LITERATURE CITED
(excepting items cited by title in text)

DAVIS, J.
1959. The Sierra Madrean element of the avifauna of the Cape District, Baja California. Condor, 61:75-84.

ELBEL, R. E., and EMERSON, K. C.

EMERSON, K. C.

GRINNELL, J.

HASBROUCK, E. M.

JACOT, E. C.

KNORR, O. A.

MARSHALL, J. T., JR.
1939. Territorial behavior of the flammulated screech owl. Condor, 41:71-78.

MILLER, A. H.

MILLER, A. H. and MILLER, L.

MOORE, R. T., and MARSHALL, J. T., JR.

OWEN, D. F.

PHILLIPS, A. J.

SHORT, L. L., JR.

SLUD, P.

Fig. 1. Author's sketches of the right foot of seven species of screech-owls, natural size, to show differences in feathering and proportions.
Fig. 2. *Otus asio*: dorsal and ventral patterns of races within the Kennicottii and Seductus groups, dorsal ground color indicated.
Fig. 3. *Otus asio*: color patterns of the Cooperi and Asio groups.
Fig. 4. *Otus trichopsis*, *O. guatemalae*, and *O. flammelolue*: dorsal and ventral black patterns with dorsal ground color indicated.
Otus barbarus

tarsus feathered
ear tufts large and patterned

Otus clarkii

lower tarsus naked
ear tufts present but not distinctively colored
wing 180

guatemalae: bigger
barbarus: same size as ochraceus
flammulatus: smaller foot

where the feathers end

Otus choliba

toes naked, ear tufts present, wing 173

Fig. 5. *Otus barbarus, O. clarkii, and O. choliba*: dorsal and ventral coloration.
Subspecies names are placed in the approximate region where each race attains its greatest distinctiveness. Because of a higher standard than the conventional one for subspecies, my 100% distinguishable races involve two awkward shifts. I synonymize *macfarlanei* into *bendirei* by the rules of priority but show the best development of *bendirei* in the geographic range of *macfarlanei*. Similarly, I show the best development of *asio* in the territory of its synonym, *naevius*. This is because the older name's type specimen comes from an area of intermediacy. On the other hand there are intermediate races whose type locality is exactly in the proper intermediate area. Some are well-known and venerable such as *cineraceus, inyoensis*, and *swenki*.

For those museum curators who prefer to retain all these valid, but decidedly intermediate subspecies, the table of synonyms in the appendix shows the correct names, and their distributions appear as "intermediate races" in the sections on intergrading in the appropriate subspecies accounts.

In summary, my disposition of well-known names from the AOU Check-list is as follows:
The intermediate race *asio* of the Check-list has its name replacing *naevius* to become the name of a distinctive subspecies.
The intermediate race *bendirei* of the Check-list has its name replacing *macfarlanei* to become the name of a distinctive subspecies.
The intermediate race *cineraceus* of the Check-list is submerged into *aikeni*.
The intermediate race *swenki* of the Check-list is submerged into *maxwelliae*. 
Fig. 6. *Otus asio*: distribution of the four race groups.
EXPLANATION OF FIGURE 7 (opposite page):

