to their songs, recorded most of them on tape, and made study skins, all but one of which (a *suttoni* given to its namesake) are in the University of Arizona collection. Overlap of the two groups, Kennicottii and Asio by their respective local races *suttoni* and *mccallii,* is a definite fact, with the former going downstream to Langtry, and the latter occurring upstream as far as Boquillas—sympatry along 120 miles of the Río Grande! The specimens show little intermediacy, maintaining the distinctive songs, and to a lesser extent, the coloration appropriate to their group.

The Langtry birds, at first glance, seem splendidly to show sympatry without interbreeding. Colonel L. R. Wolfe and I went there in October, 1961, just after establishing the sole occurrence of *suttoni* at Lajitas. Using the tape recorder, we took the five Langtry birds along less than a half mile of riparian growth; two are *suttoni* and three are *mccallii* based on all three traits of voice, bill color, and plumage coloration. I interpreted this to mean that we had luckily stumbled upon thriving, dense, twin populations behaving as full species. But Colonel Wolfe had misgivings about my racial determinations of plumage color, which were:

Identified as	Field number	Sex	Dorsal Coloration	Bill color	Voice
suttoni	5756	♂	*suttoni*	black	bouncing ball, double trill
suttoni	5757	♀	*suttoni*	black	double trill, yodels
mccallii	5755	♂	*mccallii*	green	attracted by taped whinny and long trill.
mccallii	5758	♂	*cineraceus*	green	"
mccallii	5759	♂	*hasbroucki,* with *mccallii* crown	green	"

I felt that the ventral pattern (4 *mccallii,* 1 *hasbroucki,* respectively) was of minor importance and that inconsistencies of dorsal color among the three *mccallii* were due to intergrading with *hasbroucki* which prevails not far to the north. The stage was set, I thought, for a beautiful solution to the Kennicottii-Asio problem through study of the voice, behavior, and pairing of the living birds to be accomplished the following spring.

Imagine my chagrin upon returning for a week in May, 1962, to find not a single owl in the area! About two miles up-river I found a male *suttoni,* recorded his bouncing ball songs, and observed him closely to see that he had a black bill. My "twin populations" must constitute but a single family, wiped out by the lethal tape recorder, which attracted every screech-owl within hearing. A likely disposition would be that female *suttoni* number 5757 and male *mccallii* number 5755 were a pair that had raised the motley three remaining males. Thus evidence from Langtry is converted to the concept of interbreeding between Kennicottii and Asio groups!

This was confirmed in July, 1962, when I encountered the mixed pair with grown young at Boquillas. The parents are very satisfactory examples of their races, considering their worn July plumage. One of the juveniles, which was collected, has a few adult feathers typical of fresh *mccallii* both above and below. The duetting by the pair was marvelous —a perfect demonstration of vocal compatibility. To the male's bouncing ball song and double trill the female forthrightly responded with her Asio Group long trill. She finally flew right up to the male and indulged in billing and head-preening with him. The male has a hybrid origin, for his bill is pale green! This means that his own mating to produce hybrid offspring was no isolated event. I conclude therefore that the two forms interbreed as freely as their sparse populations permit, and that they are of the same species.

GEOGRAPHIC VARIATION

Coloration.—The dorsal ground varies in texture from coarse heterogeneous in the north to fine homogeneous in the southwest corner of the range. A population extending from Idaho to central California and northern Baja California has a rather fine texture with freckled "salt-and-pepper" effect of small dots.

Along the Pacific Coast, dorsal ground color is rich fuscous in the northwest, becoming plain brown in California, blackish in Baja California Norte, and finally dark buffy or vinaceous gray at the Cape of Baja California. Inland, between the Sierra-Cascades and Rocky Mountains the color varies from plain brown in the north, cold gray in the Great Basin, pale pinkish-gray along the lower Colorado River, to dark vinaceous-gray in Sinaloa. East of the Rockies the color is again cold gray from Colorado to New Mexico and blackish over the Mexican Plateau. At the northeast edge of the Plateau, some vinaceous suffuses the black. An irregularity in the intermediate zone between prevailing gray and blackish is that the black back extends northwest and westward across southern New Mexico, whereas the gray swings around west of it to continue down into Chihuahua.

The dorsal shaft streaks are broad and generously flared into short crossbars in the north and east, but become thin and linear southwestward, reaching an extreme of fineness in conjunction with fine homogeneous background at the Cape of Baja California and the adjacent mainland of Sinaloa.

The ventral pattern is coarse and conspicuous in the Pacific Northwest. A population extending from Idaho through Central California to Baja California has uniquely fine, numerous, and very regular crossbars upon broad shaft streaks, this being less consistent in the southern half of California, but prevailing with heightened regularity and density in Baja California Norte. At the Cape, though finer and less dense, these marks are black and the sharpest of any race. In the Great Basin and lower Colorado River Valley, the bars crossing the broad black ventral streaks are brownish, vague, and broken into dots. Streaks become narrow at the lower Colorado River Valley, and reach an extreme of fineness in Sinaloa. There, the crossbars are reduced to fine wavy rows of dark rufescent dots. Along the eastern part of the range, the ventral pattern is boldly coarse and black throughout, but the crossbars become denser on the Mexican Plateau, to give that population a blackish appearance ventrally, through reduction of the intervening white spaces, exactly like that of Baja California Norte. Bill color is black, usually with the tip minutely whitish throughout the Kennicottii Group except that it becomes greenish-gray in the interior northwest, according to Allan Brooks' well-labelled specimens from Okanagan Landing, British Columbia. Elsewhere the only light bills are of specimens that have been washed or degreased.

Size and structure.—The largest race exceeds the smallest by 21% in wing-length and 82% in weight (100% = the small race). Size is large all across the northern part of the range from Alaska and Washington to Idaho. It is medium in California, the Great Basin, New Mexico, and Colorado. It is small in a continuous arc from Baja California up to the lower Colorado River and thence south along the coast to Sinaloa. This north-to-south decrease is everywhere smooth, gradual, and regular except that it levels off at a medium small value from central Arizona southeastward over the entire plateau of México. The feather coat becomes denser, longer, and fluffier toward the north. Toes become less densely feathered, and more bristly toward the south.

Voice.—Along the Pacific Coast of the United States the bounding ball (primary) song of about 12 to 15 notes, is long, and it ends in a very fine roll. Its haunting charm is entirely lost inland through curtailment of the ending. There, eight or nine notes are usual. I have heard them in Arizona, Colorado, New Mexico, Texas, Sonora, and Sinaloa (with tape recordings for all those states), Cape of Baja California and the entire Mexican Plateau. But a singer will occasionally cut down to only four; this must be the short song heard by A. H. Miller in the Sierra del Carmen, Coahuila (Condor, 1955, **57**:163-164).

At the Cape of Baja California Sur both the "bounding ball" and the "thirteen-note song" of the Cooperi Group are used for the primary song!

Wildness.—Over most of their range, screech-owls of the Kennicottii Group are tame. They are easily attracted by imitated calls to sit overhead in full view and look benignly down at you. Such tameness is the rule throughout the western United States and the Mexican Plateau. In the tropics all this changes. At the Cape of Baja California Sur and in southern Sonora you first notice that owls are playing tricks. You hear them but you don't see them. In Sinaloa it is almost impossible ever to see the bird even when calling it up with its own songs on a tape recorder. It is here and it is close, but all you ever see at night is the shaking of leaves after it flies. It has definitely selected perches screened from your view. It flushes at the slightest rustle as you try to step toward it. This is a trait which links the tropical members of the Kennicottii Group to the Seductus and Cooperi groups. One wonders if tropical Asio Group birds of southern Florida and Tamaulipas are also wild?

Distinctive races.—The following eight populations have unique color traits developed to an extreme, so that they are 100% separable from each other.

OTUS ASIO KENNICOTTII (Elliot)

Diagnosis.—Dorsal ground color fuscous of coarse texture varying from blackish-fuscous to buffy-fuscous. Pattern coarse and bold with wide ventral crossbars recurved and often enclosing a sub-basal rufous patch; red phase 7%; intermediate phase 5%; bill black or gray; size large with wing of males averaging 170 mm.; feather coat long, dense and fluffy; toes densely feathered; long primary song; tame.

Distribution.—Characters best developed along Pacific northwest coastal strip from Juneau, Alaska, south to the mouth of the Columbia River (50 fall specimens two of which, from Seattle and Glacier, Washington [if properly labelled], resemble the next race to the east, *bendirei*).

Intergrading.—In the north, *kennicottii* influences the population of *bendirei* at Okanagan Lake by making five of the twelve fall specimens richer brown dorsally. This influence is stronger up the Columbia River, just interior to the mountains, because of breeding continuity afforded through this break in the Cascades (5 fall specimens). Southward into western Oregon and humid coastal California to Cape Mendocino the birds become slightly smaller and less colorful (the intermediate race *brewsteri,* 21 fall specimens).

Habitat.—I have met this abundant owl in oak woods and low dense Douglas fir forest (second growth?) at Friday Harbor in Puget Sound (specimens), and in riparian trees along streams through lowland forests of northwestern Oregon (specimens), where it was eating crayfish.

OTUS ASIO BENDIREI (Brewster)

Diagnosis.—Dorsal color plain brown of fine texture and freckled with little dots to give a homogeneous "salt-and-pepper" background to the broad shaft streaks. Ventral pattern sharp and clear, consisting of wide streaks crossed by fine, numerous, regular bars. An intermediate red phase occurs (11% in the north) which is strikingly similar to the normal phase of New England Asio Group birds. Size largest of the species (=*macfarlanei* of the AOU Checklist), with wing of males averaging 175 mm. This northern population is the only member of the Kennicottii Group in which the bill is not black; it is greenish-gray like the Asio Group. Feather coat long, dense, and luxuriant, including that of toes; long primary song; tame. An exception to the tameness was in dense oak woodlands at Moraga, California, where C. G. Sibley and I found them very wild, perhaps due to the prevalence of great horned owls.

Distribution.—Size and color traits best developed in west Idaho, southwestern Montana and eastern halves of Washington and Oregon (19 fall specimens).

Intergrading.—In California away from the humid northwest coast and east side of the Sierras, the identical coloration is maintained (*bendirei, sensu stricto,* 60 fall specimens), while size is diminished to an average 161 mm. wing chord in males. The bill is blackish or gray.

The southward approach toward *cardonensis* of Baja California is not a smooth cline, for in southern California the pattern becomes irregular and more variable with some birds scarcely distinguishable from *Otus asio asio*—tendencies that have to be reversed upon reaching the area of *cardonensis*. The major change toward *cardonensis,* though, is increased frequency of blackish backs, which become a majority in the San Diegan district (6 fall specimens).

Of equal interest as the enormous latitudinal range of *bendirei,* over which coloration remains constant, is its occurrence on the Mojave Desert of California. There it maintains its medium size equal to Californian and Great Basin birds together with its brown color and heavy black pattern, whereas true desert populations to the east and south tend to be small, pale gray, and finely patterned. The population in riparian groves of the Mojave River at Victorville is identical with that of coastal California (3 fall, 2 more winter specimens). Over the rest of this desert (6 fall, 4 more winter specimens) the scattered brown examples from oases, Joshua trees, and piñon-juniper woods carry the stamp of *bendirei* all the way to the Panamint Mountains! Some are pale, showing mixture with the Great Basin population of *aikeni.* In wetter parts of the Pleistocene, the Mojave Desert must have supported a thriving population of *bendirei,* still entrenched at Victorville. The confusing variability over the rest of this desert must be due to the small numbers scattered in isolated pockets of habitat, where ancestry is liable to be various mixtures of Pleistocene relict *bendirei* with wanderers from desert races to the east.

Habitat.—A. H. Miller, Ward Russell and I found it in a riparian grove within open ponderosa pine forest near Sisters, Deschutes County, Oregon (specimens taken by our party). It must be rare in the arid country of south-central Oregon, where A. H. Miller, Frank Richardson and I found not one in a month's trip. But in California it is abundant in oak woodlands, in blue oak-digger pine woodlands of the Sierra Nevada foothills, sycamores and oaks along arroyos and streams, cottonwoods and willows along rivers, shade trees in suburbs (specimens from all these habitats) but not in eucalyptus plantings. It prefers level terrain with open tree growth, therefore it is rare in the mountains where canyon live oak forms tall closed stands (one seen, Mt. Lowe, San Gabriel Mountains). In a month's winter night-hunting in piñon-juniper woods of the Providence Mountains, Mojave Desert, I heard only two and collected one. The following summer, Dale Arvey and Joseph Grinnell found them to be common in nearby Joshua trees!

OTUS ASIO CARDONENSIS Huey

Diagnosis.—There is no fresh-plumaged example of this race, whose characteristics I must infer from the type series collected in April, of which the type itself is the least worn and faded, together with a January bird from near San Diego, California These inferences are strengthened by the increasing frequency of black owls toward the southern border of California, and by the correspondence of available specimens to *suttoni* of the Mexican Plateau—the blackest race of the species.

The ground color is blackish gray, or possibly blackish brown, of fine texture with freckled dots to give the "salt-and-pepper" texture as in *bendirei.* The ventral crossbars are the most regular and densest of any race of the species. Size is small, with wings of males averaging 145 mm. The effect is of a small black edition of *bendirei,* with a distinctive close-set black pattern below. This *cardonensis* ventral pattern is duplicated by occasional specimens from the Mexican Plateau and one from central Sonora. Bill black; long primary song.

Distribution.—Baja California Norte.

Intergrading.—The only available specimen from the middle of the peninsula (north latitude 27°30′, worn plumage) looks like a good intergrade with *xantusi* of the Cape.

Habitat.—I have not been to the domain of this owl in Baja California, where L. M. Huey found it in giant cardón cacti of the desert. The San Diego County, California, birds, of which he and I made tape recordings and collected a black specimen, were in live-oaks along streams and beside pastures.

OTUS ASIO AIKENI (Brewster)

Diagnosis.—Dorsal ground is pale gray (some backs slightly buffy) of coarse texture with coarse pattern of broad black streaks. The ventral pattern is of broad streaks and wide-set conspicuous crossbars. This is the palest gray race of the species and the first mentioned so far which has the short primary song. It is of medium size, with wings of males averaging 163 mm. Bill black, sometimes with whitish tip. Coloration parallels the adjacent race *hasbroucki* of the Asio Group. Please turn to that account for distinctions between the two.

Distribution.—Salt Lake region of Utah; Grand Canyon and central-eastern Arizona, away from the Gila River; Colorado Springs; Cimarron River, throughout its course in Cimarron County, west end of Oklahoma panhandle; and New Mexico, except the south (36 fall specimens).

Intergrading.—Because of the gap between eastern and western screech-owls and resulting termination of clines, *aikeni* enjoys a broad occurrence in the pure form, untouched by intergrading to the northeast: southeastern Colorado, central eastern Arizona, most of New Mexico, and extreme western Oklahoma. Westward into the Great Basin of Nevada, the Inyo region of eastern California, and the southwest corner of Utah, the size is maintained (wing of males averaging 166 mm.) but some of the backs are of fine texture and the ventral crossbars become numerous, fine, and faint (16 fall specimens =the intermediate race *inyoensis,* including an apparent migrant to the Big Sandy Valley of western Arizona). These birds can be regarded as *aikeni* tending toward *yumanensis.* A more reciprocal intergrading with *yumanensis* proceeds southwestward across the low deserts of Arizona as the birds become gradually smaller (wing of males averaging 153 mm.), the dorsal ground becomes more homogeneous and occasionally shows pink, and the pattern becomes finer (117 fall specimens =intermediate race *cineraceus,* which extends up the Gila River to reach New Mexico and also penetrates north-central Sonora).

Southward the trend toward *suttoni* is reflected in smaller size and blacker backs. But gray backs persist side-by-side with them in this area including the southern border of New Mexico; extreme southeastern Arizona, and adjacent corner of Sonora; Chihuahua; and apparently even Durango (38 fall specimens).

Habitat.—I found this form to be abundant in the cottonwood forest along Fountain Creek south of Colorado Springs, Colorado; in cottonwoods and willows of the Río Grande at Socorro, New Mexico; and in cottonwoods of the Cimarron River, Cimarron County, Oklahoma. In these places I made tape recordings of the songs, which are typical of the Kennicottii Group, and collected the specimens (in the last place with the help of G. M. Sutton and Col. L. R. Wolfe). On the Río Grande near Las Cruces, New Mexico, R. Raitt, R. Ohmart and I found it in groves of mesquite, hackberry, and exotic tamarisk (specimen). Near Seligman, Arizona, I took two in piñon-juniper woods, but I have never found it elsewhere in that habitat. In the foothills of the White Mountains, near Springerville and Eagar, Arizona, it was associated with those piñons and junipers that penetrated up into open ponderosa pine forest (specimens). In Arizona it is found in palo verde-saguaro woods of the deserts (specimens and tape recordings) and in open oak woodlands of the broader foothill valleys (specimens). It is more numerous in sycamores, cottonwoods and willows along streams both of lowlands and foothills (specimens and tape recordings), but reaches a really incredible abundance in the mesquite bosques (specimens and tape recordings). The bark of these mesquite trunks is fairly black, and the light gray owl is not properly concealed when it perches beside them. It is well concealed in cottonwood and willow trunks, however. Love for riparian groves of sycamores carries it up into the mountains to about 5500 feet, there to be associated with pines and sometimes also with *O. trichopsis* and *O. flammeolus.*

OTUS ASIO SUTTONI Moore

Diagnosis.—This is the blackest race of *Otus asio.* The blackish gray dorsal ground color varies in texture. The black pattern is bold, dense, and precise above and below. Some examples have ventral crossbars so dense and regular as to duplicate the ventral pattern of *cardonensis.* Size is small, with wing of males averaging 155 mm. The fresh fall series (of 5) obtained in the mountains above Saltillo, Coahuila, by Charles Ely, differed from contemporary specimens I took in the Big Bend of the Río Grande by having a tinge of vinaceous over the back. This bird has the short primary song and a black bill.

Distribution.—From the Big Bend of the Río Grande in Texas to the Mexican Plateau (31 fall specimens). One road kill at Tehuacán, Puebla, below the plateau (R. W. Dickerman—University of Minnesota collection).

Habitat.—I found *suttoni* inhabiting woods of piñon and oak high in the Chisos Mountains of Texas (specimen and tape recordings), and thickets of mesquite and of willows along the Río Grande at the base of this mountain (specimens with tapes). In the Sierra Madre Occidental of Chihuahua, I collected specimens in open forests of pines and oaks where the pines were *Pinus engelmanni* and *P. leiophylla;* it was not found in ponderosa pine forests at higher altitudes. It was common in riparian willows and cottonwoods at the east base of this mountain (specimens). At Sayula, Jalisco, W. Schaldach and I found it in mixed woods with tall mesquites near the lake (specimens); near Lagos de Moreno in the same state, Peter Marshall and I found a family in pepper trees along a wash (specimens). Phillips prepared a beautiful fall example which flew inside the Instituto de Biología, México, D. F., and he and I found at least one pair in oaks of the nearby Barranca de los Muertos (specimens), where *Otus trichopsis* is abundant.

OTUS ASIO YUMANENSIS Miller and Miller

Diagnosis.—This is a pale pinkish-gray, fine-textured, thinly streaked, small owl, with wings of males averaging 149 mm. The misty ventral crossbars, broken into wavy rows of brown dots, are less distinct than in any other race of the species. The thin black shaft streaks above and below have blurry edges, unlike the sharp black streaks of *xantusi* and *vinaceus.* The dorsal ground color, appreciated only in fresh fall specimens, is definitely a cold clear gray, overlaid with pink. The primary song is short; bill black.

Distribution.—The above traits are discerned in all the birds of the lower Colorado River Valley and the Colorado Desert of California (25 fall specimens). In addition, the only fresh specimen from coastal Sonora is an excellent example: U. S. National Museum no. 287564 from the Sierra Seri, on the coast opposite Isla Tiburón.

Intergrading.—The numerous specimens from central western Sonora taken by van Rossem afford only a tantalizing hint of the mingling of *yumanensis* characteristics with those of its close relative, *vinaceus,* because they are in worn, April plumage. Farther inland on the Río Yaqui, my three fall specimens show odd mixing of the two phenotypes, *cineraceus* (of the subspecies *aikeni*) and *vinaceus:* one looks like the southern Arizona population, another is *vinaceus,* the third is exactly the hypothetical fall plumage of *cardonensis* across the Gulf of California!

Habitat.—Gale Monson and I found this race to be abundant in the thick stands of willow and tamarisk along the lower Colorado River above Imperial Dam, Arizona (specimens). I have heard or seen it at Whiteriver and Cottonwood Springs in the Colorado Desert of California. It occurs in riparian trees at such oases.

OTUS ASIO VINACEUS (Brewster)

Diagnosis.—Dorsal ground of fine texture, its color thereby consolidated into a darker gray than in the races to the north, and this is strongly overlaid with a beautiful red wine color. Dorsal and ventral shaft streaks linear, fine and distinct. Fine, close-set ventral crossbars are wavy rows of dark wine-colored dots. Size small; wing of males averaging 147 mm. Uses the short style of primary song. This is the first really wild bird so far encountered on our list. Toes bristled; bill black.

Distribution.—From near the Sonora border of west-central Chihuahua and the Alamos district of southern Sonora south along the coastal plain to Culiacán, Sinaloa (8 fall specimens).

Habitat.—I found it to be common both in hills and plains in tropical deciduous woods with giant cardón, in *Lysiloma* woods, in tall mesquite and hackberries along streams, and rarely in riparian bald cypress. On the flat desert inland from Agiabampo, Sonora, the birds were spaced along winding washes arched over with trees. Don't wander there at night without a compass! My field observations cover all these habitats and I have collected specimens from all except bald cypress. I recorded the songs on tape near Alamos, Sonora, and Guamúchil, Sinaloa. At the latter place is the thickest short tree forest in which I have encountered the species (southernmost specimens), but it is not as tall nor as dense as that farther south at Mazatlán, where I have looked in vain for this owl.

OTUS ASIO XANTUSI (Brewster)

Diagnosis.—Smallest of the Kennicottii Group, with wing of males averaging 143 mm. Coloration just like its neighbor, *vinaceus,* across the Gulf of California, except that the ventral crossbars are linear, black, and at right angles to their shaft streaks. Thus the venter is black and white instead of black, pink and white. The dorsal ground, if it has any wine color at all, has less than *vinaceus.* The only recent fully-molted fall specimen is an early November bird taken from a hole in a cardón by Ed N. Harrison; its back is clear gray overlaid with pale buff instead of wine; it is practically indistinguishable, though, from the least reddish *vinaceus* backs.

This bird is wild and elusive. For a primary song it uses either the short "bouncing ball" song or the "thirteen-note song" of *cooperi,* both of pure mellow tone characteristic of the Kennicottii Group. The thirteen-note song is an even series of short hoots which rises in pitch and then falls again to the starting pitch level. The toes are bristled.

Distribution.—The Cape of Baja California Sur (5 fall specimens).

Affinities.—*Xantusi* is one of several birds of the Cape whose trans-gulf affinities show them to have preserved relatively unchanged their ancestral characteristics attained from former continuity, somehow, with populations of the Mexican mainland (Davis, Condor, 1959, **61**:75-84). And this is in spite of intergrading with dissimilar Californian races to the north. *Pipilo fuscus* is an equally good example.

Imagine the surprise at my only visit to the Cape to hear *xantusi* tuning up with the thirteen-note primary song of *cooperi!* By then I was accustomed to surprises, having found that *Ciccaba virgata* in Sinaloa sings the same song. Irby Davis later tape-recorded this from *xantusi* at San Antonio, Baja California Sur, where it comprised 15 or more notes.

Habitat.—I found it common in tropical deciduous woods with giant cardón of the desert open growth (specimens), and from there on up to the summit of the Sierra de la Laguna. It was heard along oak-lined arroyos at the foot of the mountain, in dense deciduous short tree forest of the slopes (specimen), and was fairly common in the piñon pine forest, with oaks, of the summit plateau. This is the only tropical race of *Otus asio* which occurs also in a temperate habitat.

THE SEDUCTUS GROUP

(OTUS SEDUCTUS, Balsas Screech-owl)

Diagnosis.—Dorsal ground homogeneous, of fine texture, its color warm brown overlaid with vinaceous pink; black shaft streaks above and below are sharply etched and narrow, though broader than in the race *vinaceus*. Some specimens have little paired buff spots, called ocelli, one on either side of the shaft streak. A frosted coronal band is better developed than in the Kennicottii Group. Ventral surface is closely and narrowly barred with rows of little black or pinkish dots—the ventral crossbars. Size is huge, with wings of males averaging 173 mm.; weight, 155 g. Vocalizations are the same as those of the Kennicottii Group but much louder and of an ominous, gruff, threatening quality, never sounding pure and mellow except at a distance. Some sound like two simultaneous songs at different pitch. Primary song is short. Iris dark brown (except for two out of the 41 specimens with iris color recorded; one was golden brown, the other yellowish). Very wild. No red phase; toes bristled; bill greenish.

Distribution.—From Colima southeastward to the lower Río Balsas drainage in Michoacán and Guerrero (30 specimens with unworn feathers). This known distribution is interior to the coast.

Habitat.—This owl inhabits tropical deciduous woods with giant cardón, including closed woods with bare ground beneath as at Apatzingán, Michoacán, where I found pairs nesting in June (specimens). Near the town of Colima, W. J. Schaldach, Jr., his party, and I found them abundant in more open woods with giant cacti on level terrain (specimens), the woods of the slopes being too dense and inhabited by *O. guatemalae*. These birds abounded at the edges of milpas and perched in mesquites far out in the fields. We could find none in denser or steeper growth along the coast.

Affinities.—*Seductus* is completely isolated geographically from other forms of *Otus asio*. It closely approximates the range of *Otus asio suttoni* which lives, however, in a different habitat at higher altitude on the Mexican Plateau. We measured 55 miles of highway separating the *suttoni* examples collected around Lake Sayula from *seductus* taken near Colima, but this might be narrowed to 15 miles if *seductus* occurs in tropical woods farther up the highway.