<table>
<thead>
<tr>
<th>Locality</th>
<th>Museum</th>
<th>Date</th>
<th>Phenotype (if not worn)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>KENNICOTII GROUP, SOLID CIRCLES</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pine Springs, Culberson County,</td>
<td>Denver</td>
<td>Sept 1945</td>
<td>2 9 aikeni</td>
</tr>
<tr>
<td>and 8 mi. N Guadalupe Peak</td>
<td>MVZ</td>
<td>March 1950</td>
<td>aikeni</td>
</tr>
<tr>
<td>Bell Canyon (cannot find) 70 mi.</td>
<td>Peabody</td>
<td>June 1947</td>
<td>8 sutoni</td>
</tr>
<tr>
<td>NE Van Horn, 5000 ft.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lajitas</td>
<td>Arizona,</td>
<td>Oct 1961</td>
<td>3 8 sutoni</td>
</tr>
<tr>
<td>Terlingua</td>
<td>Oklahoma</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chisos Mts</td>
<td>USNM</td>
<td>June 1901</td>
<td>8 sutoni and 2 juveniles</td>
</tr>
<tr>
<td>Boquillas</td>
<td>Univ. Texas</td>
<td>Sept 1937</td>
<td>2 sutoni</td>
</tr>
<tr>
<td>9 mi. SBoquillas</td>
<td>Big Bend Park</td>
<td>July 1962</td>
<td>2 sutoni of mixed pair,</td>
</tr>
<tr>
<td>Sierra de Carmen</td>
<td>Arizona</td>
<td></td>
<td>another lane 8 heard</td>
</tr>
<tr>
<td>Langtry</td>
<td>Chicago</td>
<td>April 1945</td>
<td>3 of aikeni phenotype</td>
</tr>
<tr>
<td>Juno</td>
<td>USNM</td>
<td>Oct 1961</td>
<td>5 4 0 sutoni</td>
</tr>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>ASIO GROUP, TRIANGLES</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sheffield</td>
<td>U. Texas,</td>
<td>July 1962</td>
<td>1 8 mccallii</td>
</tr>
<tr>
<td>Independence Creek</td>
<td>Arizona</td>
<td>July 1949,</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>July 1962</td>
<td></td>
</tr>
<tr>
<td>Boquillas</td>
<td>Arizona</td>
<td>July 1949,</td>
<td>1 8 mccallii of mixed</td>
</tr>
<tr>
<td>10 mi. WLangtry</td>
<td>Arizona</td>
<td>July 1962</td>
<td>pair</td>
</tr>
<tr>
<td>Langtry</td>
<td>Arizona</td>
<td>Oct 1961</td>
<td>3 8 mccallii, cineraceus</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>and hasbroucki</td>
</tr>
<tr>
<td>Comstock</td>
<td>USNM</td>
<td>June 1902</td>
<td>9 mccallii</td>
</tr>
<tr>
<td>mouth of Devil's River, and Del</td>
<td>Kansas, MVZ</td>
<td>Feb 1955</td>
<td>2 0 mccallii</td>
</tr>
<tr>
<td>Rio, 4 mi. N.</td>
<td></td>
<td>Dec 1954</td>
<td></td>
</tr>
<tr>
<td>Fort Clark</td>
<td>USNM</td>
<td>March 1893,</td>
<td>1 9 of hasbroucki</td>
</tr>
<tr>
<td></td>
<td></td>
<td>April and</td>
<td>phenotype</td>
</tr>
<tr>
<td></td>
<td></td>
<td>May 1898</td>
<td></td>
</tr>
<tr>
<td>Jiménez</td>
<td>Kansas</td>
<td>June 1952</td>
<td>1 8 and 1 9 mccallii</td>
</tr>
<tr>
<td>Nave</td>
<td></td>
<td>July 1962</td>
<td>1 8 mccallii</td>
</tr>
<tr>
<td>Allende, 8 mil. S.</td>
<td>Arizona</td>
<td>July 1962</td>
<td>1 8 heard</td>
</tr>
<tr>
<td>La Gacha</td>
<td>Kansas</td>
<td>Dec 1953</td>
<td>1 mccallii</td>
</tr>
<tr>
<td>La Mariposa</td>
<td>U. Texas</td>
<td>March 1938</td>
<td>9 mccallii</td>
</tr>
</tbody>
</table>
Fig. 7. *Otus asio*: overlap of Kennicottii and Asio groups at the Big Bend of the Rio Grande.
Fig. 8. *Otus trichopsis*: coloration of 129 fall and winter specimens.

(Each small square represents one museum specimen. All specimens in a vertical column are of the same dorsal/ventral coloration, named at the top of that column; all specimens in a horizontal array are from the same population. Red phase is blacked in. For brevity, the name "enano" is used for the phenotype predominant in the Chiapas-Guatemala population.)
OTUS FLAMMEOLUS

POPULATIONS

Pacific states and Idaho, idahoensis

Great Basin and southern Rockies

Southern border of USA, northern Mexico, flammeolus?

Mexico south of Tropic of Cancer, rarus

Fig. 9. *Otus flammeolus*: coloration of 32 fall-plumaged birds thought to be on their breeding grounds.
FIG. 10. Diagrammatic representations of sonograms of screech-owl songs: *Otus asio* and *Otus trichopsis*.