The affinities of *seductus,* especially its vocalizations, are all with the Kennicottii Group and its closest relative, *Otus asio vinaceus* far to the north, which it resembles in its vinaceous tint, fine pattern, and dotted ventral crossbars. But it upsets the clines of the Kennicottii Group by its large size, brown color, and somewhat broadened shaft streaks. Gruff voice, wildness, brown coloration overlaid with vinaceous-pink, and the beginnings of paired buff ocelli on either side of the dorsal shaft streaks are traits linking *seductus* with the Cooperi Group. Its large size corresponds with *Otus asio kennicottii* to the north and *Otus asio cooperi* to the south, but in both directions are interposed small forms. Then *seductus* has its unique trait of brown eyes.

I think that *seductus* and *suttoni* could mate if opportunity were presented, perhaps along some stream between Apatzingán and Uruapan, Michoacán, for instance. Then I still might find a connection between *seductus* and *lambi* somewhere in southeastern Guerrero or southwestern Oaxaca. But the main reasons why I want to keep *seductus* next to the Kennicottii Group in *Otus asio* are vocal ones. I am loath to separate two forms whose vocalizations are identical except for hoarseness and loudness. The gruff tone of *seductus* is duplicated by birds at Tucson, Arizona, when they are particularly excited by invasion of their territory (tape recordings).

THE COOPERI GROUP

(OTUS COOPERI, Pacific Screech-owl)

Diagnosis.—Dorsal texture fine, dorsal color light brown with pink or buff cast, pattern fine. Pale ocelli next to dorsal shaft marks. Ventral crossbars dotted and irregular. Prominent white frosting on sides of forehead, ear tufts, and coronal band. Toes bristled, iris yellow. Primary song is of 13 to 15 short notes rapidly delivered in a series which rises in pitch at the middle, then falls to the initial pitch level at the end. Secondary song as in the Kennicottii Group, but sometimes the initial trill is at a higher pitch than the longer following trill. Voice loud, gruff, of threatening quality as in *seductus;* the notes sound like "pup-pup-pup" as in a similar but louder 13-note song of *Ciccaba virgata*. No red phase. Extremely wild. The wing is short in proportion to the robust body as indicated by weight. Bill pale olive or greenish.

Distribution.—From Puerto Angel and the Río Tehuantepec, Oaxaca, southeastward narrowly along the Pacific Coast to Costa Rica.

Habitat.—Tropical deciduous woods with giant cardón; palms, mangroves, and woods fringing coastal mangrove swamps.

Affinities.—Completely isolated geographically from the rest of the species. Although it plays havoc with clines emanating southward from the Kennicottii Group, nevertheless after a false start it eventually carries to a logical conclusion the increasing fineness of pattern southward that parallels *Otus trichopsis* and *Otus guatemalae.* Its secondary song links it with the Kennicottii Group and *seductus,* its primary song with *xantusi,* its coloration with *vinaceus,* and its gruff voice with *seductus.* Wildness and preference for tropical deciduous woods link it with *xantusi, vinaceus* and *seductus.* Its occurrence in mangroves is unique.

Geographic variation.—Traits abruptly change in southeastern Oaxaca, then remain constant all the way from Chiapas to Costa Rica. From northwest to southeast then, size jumps from small to large, streaks from medium to fine, and dorsal ground color from pinkish brown to buffy gray. Ventral crossbarring changes from rows of pink dots to black dots clustered together so as to leave white spaces in the middle of the feather. Similarly on the back of the southeastern population, the fine freckles retract on either side of the shaft streaks so as to leave little paired buff ocelli, which are only hinted at in *seductus* and the population in Oaxaca. Voice and other traits do not change geographically. The two distinctive populations are as follows:

OTUS ASIO LAMBI Moore and Marshall

Original description.—Condor, 1959, **61**:224-225 (all others are referred to in the literature cited in the introduction).

Diagnosis.—Remarkably similar to *Otus asio vinaceus,* 940 miles away to the northwest! Ruddier than *vinaceus,* being pink on brown rather than pink on gray. Black shaft streaks are coarser than in *vinaceus* and the rows of dots comprising the ventral crossbars are bunched and pink rather than evenly spaced and blackish. Shaft streaks on the head are broad, making the crown appear darker than the back. The wing, averaging in males 154 mm., is small out of proportion to the robust body, with weights of males averaging 125 g. as against 100 g. for *vinaceus.*

Distribution.—Río Tehuantepec, at least as far up as Nejapa; Ixtapec, Puerto Angel, and the margins of Laguna Superior and Laguna Inferior, all in Oaxaca (9 unworn specimens).

Intergrading.—Transition to *cooperi* eastward is accomplished in the short space between Laguna Inferior and Mar Muerto, both in Oaxaca, and both connected, apparently, with continuous mangrove woods. The series of five unworn specimens from east of Juchitán contains one of *cooperi* color and pattern; these birds are all small, however. A little farther east, near Niltepec, I took a good *lambi* in the mangroves. This is practically at the boundary between the two lagoons mentioned above, where a hill extends seaward to divide them. The next eastward specimens are typical large, finely-marked *cooperi* at Chahuites, on the Mar Muerto (some labelled Cacoprieta or Tapanatepec).

Habitat.—I found it in rather tall deciduous woods with cardón in gullies and hillsides above the Río Tehuantepec near Nejapa (specimen), where it was common. It was not in willow groves along the river. Near the coast, 13 miles east of Juchitán, it was common in short, dense woods of the hill (specimen), and during general chorusing could be heard all over the inland fresh-water marshes, where there were palms and mesquites. At the border of Laguna Inferior, opposite Niltepec, the birds sang from mangrove woods, dry at the time of my visit in April. I collected one as he perched on the side of a palm trunk, next to a hole that he was advertising as a nest site. Chester Lamb took all these wild tropical races upon accidentally flushing them in the daytime. On the other hand, Nazario Chávez would lope through the brush at night fast enough to catch the birds in the middle of a song. That is how he built up our series of *seductus* and *lambi.*

OTUS ASIO COOPERI Ridgway

Diagnosis.—Large size with large powerful feet and bristled toes, wing of males averaging 166 mm., and their weight, 150 g. Dorsal color tawny gray, of homogeneous texture. Pattern fine; streaks extremely narrow, sharp, and black, those of the back with little pointed lateral extensions embracing light buff ocelli. Ventral crossbars reduced to a chaos of little freckled dots gathered terminally to expose subterminal white spaces on either side of the shaft streak. Shaft markings of the head are narrow, so that the crown appears no darker than the back; dorsal and ventral shaft streaks narrower than in any other race of *Otus asio.* Hoary areas of "frosting" around the forehead, coronal semicircle, and ear tufts more extensive than in other races of *Otus asio.*

Distribution.—From Mar Muerto, Oaxaca, southeastward narrowly along the coast to Costa Rica (35 unworn specimens).

Habitat.—At Puerto Ariste, Chiapas, I found this form only along the edge of the mangrove lagoons where there was a continuous fringe of a characteristic, spreading, small-leaved tree with wet, bare or grassy ground beneath (specimens). From this woodland strip the birds would spill out into smaller trees of adjacent cut-over land. In El Salvador I never saw the bird, but I heard it near Lake Olomega at the railroad station and once at the edge of deciduous forest at lakeside fields. Oaxaca and Chiapas specimens are all from so close to the coast that the mangrove edge must be inferred as the habitat; van Rossem's El Salvador specimens come from deciduous forest at the edges of lakes or rivers —all suggestive of restriction to the water's edge. But such an edge may provide the only growth open enough for *Otus asio* in these areas of tall, dense forests. In Costa Rica, judging from Slud's remarks (Bull. Amer. Mus. Nat. Hist., 1964, **128**:130), there is arid growth inland which is suitable; therefore in that country the owl spreads out away from the coast. However, one of the Chomes specimens is definitely labelled as coming from the mangroves.

THE ASIO GROUP

(OTUS ASIO, Eastern Screech-owl)

Diagnosis.—Dorsal pattern emphasizes lateral projections of the black shaft marks at the expense of a linear appearance; recurved ventral crossbars equally wide as shaft streaks. Ground color lurid by comparison with the Kennicottii Group, running to rich brown, buff, and ruddy hues. Primary song a whinny, secondary song a long trill of rapid notes at constant pitch. Iris yellow; bill yellow, green, pistachio or turquoise, never black. Red phase common, with simplified pattern. Ear tufts longer than in western races; they can be seen even when not erected.

Distribution.—East of the Rocky Mountains from extreme southern Canada to Florida and northeastern México.

Red Phase.—I can add figures for northeastern México to D. F. Owen's results for the eastern United States (Wilson Bull., 1963, **75**:183-190). My data, summarized by racial populations, show red phase frequencies of 5% to 11% on the Great Plains, increasing eastward to surpass 50% in the group of states from Missouri and Arkansas to Virginia and the Carolinas. From 2% on the Edwards Plateau and zero in the Río Grande valley of Texas it jumps to 13% in the sample of 46 skins from Tamaulipas and San Luís Potosí. Intermediate plumages, ranging from none in Tamaulipas and San Luís Potosí and 2% along the Río Grande to 7% and not correlated with frequency of the fully red phase, are in the minority, so that phase variation is bimodal and dimorphic, except that in Florida there is continuous variation with intermediates in the majority. My figures for the entire race *floridanus* are: 37% gray, 39% intermediate, and 24% red.

Fully red birds tend to have a reduced pattern: black streaks on the back are narrow or absent, red anchors are sparse on the flanks. Intermediate phase tends to preserve the entire complex pattern of normal phase markings, embellished with red to produce some colorations of breath-taking beauty.

GEOGRAPHIC VARIATION

Coloration.—Amount of patterning and darkness of the ground in the red phase agrees with geographic variation in the normal phase, so that southward the ventral surface becomes densely marked—in Florida and Texas. In the north, the red phase becomes paler from east to west. In Tamaulipas and San Luís Potosí the entire dense black pattern of the normal phase plumage is preserved, touched up ventrally with red. This may be unusual for *Otus asio,* but comes as no surprise in the genus, where we find unreduced patterns in the red examples of *flammeolus,* of southernmost populations of *trichopsis,* and of *choliba.*

Normal phase ground color is rich brown of coarse texture along the Atlantic Coast of the United States, and this becomes homogeneous, richer and ruddier southward. The pattern becomes denser southward, especially on the venter. The dorsal ground becomes pale toward the northwest in conjunction with reduction and narrowing of the pattern marks and commensurate increase in white areas ventrally. Southward into Texas the coarse-textured ground color becomes dull grayish, but the pattern is bolder and denser. All the above populations have the usual eastern dorsal pattern with emphasis upon laterally flared transverse projections of the shaft marks at the expense of a linear streaking.

In the valley of the Río Grande, however, there is an abrupt assumption of western garb, consisting of a fine linear pattern of shaft streaks emphasized upon a buffy gray, fine-textured background. The only eastern appearance on these Río Grande birds is their green bill, transverse black marks on the crown, and ventral crossbars equally wide as their shaft streaks. Some have a coarser, browner dorsal ground, and coarser black marks. This style gains in frequency southward through Tamaulipas.

Remember that these clines of color change are independent of and entirely different from those of the Kennicottii Group across the gap to the west.

Size and structure.—Clines of gradual decrease in wing length run from north to south. In the west, males average 165 mm. on the northern plains, and the wing decreases to 151 mm. in Tamaulipas, with a steep dip between the Edwards Plateau and Río Grande valley of Texas. On the Atlantic seaboard, the cline is perfectly smooth; from 162 mm. in New York, it drops to 141 mm. in Florida. A notable irregularity is the persistance of small size around the gulf coast from Florida to Louisiana, and thence up the Mississippi Valley, where at any given latitude, wing length will be less in the valley than off to the east or west. As in the Kennicottii Group, the feather coat becomes denser and fluffier to the north, including that of the feet. In the south, the toes are more bristly than plumed.

Voice.—Geographic variation produces regional differences in rendition of the whinny (primary song). The sonagraph shown is of a southern Georgia male, with a typical whinny such as I have heard there and in Louisiana. This is a long cry which starts upward in pitch, then falls gradually and takes on a vibrato or tremolo for about the last third. The male from Ithaca, New York, has a coarser and longer tremolo, and sounds more like a horse. On the Edwards Plateau of Texas the ten or a dozen males heard and recorded by Colonel Wolfe and myself had the tremolo very fine and short—just a terminal vibrato. Even this is eliminated by the birds of the Río Grande valley. They utter only the inflected cry. We did not hear the primary song often there, but noted it in four birds and recorded it in two from Langtry to the Big Bend. Irby Davis recorded the same song in a female at the mouth of the Río Grande. This kind of variation is analogous to the geographic differences in length of terminal trill of the primary song of the Kennicottii Group, except that the ends of this vocal cline are so different that you might not recognize them as the same species if you were not acquainted with the intergrading voice on the Edwards Plateau, and with the secondary song common to all.

Distinctive races.—Five populations at the ends of clines show unique color characteristics developed to extremes. The curious reversal of clines south of the Río Grande will be noted under the account of *mccallii,* rather than as a unique race, *semplei. Semplei* is not as strongly differentiated as the others, which may be characterized as follows:

OTUS ASIO MAXWELLIAE (Ridgway)

Diagnosis.—This is the palest and least marked population of *Otus asio.* Fall dorsal ground of coarse texture is presumably pale buffy gray; dorsal shaft marks are small and inconspicuous. Ventrally there is excessive white showing because the pattern is thin and sparse. The red phase is pale; 7% of the specimens show it, and 6% are intermediate. Size is large, with wing chord of males averaging 165 mm. The bill is presumably yellow in life, but the slightly less distinctive population from western Kansas has a pale grayish-green bill. Feather coat dense, long and fluffy, including that of the feet.

Distribution.—These traits are seen in 14 fall specimens from eastern Montana south to the region of Denver, Colorado. Some individuals visit Colorado Springs in winter (2 fall specimens) and there is a visitor to Comanche County, Kansas, which seems to be in fall feather (but labelled "March, 1948," Denver Museum).

Intergrading.—Eastward, as *asio* is approached, the back becomes darker, browner, and the pattern bolder; there is a small drop in wing length to the size of *asio* (16 fall specimens from North Dakota, Minnesota, northwestern Iowa, western Nebraska, western Kansas, and the panhandle of Oklahoma, of an intermediate population known as *swenki*).

Habitat.—Colonel Wolfe and I found this subspecies (as the intermediate population *swenki,* specimens, tape recordings) in cottonwood forests along the Arkansas River at the Kansas-Colorado border and on the Cimarron River north of Elkhart, Morton County, Kansas. One eastern screech-owl was seen and tape recorded at a branch of the Canadian River near Tascosa, northeast Oldham County, Texas. These localities along the 102nd meridian are the farthest west that I have found the eastern screech-owl (except on the Río Grande, where it reaches 103). The cottonwoods along these rivers are much smaller than those of the far west, even when old and full of the holes necessary for owls. Distribution is interrupted by the young stands, too small for holes, possibly produced by periodic sweeping away of the mature forest in floods.

OTUS ASIO HASBROUCKI Ridgway

Diagnosis.—Dorsal ground color plain, of coarse texture, buffy gray with a bold black pattern. Venter densely marked with coarse black streaks and crossbars. The red phase (5%, intermediate 1%) is dark red like eastern birds, but more heavily patterned. Size is medium, with wing of males averaging 161 mm. The bill is light greenish. The primary song has a "tight," short, terminal vibrato. This is the only population of the Asio Group which resembles its neighbor of the Kennicottii Group confronting it across the distributional gap to the west. The neighbor is *aikeni,* which *hasbroucki* resembles in medium size, coarse-textured gray or buffy gray dorsal ground color, and bold coarse black pattern. It differs from *aikeni* in voice, possession of the red phase, green bill, transverse flaring of dorsal shaft marks, buffier dorsal ground, and narrower ventral streaks (of same width as crossbars). Except for the red phase and clear-cut distinction in voice and bill color, these are differences of degree so that color analysis of possible hybrids will be difficult.

Distribution.—Central Texas (17 fall specimens), best developed on the Edwards Plateau.

Intergrading.—The southeastward approach to *floridanus* should prove interesting because of the size difference, if more specimens become available. Vocally, *hasbroucki* is intermediate between *asio* and *mccallii.* Abrupt intergrading in color, simply by *mccallii* coloration turning up in the range of *hasbroucki,* and *vice versa,* is known from a few spring specimens. This is the same cleavage into two phenotypes as is seen in the hybrids between *suttoni* and *mccallii!*

Habitat.—Colonel Wolfe and I found this owl abundantly in the large live-oaks around Kerrville, Texas, on the Edwards Plateau (specimens, with tape recordings of whinny and trill). They were tame in parks, gardens, and dooryards, but were wild in the vast woodlands away from town. Farther to the southwest I found presumably this race (July specimens too worn for identification, tape recordings of trill only), a pair to each oak mott along Independence Creek, Terrell County, Texas, and one male in riparian mesquites on the Pecos River near Sheffield. Independence Creek has willows, mesquites, and an occasional cottonwood, which the eastern screech-owls avoided in preference for the widely separated clumps of oaks (= mott).

OTUS ASIO MCCALLII (Cassin)

Diagnosis.—Dorsal ground buffy dark gray, of fine texture, streaked in western screech-owl style, so that the back resembles the western races *xantusi* and *vinaceus,* though with broader streaks. Ventral pattern of fine, dense, black marks of eastern screech-owl style with crossbars as wide as shaft streaks. Red phase absent from large Río Grande series; intermediate red phase, 2%. Bill pale green or turquoise. Size small, with wing of males averaging 151 mm. Primary song lacks the terminal tremolo.

Mccallii differs from its nearest neighbor, *suttoni* of the Kennicottii Group, which it overlaps with limited hybridizing, in the following: songs are the inflected cry (counterpart of the whinny) and long trill rather than the "bouncing ball" and double trill; bill green or turquoise rather than black; ventral shaft streaks narrow, of same width as crossbars instead of broad and wider than crossbars; dorsal ground homogeneous and buffy gray instead of coarse and blackish.

Distribution.—Valley of the Río Grande from Big Bend to the mouth (25 fall specimens, 19 of *mccallii* phenotype dorsally, 6 of *semplei* phenotype).

Habitat.—I found *mccallii* sparsely distributed along the Río Grande in the infrequent large groves of willows (specimens, tape recordings). Occasionally the birds went into adjacent mesquites. Farther down in Coahuila I heard one call at dusk from an oak mott, and I picked up a road kill where the highway went through an extensive mesquite bosque.

Remarks.—In Coahuila and San Luís Potosí, where the distributions of *suttoni* and *mccallii* run side-by-side for about 600 miles, there is not the slightest indication of gene exchange. The 9 fall specimens of *suttoni* and 20 fall or unworn examples of *mccallii* are very different from each other.

Southward from the Río Grande, clines of the Asio Group are reversed. The red phase appears, and assumes the dense black pattern of the normal phase in San Luís Potosí and southern Tamaulipas. There also the dorsal ground and pattern become respectively ruddier and coarser (=the intermediate race, *semplei,* 17 fall or unworn specimens, of which 5 are *mccallii* phenotypes, 12 of *semplei* coloration). The bill is grayish yellow or yellowish green. Other peculiarities of *mccallii* that we have already discussed are its primary song lacking the tremolo or whinny, western style back streaks and fine-textured dorsal ground, abrupt drop in size as contrasted with *hasbroucki,* "bimodal" intergrading with *hasbroucki* in color accomplished as with size over a short distance, ability to interbreed with the Kennicottii Group, simultaneous ability to preserve some pure pairs in the zone of overlap.

OTUS ASIO ASIO (Linnaeus)

Diagnosis.—Fresh fall specimens of rich brown, coarse-textured dorsal ground, varying to buffy, gray, or ruddy. Coarse dorsal pattern; ventral pattern coarse and sparse. Red phase 39% (intermediate 4%), rich dark rusty in fresh fall plumage, varying in dorsal pattern from narrow black streaks to none; venter with pattern of red anchors. Primary song like the whinny of a horse. Size medium; wing of males averaging 162 mm. Bill blue-gray, greenish, or pistachio. Feather coat luxuriant; feet densely feathered.

Distribution.—These characters are best developed in southern Ontario, the New England states, New York, Pennsylvania, northern Ohio, and southern Michigan (75 fall specimens). I have not seen the migrants; presumably they are large individuals found in southeastern states in winter.

Intergrading.—Intergrading up and down the Mississippi drainage is confusing to me because I have not yet examined simultaneously the collections from the pertinent states. In Kansas and Oklahoma (35 fall specimens) many are dull colored with dense black pattern suggesting *hasbroucki.* Size decreases down the Mississippi and its tributaries (44 fall specimens =the intermediate race *asio* of the AOU checklist); influence of *floridanus* is shown in Arkansas where wings of males average 148 mm. and where richer colors and finer, denser patterns appear, but without the intermediate red variants of *floridanus.*

Southward down the Atlantic coast, intergrading is clear and gradual (the intermediate population *asio* of the AOU checklist, wing of males averaging 152 mm., 28 fall specimens) as the size difference is bridged between large New England and small Florida birds.

Habitat.—Woodlands, presumably. My only encounter with this hard-to-find "critter" was in dense broad-leaved trees beside a river at Ann Arbor, where Richard Crossin called up a male by whistling an imitation of the long trill, using the saliva on rolled tongue technique. I have failed to find it in deciduous woodlands at Lawrence, Kansas; St. Louis, and the Ozark Mountains, Missouri; the vicinity of Carlisle, Pennsylvania; Cape May, New Jersey; and the Washington, D. C. countryside .

OTUS ASIO FLORIDANUS (Ridgway)

Diagnosis.—Dorsal ground color ruddy brown of fine texture, with dense pattern; venter densely patterned. Extreme red individuals similar to the red phase of *asio.* Variation with respect to redness is continuous, with intermediates comprising the majority. Size smallest in the species; wing of males averaging 141 mm. Toes bristled; bill pale greenish horn, tip whitish horn (Allan Brooks).

Distribution.—Traits best developed on the Florida Peninsula, but detectable westward along the gulf coast to the mouth of the Mississippi (16 fall specimens).

Habitat.—Wade Fox and I tape-recorded this bird in a willow thicket on a levee of the Mississippi River in New Orleans. We heard others in the swamp forest. In extreme southern Georgia, I made tape records of three males in oak woodlands at the home of Ed Komarek, near Tallahassee, Florida. Barred owls abounded in the same locality.

OTUS TRICHOPSIS, Whiskered Screech-owl

Diagnosis.—Otus trichopsis closely resembles *Otus asio,* from which it is distinguished afield only by voice. Its territorial song is of about eight notes of fairly even pitch and timing. The syncopated duetting song is of short and long notes like Morse code, all on the same pitch. The usual phrase, two "dots" and three "dashes," is delivered thrice without pause and terminates with an extra "dash." Both species have plumed or bristled toes, which become more bristly southward and when worn. In the hand, *Otus trichopsis* can be determined by its small feet—much smaller than in the smallest races of *Otus asio*—and absence of white bars on the inner web of the outermost primary. It is always smaller and more coarsely patterned than whatever race of *Otus asio* is in the same region or latitude.

The whiskers on the face are longer and more numerous than in *Otus asio.* They are especially luxuriant on the upper part of the facial disc, where each feather has about six long, soft, black hair-like extensions of the rachis and adjacent five distal barbs. In *Otus asio* these are not as long, and they number only three per feather. The juvenile plumage is more coarsely barred than that of *Otus asio.* The iris is yellow; ear tufts are present but not noticed unless the bird elevates them while roosting. There is a variety of calls including barks besides the two kinds of song mentioned above. The female utters the same songs and barks at higher pitch; in addition she has a descending note, "kew." This owl is sedentary, has a small territory, and is usually found in pairs all year. It feeds from perches in trees by catching invertebrates at the end of a short flight to the ground or to another branch. It prefers denser groves and higher altitudes than does *Otus asio.* There is pronounced geographic variation in color, with a red phase appearing in the south. Voice and ecology remain the same. Geographic and sexual variation in wing chord and weight are imperceptible.

Distribution and areas where absent.—From southern Arizona, Chihuahua, and southern Nuevo León southeast to Nicaragua. I could not call up the species in pines at Sarabia, Oaxaca, at low altitude on the Isthmus of Tehuantepec; in piñon pine and oak of the Chisos Mountains, Texas; oak and piñon pine forest at the Cape of Baja California; pine-oak woodland of the Peloncillo Mountains, Hidalgo County, New Mexico; and Arizona, north of the north slope of the Santa Catalina Mountains, Pinal County. I could find no member of the genus in pine-oak woods and forests of southern Sonora near the Chihuahua boundary; van Rossem took *trichopsis* both north and south of the area I visited, however.

Habitat.—The whiskered screech-owl lives in dense groves of oaks within pine-oak woodland of mountains. It ranges down into dense oaks at elevations lower than pines in Arizona, Sonora, Distrito Federal, and Chiapas. In Chiapas and El Salvador its ecologic spread is from oaks within upper tropical woodlands through oak woodland, pine-oak forest and pine forest to the lower part of the cloud forest. I have made tape recordings in Arizona and have collected specimens in Arizona, Sonora, Chihuahua, Sinaloa, Michoacán, Veracruz, Oaxaca, Chiapas and El Salvador. My detailed field notes cover occurrence in all the habitats and states mentioned above.

Response to man-made changes.—Fire protection in the mountains of southern Arizona, resulting in considerable thickening of woodland and forest growth, may have increased *Otus trichopsis* at the expense of *Otus asio*. Surely the species will continue to abound wherever dense vegetation is allowed to remain on steep north-facing mountainsides and in narrow shady canyons. A pair nested in one of my nest boxes at Hitchcock Campground, Santa Catalina Mountains, Arizona, in the summer of 1963.

In México, where naturally occurring fires have not been curbed, the woodland and forest are tall, open, and more favorable for *O. asio* and *O. flammeolus* than *O. trichopsis*. Logging further opens up the growth and further restricts *Otus trichopsis* to such dense stands as remain on steep slopes and in deep canyons. Yet in such places it is incredibly abundant, and one hopes that vegetation will be allowed to persist in some of these splendid Sierra Madrean barrancas. In Chiapas, it shows great tenacity in occupying all dense groves and pockets remaining after incomplete logging and in areas partly opened up for agriculture. In El Salvador, it lived in considerable numbers within coffee fincas—an artificial forest of tall shade trees over an understory of coffee bushes, and therein may be its salvation!