(*Otus cooperi* was recorded by Irby Davis. The opening trill of its primary song is not frequently used; it and the first trill of the double trill are confused on the sonograph, and do not agree with what the ear discerns, especially when the recording is played slowly. The sonogram is reproduced here mainly because it is the only known recording of this owl; it is atypical and unfortunately does not support the author's claim that *cooperi* is conspecific with *asio*, based on his field notes and diagrams of normal songs of *cooperi* males. The rest of the owls were all recorded by the author.)
Fig. 11. Diagrammatic representations of sonagrams of screech-owl songs.

(Otus guatemalae was recorded by Irby Davis, O. choliba by Paul Schwartz, and O. scops by Tsuruhiko Kabaya. The rest were recorded by the author.)
Fig. 13. *Otus asio*, Kennicottii Group: ventral view of same specimens shown in Fig. 12.
Fig. 14. *Otus asio*, Kennicottii Group: lower, tending toward *cardomensis* phenotype but ventral pattern insufficiently dense (see Fig. 15), San Diego County, California; center, *suttoni*, México, D. F.; upper, *santus*, Baja California Sur (with ventral cross-bars atypically vague—see Fig. 15).
Fig. 15. *Otus asio*, Kennicottii Group: ventral view of same specimens shown in Fig. 14.
Fig. 17. *Otus asio*, Kennicottii Group: ventral view of same specimens shown in Fig. 16. Observe that *cinereus* is intermediate in all respects between *yumanensis* and *aikeni*. 
Fig. 18. The vinaceous screech-owls of the Pacific coast of México. *Otus asio*, Kennicottii, Seductus, and Cooperi groups: bottom to top—vinaceus, coastal Sinaloa; seductus, Colima; lumbi, Oaxaca.
Fig. 19. The vinaceous screech-owls of the Pacific coast of México—ventral view of the same specimens shown in Fig. 18.
Fig. 20. *Otus asio*, Cooperi and Asio groups: bottom to top—*cooperi*, Costa Rica; *maxwelliae*, Colorado; *asio*, Iowa.
Fig. 21. Ventral view of same specimens shown in Fig. 20. (Note: All figures of plumage are of the normal phase; none is of the red phase, either in the drawings or in the photographs.)

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Fig. 22. *Otus asio*, Asio Group: top to bottom—*mccalli*, Langtry, Texas; *hasbroucki*, Kerrville, Texas; *florianus*, Florida.
Fig. 23. *Otus asio*, Asio Group: ventral view of same specimens shown in Fig. 22. The upper specimen, *mccalli*, has atypical coarse ventral markings (see Fig. 31).
Fig. 24. *Otus asio* and *Otus trichopsis*: bottom to top—*Otus asio simplex*, San Luis Potosí; *Otus trichopsis aspersus*, Arizona; *Otus trichopsis* sp.?*, San Luis Potosí; *Otus t. trichopsis*, México, D. F.
Fig. 25. *Otus asio* and *O. trichopsis*: ventral view of same specimens shown in Fig. 24.
Fig. 26. *Otus trichopsis* and *Otus guatemalae*: bottom to top—*Otus trichopsis* ssp.? Chiapas; *Otus trichopsis mesamericanus*, Mt. Cacaguatique, El Salvador; *Otus guatemalae hastatus*, Sonora; *Otus guatemalae cassini*, Tamaulipas.
Fig. 27. *Otus trichopsis* and *O. guatemalae*: ventral view of same specimens shown in Fig. 26.
Fig. 28. *Otus guatemalae*: bottom to top—*thomsoni*, Yucatán; *guatemalae*, Honduras; black *guatemalae*, Guatemala; *dacrystactus*, Nicaragua. *(Note: Even though I do not recognize all races, I use their names for discernible phenotypes.)*

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Fig. 29. *Otus guatemalae*: ventral view of same specimens shown in Fig. 28.
Fig. 30. *Otus guatemalae* and *Otus flammeolus*: bottom to top—*Otus guatemalae* vermiculatus, Panamá; *Otus flammeolus*, black Great Basin-southern Rocky Mts. phenotype, Hualpai Mts., Arizona; *O. flammeolus*, typical phenotype, Catalina Mts., Arizona; *O. flammeolus*, red rano phenotype, Davis, California.
Fig. 31. *Otus guatemalae* and *O. flammeolus*: ventral view of same specimens shown in Fig. 30.
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