Overlap with other species of **Otus**—I have always been intrigued by the simultaneous occurrence of this and other species of *Otus* in places where ecologic complexity of steep mountains brings together appropriate mixtures of vegetation. Thus *Otus asio, Otus trichopsis,* and *Otus flammeolus* have been found on overlapping territories at suitable spots of around 5,500 feet altitude in mountains of Arizona, Sonora, and Chihuahua (Marshall, Pac. Coast Avifauna no. **32,** 1956). Ordinarily they are altitudinally separated by preference respectively for open woodland, closed pine-oak woodland, and tall pine forest. *Otus trichopsis* and *Otus asio* occurred together in pine-oak forest of Michoacán. I was pleased also to find them both in oaks of a steep barranca back of Allan Phillips' house, within walking distance of the heavy traffic of México, D. F. Doubtless *Otus trichopsis* and *Otus guatemalae* occupy the same dense upper tropical woodlands in the highlands of Chiapas. I tried to find the latter at several spots where Sr. Miguel Alvarez del Toro had collected specimens. Not knowing the song of *guatemalae,* I gave imitations of such *Otus* that I knew, and invariably called up *trichopsis!*

GEOGRAPHIC VARIATION

The trends from northwest to southwest are: (1) dorsal ground changing from gray through blackish to brown, (2) pattern from medium to coarse to fine, (3) increasing rufous decoration of the gray phase, (4) appearance of a red phase in the south.

In fall and winter plumage (129 skins) the dorsal ground color is seen to be light gray in the northwest (Arizona, Sonora, Chihuahua). It is blackish at the southern end of the Mexican Plateau (Michoacán, Zacatecas, Distrito Federal, Veracruz) and is peculiarly bimodal with both dark and light extremes in the intervening and surrounding areas. In the northeast (Nuevo León, San Luís Potosí) the birds seem intermediate or perhaps brownish gray but they are faded and not far enough into the molt to be compared. In Chiapas and Guatemala, this ground color is dark brown; whereas in central El Salvador, Honduras, and Nicaragua, it is reddish brown.

The dorsal pattern of black shaft streaks and crossbars is moderately coarse in the northwest, coarse on the south end of the Mexican Plateau, moderately fine and variable in Chiapas and Guatemala, and is fine in the southeast. The ventral pattern consists of broad black shaft streaks with narrow black crossbars in the northwest; on the south end of the Mexican Plateau they are broadest and the wide crossbars alternating with white squares give a checkerboard effect. Intervening and surrounding areas possess both checkerboard and medium patterns, with the northwestern type cropping up as far south as Oaxaca. South of the Isthmus of Tehuantepec, in Chiapas and Guatemala, some rufous color decorates the crossbars. These are variable in thickness, but average rather fine and are paired, with consequent increase in the intervening light portions. The shaft streaks are reduced in width so that the overall ventral pattern is medium fine. In central El Salvador, Honduras, and Nicaragua, the ventral pattern is fine, with much rufous decoration, and the crossbars are bunched into two's and three's.

The red phase.—A bright rufous color phase occurs irrespective of age or sex from Sinaloa southeastward in varying percentages, but of high frequency in Jalisco and Michoacán (33%). Because the normal phase becomes browner and finally tinged with rufous toward the southeast, there is somewhat less contrast between the two phases there than north of the Isthmus of Tehuantepec.

Geographic variation in pattern of the red phase parallels that of the normal phase except that the black dorsal crossbars are absent in the northern examples. The dorsal marks are black. The ventral ones are rufous, proceeding southeastward from coarse checkerboard through medium fine doubled to fine bunched, exactly as in their normal phase counterparts. The dorsal ground is bright rufous north of the Isthmus of Tehuantepec, dark chestnut in Chiapas and Guatemala, and dull chestnut rufous in El Salvador and Honduras.

Parallelism.—In northeastern México, where *Otus guatemalae* reaches its darkest extreme of blackish-brown with coarsest pattern, we find that *Otus trichopsis* is also dark and coarsely marked. In this area, both species are precisely the same color, as known only from old skins which have doubtless turned brown from an original dark gray or brownish gray. Apparently they are separated by habitat and altitude in that area of México; but in Chiapas, they overlap and both have a peculiar dark coffee color.

Parallelism with *Otus asio* in southern Arizona is so close that the only color differences are the coarser dorsal texture and broader streaks of *trichopsis*. There, both species are pale gray with a ventral pattern of wide black streaks and medium crossbars. The Mexican Plateau supports the blackest and most coarsely marked race of each species. In these areas where the resemblance is so close, the two coexist in the same habitat. South of the Mexican Plateau their ranges diverge, but both nevertheless become progressively more rufous-brown and more finely patterned as they continue toward the southeast in their respective habitats and altitudes. Their red phases, although far removed geographically, show parallel reduction of dorsal black pattern in the north and adherence to normal phase pattern in the south.

Distinctive races.—Three homogeneous populations are one hundred per cent distinguishable from each other in color of fall and winter specimens. They occupy the extremes of the geographic range (northwest, southeast) and of altitude (southern Mexican Plateau). Together, they encompass less than half the area of the species; nevertheless, I recommend that they alone receive racial scientific names. Let all the examples of variable, intervening, intermediate, and indeterminate populations be filed away and catalogued geographically by states! The figure on coloration shows that a fourth population is rather well distinguished. Over its broad area of occurrence in Chiapas and Guatemala it is at least consistent in its variability. But it has no extreme traits of its own, since it is intermediate between *trichopsis* and *mesamericanus,* as defined below. The important races can be characterized as follows (remember that grays and blacks will show as light and dark brown in all but the most recent fall specimens):

OTUS TRICHOPSIS ASPERSUS (Brewster)

Light gray; broad black shaft marks, medium ventral crossbars; no red phase. Arizona, Sonora, and Chihuahua.

OTUS TRICHOPSIS TRICHOPSIS (Wagler)

Blackish; broad black marks, coarse ventral crossbars in checkerboard pattern; bright red phase lacking dorsal crossbars. South end of Mexican Plateau from Michoacán through Distrito Federal to Veracruz.

OTUS TRICHOPSIS MESAMERICANUS van Rossem

Brown (with rufous lateral edges to back feathers); fine pattern with ventral crossbars grouped by two's and three's; dull red phase with same fine pattern as the normal phase. Central El Salvador, Honduras; Nicaragua.

OTUS FLAMMEOLUS, Flammulated Owl

The flammulated owl is the smallest species of the genus. It is characterized by proportionately long wings, tiny feet, brown eyes, densely feathered tarsi, and bare toes. Erectile ear tufts are no longer than the adjacent feathers of the head. The song of the male is a hoot sometimes preceded by one or two grace-notes a third lower in pitch. The extraordinary low pitch and resonant quality of this hoot is made possible by a relatively large syrinx with thickened tympaniform membranes (Miller, Auk, 1947, **64**:133-135). Unlike the other members of the genus which I have heard, the female's song does not correspond with that of the male. Hers is much higher in pitch, is quavering, and of whining quality. The coloration, of standard *Otus* style, is subject to uncommon individual variation, ranging in dorsal color from pure cold gray, through various shades of gray with rufous superimposed, to red, without cleavage into two color phases. The pattern of shaft streaks and ventral crossbars is always prominent, although it varies from coarse to fine. Red individuals retain the full black pattern. Sexual dimorphism in wing chord and weight is nil, although the six longest-winged birds of 148 measured are females.

Otus flammeolus (Kaup) is migratory, with some showing up in the lowlands in spring, fewer in fall, and with winter specimens taken south of the known breeding range. For arrival and departure dates see Phillips, Marshall and Monson, *Birds of Arizona,* 1964, p. 50. It summers from southeastern British Columbia to Mt. Orizaba, at the south end of the Mexican Plateau. (Specimens from the Sierra Madre del Sur of Guerrero, where it may breed, were presumably taken in late August, as well as in October and December—by W. W. Brown.) George M. Sutton found a female incubating eggs at Cofre de Perote, Veracruz, and this remains the southernmost nesting record. I could not find the bird there, for the forest floor has been picked so clean that even *Junco phaeonotus* has to nest in the lower pine branches. and *Otus flammeolus* requires considerable understory vegetation. It is a bird of mountain pine forests, catching its prey of moths and other insects in mid-flight or upon the foliage and branches of trees and understory brush at the end of a flight. It perches high in pines when calling, maintaining effective concealment in the angle between branch and trunk.

While *Otus flammeolus* is unquestionably related to *Otus scops* of the Old World through similarity in structure, coloration, and migratory habit, I cannot conceive that they are conspecific. The basic note of *Otus scops'* song is a high-pitched chirp, making a complex noise figure on the sonagraph, rather than the musical low tone of *flammeolus; Otus scops* is larger than *flammeolus* and has long ear tufts, yellow eyes, and a real red phase.

Little has been added to our knowledge of flammulated owls since the basic accounts of Jacot (Condor, 1931, **33**:8-11), Marshall (Condor, 1939, **41**:71-78), and Phillips (Wilson Bull., 1942, **54**:132-137), which introduce to us an abundant insect-hunter in pine forests of the western United States, migratory, males territorial and persistent hooters. Little is said about family life, behavior, and the elusive female. After several people learned how to imitate the song, we filled in the distribution to include just about every open ponderosa pine forest with understory brush in Washington, Oregon, California, Nevada, Arizona, Texas, Sonora, and Chihuahua. The main contributors have been Bob Dickerman, Ned Johnson, Alden Miller, Allan Phillips, Ward Russell, and myself, not to mention bird-banders who now take the flammulated owl in nets. Farther south in Mexico it becomes increasingly difficult to locate undisturbed forests in which to look for this owl. I put up nest boxes in the Santa Catalina Mountains of Arizona, but they attracted only chipmunks and *Otus trichopsis.* Nevertheless, I recommend nest boxes as the best way to solve the remaining problems concerning this mysterious little bird, including Ned Johnson's idea that it hibernates. I have made tape recordings in Arizona and Texas, and have specimens and field notes from all the states mentioned above, except Nevada.

The only recent contribution is Phillips' discovery of a black, heavily marked Great Basin-Rocky Mountains race, of which he collected a series in the Hualpai Mountains, western Arizona, in 1950-1951. These specimens were mostly in fresh fall plumage, easily collected during resumed singing after completion of the fall molt. We lack sufficient fall-plumaged birds from other states properly to evaluate this race, but it is different from our fall series of southern Arizona. We still do not know to which population the type of *flammeolus* pertains, or where the type locality is, and it seems best at present to recognize no races of the species, at least none at the 100% distinction level that I am maintaining in the rest of this paper. (Two to four conventional races could be supported, however.) Phillips cautions that there may be pattern differences among populations which are obscured by, or which we fail to notice because of preoccupation with, the amount of red superimposed. The present state of our knowledge does not permit a really confident allocation of migrants and winter visitors to breeding population of origin.

Geographic variation.—There is a smooth cline of increasing wing length from southeast to northwest, correlated, no doubt, with distance of migration. Wing chord and weight of males presumed to be on their breeding grounds vary from about 129-137 mm. and 49-60 g. in the northwest to 122-123 mm. and 45-57 g. in the south. Clines of color differences (32 fall specimens on breeding grounds) radiate from the Great Basin-Rocky Mountain population, which is the extreme for blackness, least red trimming, largest and blackest ventral shaft streaks. From there the birds become redder and more finely patterned, reaching the extreme of fine pattern in the Pacific Northwest, and the extreme of redness in the southeast, on the Mexican Plateau.

OTUS CHOLIBA, Tropical Screech-owl

Not having encountered this species in the field, I have nothing to add to what is in the key and synopsis except for the songs, kindly loaned by Irby Davis and transferred to sonagrams by John William Hardy. Paul Schwartz, who recorded these songs in Venezuela, writes that they are not primary and secondary in the sense of *asio* and *trichopsis.* The plain song is the more belligerent—a response to playback of tape. The usual, more varied song, is used in antiphonal singing by adjacent males on territories. He has not heard duets by the pair in *choliba.* The red phase is known in our area from only two specimens, one with simplified pattern, the other with the same pattern as the normal phase. In South America the red phase with reduced pattern is more frequent. Our Middle American race is *luctisonus* Bangs and Penard, one of several South American subspecies.

OTUS GUATEMALAE, Vermiculated Screech-owl

Diagnosis.—The vermiculated screech-owl has the normal style of *Otus* coloration but there is less contrast between the ground color and the shaft pattern than in other species. The dorsal pattern is of transverse black five-pointed hastate marks—shaped like a pagoda—upon a homogeneous background. The red phase varies from this same pattern, through streaks, to no pattern at all. Recent freshly-molted specimens show that the fine ventral pattern is on a pure white ground. The toes are naked and very long for this medium-sized owl. The iris is yellow, the bill greenish, the feet pale grayish with darker claws. The tarsus is feathered, but at the distal third the plumes are thin in the population of Costa Rica and Panamá. There also, the pattern of most individuals is blended with the ground color and fragmented into vermiculations. The song is a long trill on one pitch, like a spadefoot toad (*Scaphiopus*). It starts softly, gradually swelling until it is extremely penetrating; then it cuts off abruptly. But for the crescendo it would scarcely be distinguishable from *Chordeiles acutipennis* and eastern *Otus asio*. The latter is shorter, however. I can find no sexual difference in wing chord and weight, but the four longest-winged among 75 sexed skins are females.

Distribution.—Sonora and Tamaulipas to South America.

Habitat.—Dense, tall, continuous, broadleaved woods (and rain forests?) from tropical deciduous woods and thorn forests of lowlands and foothills up into oak woodlands. This species utilizes denser tropical woods than does *Otus asio;* accordingly, it fills blanks in distribution of the latter species, for instance the humid strip from Sinaloa to Colima.

Proximity to other species of **Otus.**—I have not been able to observe this species together with other members of the genus but must presume that it coexists with *Otus trichopsis,* as mentioned under that species. There is little chance of overlap with others, such as *Otus asio,* which require more open growth. I have found them one-half mile apart in Sonora, 10 miles apart in Colima, and L. Binford has taken *guatemalae* 13 miles north of where R. Dickerman took *O. asio* at Puerto Angel, Oaxaca.

GEOGRAPHIC VARIATION

Clines of geographically variable traits radiate outward toward the outposts of the species from a central, variable, dark population occurring from the Isthmus of Tehuantepec to Honduras. It contains some pale specimens identical in coloration with remote races. Its sooty or fuscous dorsal ground color extends northward to include Tamaulipas; tawny brown backs (ruddy when fresh) radiate towards Yucatán, Sonora, and Nicaragua; and a lighter, reddish-brown, speckly back prevails southward into Costa Rica and Panamá. The dorsal pattern is bold and distinct in the north, and in Yucatán and Nicaragua; variable in the central section; and fine and blended in the southeast. The ventral pattern includes conspicuous sharp black streaks in Sonora, Tamaulipas, and Yucatán. They narrow to the vanishing point southward and become lost in the vermiculations. The central population includes every variety of ventral crossbars. Peripherally, they stabilize in Yucatán with narrow black bars, in Sonora and Sinaloa with rows of black dots, from Nicaragua to Panamá with vermiculations, and in Tamaulipas with solid black crossbars as wide as their shaft streaks, like *Otus trichopsis* of the same region. In summary, there is a distinct, sparse, bold pattern in the north (including Yucatán) which becomes variable in the center, and then indistinct, blended, and vermiculated in the southeast. In the red phase the ventral pattern is the same as that of the normal phase; dorsally the pattern may be reduced, but there is no such reduced specimen from the northwest.

Size increases from north to southeast. The smallest birds are *cassini* with wing chord of 143-150 mm. (except for one male of 134 mm.!); the largest are *guatemalae* at 152-172 mm.; *hastatus* is intermediate between these; and *vermiculatus* is slightly shorter than *guatemalae.*

Parallelism.—Similarity to *Otus trichopsis* is discussed under that species. Additionally, *Otus guatemalae* has remarkable parallels among its own races, remote from each other geographically. The dorsal color and dorsal pattern of the Yucatán, Sonora and Nicaragua populations are identical. Apparently the first two have responded to vegetation of arid regions, where bold pattern and light background enhance concealment. (A molting Yucatán bird shows that the really fresh feathers in these populations are the same color as backs from Nicaragua!)

Distinctive races.—Four distinctive Middle American races can be recognized in the 104 adult specimens I have seen, unfortunately not segregated by wear or vintage. Two more will deserve recognition if further study shows consistency of the interesting Yucatán *thompsoni* (15 specimens), and Nicaraguan *dacrysistactus* (4 specimens, including one from eastern Honduras) populations. Their dorsal coloration is that of *hastatus* but ventrally the first has a unique pattern and the second has the underparts of *vermiculatus.*

OTUS GUATEMALAE HASTATUS (Ridgway)

Diagnosis.—Light tawny-brown dorsal ground, upon which are neat, black, pagoda-shaped marks. Distinct black ventral streaks are crossed by wavy rows of little black dots. Red phase of identical pattern.

Distribution.—Sonora and Sinaloa (16 specimens).

Intergrading.—Southward down the Pacific Coast from Nayarit to Puerto Angel, Oaxaca (12 specimens), the birds are more variable, their ventral crossbars become irregular and are not freckled, and some dark backs like *guatemalae* appear.

Habitat.—In southeastern Sonora, east of the Guirocoba Ranch, Rodney Montgomery collected the female of a pair and took me back the same evening for my first encounter with this species which had eluded me for years. The male was calling in a dense tropical deciduous woodland. Near Cosalá, Sinaloa, Jim Werner and I heard a male sing in similar woods with giant cacti added. At neither of these places was the bird actually seen. Both represent the kind of dense habitat in which we have never been able to find *Otus asio.* Phillips and I easily called up a pair by imitated whistles in October in a hillside oak woodland in Nayarit.

OTUS GUATEMALAE CASSINI (Ridgway)

Diagnosis.—The smallest, blackest, and most coarsely patterned race in our area, almost as coarse as *Otus trichopsis trichopsis.* Ventrally the strong black streaks and equally distinct perpendicular crossbars look like the checkerboard pattern of *trichopsis.* The red phase is not yet known north of Jalapa, where a cotype of this color is small enough to qualify as *cassini.*

Distribution.—Caribbean coast of México in southern Tamaulipas, San Luís Potosí, and northern Veracruz (8 specimens).

Habitat.—I have not encountered this race. It ranges up into foothill tropical woods as far as oak-sweetgum in Tamaulipas, where Wm. B. Heed heard three on an evening in late August (Byron Harrell, *The birds of Rancho del Cielo,* 1951, Masters thesis, Univ. of Minnesota).

OTUS GUATEMALAE GUATEMALAE (Sharpe)

Diagnosis.—Equally as dark as, but more finely patterned and larger than, *cassini.* Gray-brown dorsal ground with black pagoda marks. Ventral pattern of narrow shaft streaks crossed by numerous sooty vermiculations or wavy lines. The overall effect is dark, through crowding out of the light parts of the feathers.

Distribution.—Southern Veracruz to Honduras (32 specimens).

Intergrading.—The Nicaraguan population is ideally intermediate between this and *vermiculatus* to the southeast for it combines a ruddy dorsal coloration of freshly-molted *hastatus* with the ventral pattern of *vermiculatus.* There is at least one *guatemalae* style specimen from the range of *vermiculatus* (Utivé, Panamá), and *vice versa,* several from Veracruz to Honduras showing a breakdown of pattern into vermiculations.

Habitat.—I visited numerous type localities and other spots where specimens had been taken in Chiapas and Veracruz without finding the bird. But the habitats were tall tropical woods ranging from lowland rain forest up to oaks.

OTUS GUATEMALAE VERMICULATUS (Ridgway)

Diagnosis.—The reddest and most finely and inconspicuously patterned race. Ground color reddish-brown; pattern of transverse wavy vermiculations is fine, dense, blended, and scarcely darker than the ground. Ventral shaft marks obsolete. Sparsely feathered or bare distal end of tarsus is apparently due to the feathers having been rubbed off, because fresh-plumaged specimens are fully feathered (U. S. National Museum, collected by Alexander Wetmore). Irby Davis writes that he has recorded *vermiculatus* on tape and finds the song similar to that of *guatemalae* which he recorded in Chiapas, except that it is of higher pitch. I suspect it is the voice of the female. I have no doubt that *guatemalae* and *vermiculatus* are conspecific, even though I have not met the latter in the field.

Distribution.—From Costa Rica at least through Panamá (17 specimens).

OTUS BARBARUS, Bearded Screech-owl

The white bridle on the head of *Otus barbarus* (Sclater and Salvin) is conspicuous. Plumage is of the spotted type, not typical *Otus* pattern. I have nothing to add except to mention my chagrin at not finding it where it was collected by Robert W. Dickerman, and to call attention to his record and that of Alfred Lunt Gardner, both from high pine forests of Chiapas. Some fresh-plumaged birds tend to have the tarsus feathered for its entire length on top; beneath, it is bare near the joint with the hind toe.

OTUS CLARKII, Bare-shanked Screech-owl

In many specimens of *Otus clarkii* Kelso and Kelso, the spotted ventral pattern is beautifully done in white, rufous, and black, with narrow black trimming to the white and rufous areas. But in others, the three colors do not "print" in proper alignment, so that the black trim does not match the edges of white or rufous areas, and the pattern is jumbled. I hope we can learn something about this largest screech-owl of our area before its forest habitat is eradicated.

CONCLUSIONS

(See also hypotheses in the introduction.)

Seven species of *Otus* occupy North and Middle America, where they overlap without interbreeding, in such combinations as their distributions and habitats permit. Five are endemic to this continent. *Otus guatemalae* and *Otus choliba* continue across the isthmus of Panamá to range over much of South America. One pair of similar species is peculiar, with restricted distribution in mountain forests of Middle America, and colored in spots and bars. They are *Otus barbarus* and *Otus clarkii,* widely separated geographically and differing greatly in size. The others are of normal *Otus* coloration, patterned with black shaft streaks and crossbars. *Otus flammeolus,* of pine forests, occurs higher in the mountains than the others. It is related to the *Otus scops* group of the Old World, but differs so much from *O. scops* in voice as to be unhesitatingly placed in a separate species. *Otus trichopsis* and *O. asio* constitute a pair unique in feathered toes, more alike than any other two among the seven species. Neither is closely related to *Otus bakkamoena* of Asia. They overlap geographically, occur together in the same habitat frequently, and do not interbreed. Reproductive isolation is through recognition of the different timing of notes in the songs; one species never responds to the songs of the other even though the notes are of similar quality and pitch.

Otus guatemalae is a medium-sized inhabitant of dense tropical woods (and forests?). It tolerates denser growth than any other species of the genus in our area, thus resembling *Otus trichopsis* which it overlaps at the junction of tropical and temperate woods. It converges upon *Otus trichopsis* in northeastern México in details as well as in overall appearance of the cryptic coloration. There, also, *Otus guatemalae* is of smaller size than elsewhere in Middle America; its size increases from north to south. Of standard bold color pattern in the north, this species effects the greatest transformation in the genus, for in the southeast its pattern becomes so fine that it almost vanishes! Individual variation, intergrading, and vocal similarity show that these races are conspecific, however. Geographic variation in coloration is a crystallizing out, at the periphery of the range, of homogeneous distinctive races, from a central highly variable hodge-podge. Four subspecies are recognized. There is infraspecific parallelism in coloration by populations remote from each other but apparently occupying similar environments. *Otus guatemalae* seems not to be closely related to other North and Middle American members of the genus. It has long, bare toes. Its song is like eastern *Otus asio,* but I do not believe this indicates relationship.

Otus flammeolus, a moth-catcher, is the smallest member of the genus, but has relatively the largest wings. A migrant, its wing length increases to the north and northwest, doubtless as an adaptation to longer travel by those populations. Clines of increasing redness and finer pattern radiate out from the blackish, heavily marked population of the Great Basin-Rocky Mountain region. No subspecies are recognized here.

Otus trichopsis is a smaller, more coarsely-patterned, weaker-footed edition of *Otus asio,* occupying a broad span of latitude over which it preserves unchanged its size, distinctive vocalizations, and restriction to montane woodlands. The mellow quality, constant pitch of notes in the songs, and gray coloration of *Otus trichopsis* are most similar to the western section of *Otus asio;* indeed coloration closely parallels those races of the Kennicottii Group which occupy the same region. This is an evolutionary response to the same forces selecting for cryptic coloration. But such extremely close resemblance suggests that similar sets of genes are involved, and is further indication of recent common ancestry. *Trichopsis* differs in timing of notes in the song, smaller size, small feet, and preference for dense woods at high altitude. Presumably it will have evolved from a segment of the Kennicottii Group isolated in an area of high altitude and dense woods, where smallness would be an advantage in manuevering through the foliage. Food preference will have been for smaller invertebrates than those sought by the common ancestor, with more being taken in trees than on the ground. How would the smaller foot be advantageous? Either it is better for grasping small prey, or its use for capturing has been abandoned in favor of the bill. The small foot would then facilitate perching on twigs. Unfortunately, my many hours of observations fail to resolve whether this owl captures with the foot or bill. Red-light views of foraging captives or wild birds are needed.

Evolution in *Otus trichopsis* below the species level will have been a settling out, from a heterogeneous stock, of three homogeneous populations in areas of extreme environmental conditions: aridity and winter cold in Arizona and environs, high altitude and cold of the southern Mexican Plateau, high humidity or heavy rainfall in Honduras and Nicaragua. These climates may sponsor characteristic color and texture of bark and leaf to which the cryptic coloration of the local owls conforms. This is not to imply that the more variable intermediate populations are less well adapted. Their ambivalence probably corresponds with a more varied local flora in which they must find concealment. Three subspecies are recognized. The northern limit of the species is at the end of the kind of dense, continuous oak woodlands that it likes. I have not been south of El Salvador, but I expect that the southern limit is imposed by termination of suitable oak and pine groves also.

Otus asio has gross feet for catching large invertebrates and small vertebrates on the ground under trees. It is the only one of the four species I measured which shows sexual dimorphism in size. The females average larger than the males. It is a composite of four geographically isolated incipient species, three of which are wide-ranging and spectacularly variable racially. Eight subspecies are recognized in the Kennicottii Group, one in the Seductus Group, two in the Cooperi Group, and five in the Asio Group. Similarities indicating relationship between groups are in geographically variable traits, often developed in only one racial population at a geographic outpost of its group. These affinities can be represented as follows:

	KENNICOTTII	SEDUCTUS	COOPERI	ASIO
Red phase	*kennicottii*			Asio Group
No red phase	rest of Kennicottii Group	*seductus*	Cooperi Group	northern *mccallii*
Plumage similarity	½ red phase of northern *bendirei*			normal phase of *asio*
Bouncing ball song	Kennicottii Group	*seductus*		
Double trill	Kennicottii Group	*seductus*	Cooperi Group	
13-note song	*xantusi*		Cooperi Group	
Gruff voice	*	*seductus*	Cooperi Group	
Fine linear pattern	*vinaceus, xantusi*			*mccallii*
Vinaceous pink	*vinaceus*	*seductus*	*lambi*	
Greenish bill	northern *bendirei*	*seductus*	Cooperi Group	Asio Group
Wild	*vinaceus, xantusi*	*seductus*	Cooperi Group	
Hybridize	*suttoni*			*mccallii*

*Gruff only when belligerent: tape recordings, *aikeni,* Tucson, Arizona.

Table 1. Lines of Relationship between Incipient Species in *Otus asio.*

The only known geographic approach or overlap between any of these groups is along the Big Bend of the Río Grande, where at least one, and probably two, mixed pairs with offspring have been found along with a pure pair of *mccallii* (Asio Group) and pure individuals of *suttoni* (Kennicottii Group). Their habitat is a fringe of small mesquites and willows along a river which crosses a desert, consequently the population is thin and the evidence meager. It is hoped that these conclusions may nevertheless be justified:

1. There is as much interbreeding between the Kennicottii and Asio groups as opportunity affords in this narrow habitat. We have not a zone of hybridization or intergrading, but a single file of individuals whose potential mates are few and far between, and who pair up as best they can.

2. The fairly even split of specimens into *suttoni* and *mccallii* dorsal color categories may be due to simple inheritance with dominance. (I am indebted to Dr. James R. Crook for this suggestion.) However, the variation at Langtry must arise from recombination of parental *suttoni* and *mccallii* genes, not from influence of *hasbroucki.*

3. The Arkansas River in eastern Colorado and the Cimarron River in western Kansas provide similar opportunities for contact.

4. Because common screech-owls are sedentary and riparian habitats are narrow, interbreeding fails to homogenize the population along a river. For instance, the Colorado River originates in the domain of the race *aikeni* but supports *yumanensis* at its mouth; the Río Grande has *aikeni* as far down as Socorro, *suttoni* in the Big Bend, and unadulterated *mccallii* from Del Rio to the Gulf of México.

5. There is perfect vocal compatibility between the two groups; differences in song do not interfere with the formation and maintenance of the pair bond.

6. *Otus kennicottii* and *Otus asio* are one and the same species.

7. Since *Otus seductus* and *Otus cooperi* are more similar to *Otus kennicottii* than is *Otus asio,* they likewise must be joined to the single species.

Mccallii, considering all its peculiarities, must have enjoyed a period of isolation from which it is now emerging to intergrade precipitously with *hasbroucki* and to hybridize with *suttoni* in only one area along hundreds of miles of possible contact! Perhaps it deserves incipient species rank, intermediate between the Kennicottii and Asio groups.

The seven species and the four race groups within *Otus asio* differ from each other in biological traits such as voice, habitat preference, and distribution. They also differ in proportions and amount of feathering on the feet. Their geographic variation in cryptic coloration is parallel in different species inhabiting the same general region. This shows that coloration matching the roost and foraging site in trees must be the result of natural selection by predators, and suggests also that the owls must individually choose their roost to match their coloration, especially as to whether the latter is red, intermediate, or normal phase.

Parallelism is the cue for picking traits of evolutionary importance in analyzing geographic variation. It is a handy memory device to use subspecies names to designate certain racial styles of coloration as well as the geographic area where a style prevails. The facts of geographic variation in this genus are too cumbersome to handle any other way. Formal subspecific trinomials can be profitably used for the 100% distinctive racial populations, with geographic limits to contain only the area where the distinctive trait predominates.

Geographic variation follows some of the same trends seen in other highly variable species (*sensu lato*), for which I cite the most recent revision encompassing the entire distribution in order that you can make comparisons: *Colaptes auratus* (Short, Bull. Amer. Mus. Nat. Hist., 1965, **129**:307-428), *Junco hyemalis* and *Passerella iliaca* (Phillips, Marshall and Monson, *Birds of Arizona,* 1964, Univ. Ariz. Press, Tucson) and *Melospiza melodia* (Marshall, Auk, 1964, **81**:448-451). These trends may be summarized under Phillips' Law which states that size decreases from north to south in lowland species; the reverse obtains in those which live at increasingly higher altitudes in the mountains southward. This works for *Otus asio* in the United States, but not for *Otus flammeolus.* The remaining tropical forms do not follow such a rule involving response to cold winters. Gloger's Law is followed, in a general way by *Otus* and the others, whereby we find rich, dark coloration on humid coasts, pale gray colors in deserts. Occurrence of blackish races of screech-owls in interior arid uplands demands a fuller explanation: that geographic differences in coloration are connected with concealment against the kind of bark and foliage prevailing in given climatic area, not with climate itself. Nothing in this racial variation suggests the geographic, biologic, and morphologic differences shown by the species and incipient species. Infraspecific variation should be regarded as a perfection for living in the local environment, which makes the species a better species there.

Character displacement is an observation, undocumented for any birds of known ecology, that racial divergence of two similar species where their ranges overlap is greater than in areas where they occur alone. Presumably these differences would be in traits effecting species recognition, to prevent mixed matings, and in size and proportions of the bill and feet which would facilitate taking different prey in the same habitat so as to avoid competing for food. The reverse of "character displacement" occurs in the genus *Otus*. Considering their similarity and actual convergence in appearance, screech-owls could hardly depend on coloration or structure for species recognition. Each knows its own kind by the distinctive temporal pattern of the song—the duration and timing of the notes. Duetting by the male and female is a standard nightly ritual in *Otus asio, O. trichopsis* and *O. guatemalae* insuring that pairs will be formed within the same species. Full species of *Otus,* having evolved distinctive songs and tolerance for a unique habitat, need no further modification of song when they finally extend their ranges to overlap each other. Their songs are no more different in the area of sympatry than elsewhere. So much for species recognition. As for competition, I have found no evidence for it; admittedly this might be forthcoming only during a critical reduction of food supply. But in the normal life of the coexisting *Otus asio, O. trichopsis* and *O. flammeolus* that I have studied they have behaved as if they were oblivious of each others' existence. Their territories are often superimposed. Structural differences—size, proportions, bill measurements—among these species and *Otus guatemalae* are no greater in the area of overlap than elsewhere. Character displacement has not played a role in their racial adaptation.

Turning now to the incipient species we have a perplexing situation because their geographic separation denies us the opportunity of seeing if they can all interbreed. But there is indirect evidence that they can, and this is strengthened by the similar but clearer case of the brown towhee, *Pipilo fuscus* (Marshall, Condor, 1964, **66**:345-356). Its two geographically isolated race groups, the incipient species *Pipilo crissalis* and *P. fuscus,* have different territorial songs, yet their pair-forming squeals and ecology are the same and we can conclude that they are conspecific. *Pipilo crissalis* has given rise to the new full species *P. aberti* at some time following its isolation from *P. fuscus. Pipilo aberti* is distinct both vocally and ecologically and it overlaps the parent species without interbreeding, in some marginal habitats suitable for both. In *Otus asio,* the four geographically isolated incipient species (with one exception) have different primary songs yet their pair-forming duets (secondary songs) and ecology are similar so that again we can conclude that they are conspecific. *Otus kennicottii* has given rise to the new species *O. trichopsis* at some time since it became isolated from *O. asio. Otus trichopsis* is distinct both vocally and ecologically and it so exists with the parent stock in some marginal habitats suitable for both, without interbreeding. The following is a possible course of this evolution in both *Pipilo* and *Otus:*

1. Evolution of geographic races.

2. Geographic isolation of western from eastern race groups by unfavorable habitat (Colorado Desert for *Pipilo,* dense oaks for *Otus*).

3. Development of a different song by the isolated race group—the incipient species stage.

4. Presentation of a new habitat available for occupancy by the genus (riparian woodland for *Pipilo* and montane dense oaks for *Otus).*

5. Exploitation of the new habitats by the incipient species *P. aberti* and *O. trichopsis* leading to ecologic distinction and full species rank permitting:

6. Geographic overlap with the parent species and coexistence in marginal habitats without interbreeding.

What is going to happen to *Pipilo crissalis* and *P. fuscus,* to *Otus kennicottii* and *O. asio?* Will civilized habitats bring them into breeding continuity and so break down their advance toward the species level? I cannot see how they will ever progress farther unless they acquire some really spectacular ecologic differences, as did *Pipilo aberti* and *Otus trichopsis.* The point is that if and when ecologic differences are evolved, they are going to take hold of the vocally distinct subspecies groups. They, and not the individual subspecies, will carry on evolutionary divergence. I am indeed happy and proud to present the reader with real incipient species, qualitatively of higher order than mere subspecies, in *Pipilo fuscus* and *Otus asio.*

ACKNOWLEDGMENTS

I thank the officers of the countries and states visited for permission to collect screech-owls; curators of the museums listed in the appendix for the loan of, or opportunity to see, specimens; Irby Davis and the Cornell Laboratory of Ornithology for the loan of tape recordings; John William Hardy and Miwako Tamura for making the sonagrams; John Davis and Ernst Mayr for interpreting Peters' weird and now defunct taxonomy of *Scops asio* var. *enano;* K. C. Emerson for taxonomic implications of Mallophaga, and Theresa Clay for identification of Mallophaga from *Otus asio seductus;* Eugene Eisenmann for advising not to coin a new set of common names ending in Scops-owl; Herbert Friedmann for criticism of the manuscript; the University of Arizona, the National Science Foundation, and the Western Foundation of Vertebrate Zoology for financial support and transportation; Elsie Marshall and Sally Lee for typing; Gene Christman and the Museum of Vertebrate Zoology for facilities to prepare the graphs; and the following who have collected a beautiful array of fall-plumaged skins:

Miguel Alvarez del Toro
Nazario Chávez
Richard C. Crossin
Robert W. Dickerman
Charles Ely
Santos Farfán B.
Alfred Lunt Gardner
Mr. and Mrs. R. R. Graber
Ciro Gonzales
Ed N. Harrison
Chester C. Lamb
Hugh C. Land
Seymour H. Levy
Peter Marshall
Alden H. Miller
Robert Ohmart
Allan R. Phillips
Warren Pulich
Warren Rook
Wm. J. Schaldach, Jr.
George Miksch Sutton
Alexander Wetmore
Dale Zimmerman

Field trips were made particularly enjoyable through collaboration with friends and relations, among whom I am especially grateful to Dale Arvey, Joseph Brauner, Richard Felger, C. H. Lowe, Jr., Peter Marshall, Woodridge Metcalf, A. H. Miller, Loye Miller, Gale Monson, Rodney Montgomery, Robert Ohmart, A. R. Phillips, Ralph Raitt, W. C. Russell, W. J. Schaldach, Jr., W. J. Sheffler, C. G. Sibley, R. A. Stirton, G. M. Sutton, John Tucker, Ray Turner, S. P. Welles, James Werner, and Colonel L. R. Wolfe.

APPENDIX

SYNOPSIS OF NORTH AND MIDDLE AMERICAN SCREECH-OWLS

This sets subspecies boundaries at the half-way point along clines, for the use of museum curators.

1. *Otus asio*	Any open woods. Alaska, southern border of Canada and Maine to Costa Rica, with two gaps along Pacific Coast of México and absent from Caribbean slope south of Tamaulipas.
a. Kennicottii Group	The West, from southeastern Alaska to Baja California, Sinaloa, and the Mexican Plateau.
1) *kennicottii*	Juneau and Sitka, Alaska, to coastal Oregon.
2) *bendirei*	Okanagan, British Columbia, and Idaho (large) to southern California (smaller), east of the Cascades but west of the Sierra Nevada, though including Mojave Desert.
3) *cardonensis*	Baja California Norte.
4) *xantusi*	Baja California Sur.
5) *aikeni*	Nevada, eastern California, Utah, Arizona, north-central Sonora, New Mexico, southeastern Colorado and extreme western Oklahoma.
6) *suttoni*	Mexican Plateau north to Big Bend of Texas and Guadalupe Canyon, Arizona.
7) *yumanensis*	Colorado Desert, lower Colorado River, and northwestern Sonora.
8) *vinaceus*	Central Sonora to Culiacán, Sinaloa.
	GEOGRAPHIC GAP
b. Seductus Group *seductus*	Colima and Río Balsas basin in Michoacán and Guerrero, México.
	GEOGRAPHIC GAP
c. Cooperi Group	Isthmus of Tehuantepec to Costa Rica.
1) *lambi*	Oaxaca: Río Tehuantepec and the Pacific Coast from Puerto Angel to Laguna Interior.
2) *cooperi*	Pacific Coast from Mar Muerto (Chahuites), Oaxaca, to Costa Rica, preferring edge of mangrove swamps.
d. Asio Group	East of the Rocky Mountains from border of Canada to Florida and northeastern México.
1) *maxwelliae*	Southern Saskatchewan, southern Manitoba, Montana and Dakotas to Wyoming, western Nebraska, western Kansas and northeastern Colorado.
2) *hasbroucki*	Central Kansas, Oklahoma and Texas.
3) *mccallii*	Lower Río Grande (no red phase) to the southern border of Tamaulipas (red phase common).
4) *asio*	Minnesota, peninsular Michigan, Montreal and southern Maine south to Missouri and northern portions of Mississippi, Alabama and Georgia.
5) *floridanus*	Florida and the Gulf Coast west at least to Louisiana and up the Mississippi to Arkansas.
2. *Otus trichopsis*	Pine-oak woods. Arizona to Nicaragua.
1) *aspersus*	Southeastern Arizona, Sonora, Chihuahua.
2) *trichopsis*	Sinaloa and Nuevo León to Oaxaca.
3) *mesamericanus*	Chiapas to Nicaragua.
3. *Otus flammeolus*	Pine forest. Southern British Columbia to south end of Mexican Plateau; winters in México and Guatemala.
4. *Otus choliba*	Costa Rica and Panamá (several races in South America).
5. *Otus guatemalae*	Tropical woods. Southern Sonora to South America.
1) *hastatus*	From southeastern Sonora south along the Pacific Coast to Oaxaca.
2) *cassini*	Tamaulipas to central Veracruz.
3) *guatemalae*	Southern Veracruz and Yucatán to Nicaragua.
4) *vermiculatus*	Costa Rica and Panamá.
6. *Otus barbarus*	Pine Forest. Chiapas and Guatemala.
7. *Otus clarkii*	Mountains in Costa Rica and Panamá.

SYNONYMS RESULTING FROM DISTRIBUTIONS ASSIGNED IN SYNOPSIS

Distinctive Races 100% separable by coloration	Valid Conventional Races—least consistent difference discerned by an expert, here considered synonyms	Superfluous names
Species *OTUS ASIO*		
kennicottii	*brewsteri*	*saturatus*
bendirei	*macfarlanei*	*quercinus*
cardonensis		*clazus*
xantusi		
aikeni	*inyoensis, cineraceus*	*mychophilus*
		gilmani
suttoni		*sortilegus*
yumanensis		
vinaceus		*sinaloensis*
seductus		
lambi		
cooperi		*chiapensis*
maxwelliae	*swenki*	
hasbroucki		
mccallii	*semplei*	
asio	*naevius*	
floridanus		
Species *OTUS TRICHOPSIS*		
aspersus		
trichopsis		*enano, guerrerensis, pinosus, ridgwayi*
mesamericanus	Chiapas-Guatemala population	*pumilus*
Species *OTUS FLAMMEOLUS*		
	idahoensis, Great Basin-Rocky Mt. population, *flammeolus, rarus*	
Species *OTUS GUATEMALAE*		
hastatus		*tomlini*
cassini		
guatemalae	*thompsoni, dacrysistactus*	*fuscus, marmoratus*
vermiculatus		

Table 2. Revised synonymy of North and Middle American *Otus*.

COMMENTS ON TYPE SPECIMENS

I examined all type specimens except the eight marked lost or not seen. An asterisk means that the type is colored like unworn average specimens from its local population. The trouble with the others is that they are worn or that they are variants of their population, approaching the coloration of a neighboring population.

Species *Otus asio*

aikeni (Brewster) Worn and stained.
asio (Linnaeus) Not seen.
bendirei (Brewster)*
brewsteri Ridgway*
cardonensis Huey*
chiapensis Moore*
cineraceus (Ridgway)* From a population too much like *aikeni.*
clazus Oberholser* I synonymize this with *cardonensis* because it is black, but we need fall specimens from Baja California Norte before we decide whether to include *cardonensis* on the California list.
cooperi (Ridgway)*
floridanus (Ridgway) Red phase.
gilmani Swarth Worn and faded.
hasbroucki Ridgway Very odd; fine texture, not representative; looks like the Kennicottii Group.
inyoensis Grinnell* Beautiful fall skin, identical with *aikeni* dorsally.
kennicottii (Elliot)* Tends toward the intermediate red phase.
lambi Moore and Marshall*
macfarlanei (Brewster)* The female is an excellent example.
maxwelliae (Ridgway)*
mccallii (Cassin)* The type is a flat skin with the neck extended and ruffled to reveal the light bases of the feathers. This gives an incorrect impression of "coarse mottling." Compressed into normal shape it shows the fine texture and pattern as diagnosed in my account of *mccallii.*
mychophilus Oberholser Looks more like *cineraceus* than *aikeni* but is in the area of the latter.
naevius (Gmelin) Not seen.
quercinus Grinnell Worn.
saturatus (Brewster) A good example of the blackish variant of *kennicottii.*
seductus Moore*
semplei Sutton and Burleigh*
sinaloensis Moore Worn and dull.
sortilegus Moore Worn and brown, nesting.
suttoni Moore*
swenki Oberholser Not seen.
vinaceus (Brewster)*
xantusi (Brewster) A variant unfortunately resembling *yumanensis.*
yumanensis Miller and Miller* Shows some of the pink, even though it is a spring bird.

Species *Otus trichopsis*

aspersus (Brewster) Tends toward *trichopsis.*
enano (Baird and Ridgway)* From Oaxaca, is a good example of blackish, coarse *trichopsis.* The cotype from Guatemala, summarily stripped of its credentials by Peters, is a good example of the Chiapas-Guatemala population.
guerrerensis van Rossem Not seen. There seems to be no distinction of this population from *aspersus* except greater variability and possession of a red phase. It may prove valid when skins other than those of W. W. Brown become available from the Sierra Madre del Sur. I predict, however, that they will be the same as the five beautiful fall skins collected from adjacent Oaxaca and just loaned me by A. R. Phillips. These straddle *aspersus* and *trichopsis* in the same bimodal way as do the series on the other side of Guerrero, in Jalisco and Colima.
mesamericanus van Rossem. This skin is the least ruddy of its series but otherwise is characteristic of the race in central El Salvador, Honduras and Nicaragua. It comes from an area of intermediacy with the Chiapas-Guatemala population.
pinosus (Nelson and Palmer) A juvenile. I collected two freshly molted adult topotypes (Western Foundation and Sheffler collections); they are *O. t. trichopsis.* The pine forests of Las Vigas, at 8,000 feet, are above the altitudinal limits of *O. guatemalae.* The bristled toes and all other features of the type agree with the species *Otus trichopsis.* Its dark color is to be expected in this area where the adult plumage is blackish.

pumilus Moore and Peters Has too few back feathers, which tend toward the Chiapas-Guatemala population, but it comes from an area where typical full-sized, ruddy, fine-marked *mesamericanus* prevails.

ridgwayi (Nelson and Palmer) A red juvenile.

trichopsis (Wagler) Lost.

Species *Otus flammeolus*

flammeolus (Kaup) Not seen. I am provisionally using this name for the moderately red, moderately fine-patterned, short-winged population of southern Arizona, southern New Mexico, western Texas and northern México. But the type must be examined to see if it really is a migrant of one of the northern populations.

idahoensis (Merriam)* Is a good example in coloration, but is at the low extreme of wing length, just the reverse of the true racial situation.

rarus Griscom Not seen.

Species *Otus guatemalae*

cassini (Ridgway)*

dacrysistactus Moore and Peters*

fuscus Moore and Peters Dirty.

guatemalae (Sharpe) Not seen.

hastatus (Ridgway)*

marmoratus (Nelson) Is a variant of *thompsoni* phenotype from the range of *guatemalae*.

thompsoni Cole*

tomlini Moore Worn.

vermiculatus (Ridgway)*

RED AND INTERMEDIATE RED PHASE SPECIMENS IN THE KENNICOTTII GROUP

Red Phase		
Otus asio kennicottii 9		
Dall Id., Alaska	Chicago Nat. Hist. Mus.	1 (159309)
Vancouver, B. C.	Chicago Nat. Hist. Mus.	4 (100307, 100308, 159302,159303)
Vancouver, B. C.	MCZ	3 (probably 321596, 321597 and 321598)
Sumas, B. C.	MCZ	1 juvenile (probably 244717)
Intermediate Red Phase		
Otus asio kennicottii 7		
Sitka, Alaska	USNM	1 (45847)
Chilliwack, B. C.	MCZ	1 (probably 244718)
Sumas, B. C.	AMNH	1 (476831)
Bellingham, Washington	AMNH	1 (753869)
San Juan, Id., Washington	MVZ (JTM)	2 (87205, 87206)
Tillamook, Oregon	San Diego Nat. Hist. Mus.	1 (22124)
Otus asio bendirei (northern) 7		
Vaseau Lake, B. C.	MVZ	1 (101678)
Okanagan, B. C.	AMNH	1 (360442)
Columbia Falls, Mont.	AMNH	1 (753861)
Yakima, Wash.	Sheffler	1 (4828)
Ft. Walla Walla, Wash.	USNM	1 (87888)
Rufus, Ore.	San Diego Nat. Hist. Mus.	1 (22109)
Devil's Lake, Ore.	Yale Peabody	1 (9375)
Otus asio cardonensis 1		
Jacumba, Baja California Norte	MCZ	1 (252208)
Otus asio suttoni 1		
México, D. F.	Univ. Ariz.	1 (JTM 5826)

MUSEUMS

I examined unworn Middle American specimens and those from the prebasic molt through December for the United States and Canada in the following museums:

American Museum of Natural History
*University of Arizona
*Big Bend National Park
California Academy of Sciences
University of California at Los Angeles
Carnegie Museum (including specimens formerly in Cleveland Museum)
Chicago Natural History Museum (briefly)
Colorado College
Cornell University
Denver Museum
Charles Ely
*Instituto de Biología, Universidad Nacional Autónomo de México
University of Kansas Natural History Museum
Los Angeles County Museum
*Louisiana State University (including W. J. Sheffler and J. T. Marshall collections)
*University of Michigan Museum of Zoology (*skeletons only)
University of Minnesota (a few only)
Museum of Comparative Zoology
*Museum of Vertebrate Zoology
Occidental College Moore Zoological Laboratory
Allan R. Phillips
San Diego Natural History Museum
Southwestern Research Station
*George Miksch Sutton
*United States National Museum
University of Utah
Walla Walla College
*Western Foundation of Vertebrate Zoology

*contains specimens collected by the author

I have slighted one really fine collection by spending insufficient time at the Chicago Natural History Museum. I noticed the pure red phase specimens from British Columbia there, an excellent example of *O. asio lambi* resplendent in its pink fall plumage, and a nice series of *Otus trichopsis* from Chiapas. The best prepared and most uniform skins, best arranged, easiest to find and to study are unquestionably those of the Museum of Comparative Zoology, where even the type specimens are right in with the series they typify. The most valuable collections, containing the largest proportion of fresh fall skins as well as the greatest number of little-known forms from México are those at the University of Arizona, Western Foundation of Vertebrate Zoology, and Louisiana State University. The latter now contains the Sheffler collection which includes much of my Arizona and Mexican material, as well as the remarkable collections made in San Luís Potosí by the staff of that museum and their Mexican colleagues.

SUGGESTIONS FOR PRESERVING SPECIMENS

There is no excuse for taking specimens of *Otus* in worn plumage of late winter, spring, or summer except for intergroup hybrids and *Otus flammeolus* off its breeding grounds. Worn, caged, and zoo specimens can be given to biology classes to demonstrate polymorphism and geographic variation. Specimens of W. W. Brown and J. H. Batty, with their fictitious labels, should also be given away.

Here are suggestions for preparing screech-owl skins. First, the specimen should be weighed. Even a pocket-sized spring balance gives valuable data. The "Pesola" scales made by Oskar Ludi of Switzerland will fit into your pocket and are extremely accurate. They are called *Pesola Dynamometers* and are made in sizes of 10g., 30g., 100g., 300g., 500g., 1 kilo, etc.

It is best to preserve the skin with the bill pointing along the longitudinal axis, so that the crown and nape can be seen in the same view with the back. The neck stick should run down the throat leaving a crook at the back of the neck into which can fit the bases of the dorsal tract feathers. Ordinary preparation, with a stick down the back of the neck, pushes these feathers dorsad, exposing their light bases, and giving a false impression of pale spotting. Some collectors prefer to skin the owl's wings down to the wrist as the easiest way to clean the meat off the ulna and remove the radius. But it is important that the wing be restored to its natural disposition by pulling the secondaries back (proximad) along the ulna, and hooking the innermost ones forcibly around the elbow, so as to keep all the flight feathers in proper alignment. C. C. Lamb, W. J. Schaldach, Jr., and their assistants are about the only professional collectors I know who do not leave the secondaries telescoped down the ulna, causing the primaries to be straightened unnaturally, and throwing a fold of skin around the exterior of the wrist so that the wing cannot be measured!