

THE RELATION OF FEATHERING OF FEET OF AMERICAN
OWLS TO HUMIDITY OF ENVIRONMENT AND TO
LIFE ZONES.

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THE extent of feathering on the feet of American Owls varies from a more or less bare tarsus and entirely bare toes to a densely long-feathered tarsus and toes. The extent of this feathering is of interest to the naturalist as being apparently an adaptation for protection from cold, in the case of the long-feathered type. It is of importance to systematic ornithologists, who have used it as a key character for genera, subgenera, species, and subspecies.

Whether feathering is a protective adaptation or whether it is of phylogenetic significance are matters open to question. The purpose of the present paper is not to answer these questions, but to show the relationship, if any, of types of foot feathering to humidity and life zones. Previously, zones have usually been considered in connection with bird life as a whole, or with plant and animal life in general.

Method of Study. More than one type of foot feathering may be found in one genus, and even in one species, when such species is divided into subspecies e. g. Northern Barred Owl (*Strix v. varia*) with densely short-feathered toes, and Florida Barred Owl (*Strix v. georgica*) with toes mostly bare; Sartorius' Stygian Owl (*Asio stygius robustus*) with toes sparsely feathered, and Stygian Owl (*Asio s. stygius*) with toes bare. But only one type of toe feathering is found in one subspecies or in one species not divisible into subspecies. The subspecies and the undivided species are therefore used as the taxonomic unit in this study.

Type of foot feathering in Owls does not vary with age as some have thought. There is no proven instance, for example, of the young of any form having feathered toes and the adult having bare toes, or vice versa.

The feathering of the feet of the 192 forms of American Owls seems to fall roughly into 5 types:

1. *Toes and part of tarsus bare.* Tarsus bare of feathers all the way around for part or all of its length. Toes entirely bare of feathers. Forms with only hind side of tarsus bare, as in *Tyto* and *Speotyto*, are not considered a distinct type as this condition may be due to the bird's habit of frequently crouching with the tarsus flat to the ground. Examples: Cuban Bare-legged Owl (*Gymnasio lawrencii*), Chapman's Wood Owl (*Ciccaba aequatorialis*).

2. *Toes bare.* Tarsus fully feathered and at least half of sides and upper surface of toes bare of feathers. Examples: Cholibá Screech Owl (*Otus choliba*), Florida Barred Owl (*Strix varia georgica*).

3. *Toes sparsely feathered or bristled.* Feathers or bristles somewhat

thinly distributed over most of upper surface and sides of toes. Examples: Screech Owl (*Otus asio asio*), Barn Owl (*Tyto alba*).

4. *Toes densely short-feathered.* The density of feathering much greater than in the preceding type, sufficient to hide most of upper surface of toes from view. Feathers short in comparison to size of bird, not tending to conceal part of claws. Examples: Great Horned Owl (*Bubo virginianus*), Short-eared Owl (*Asio flammeus*).

5. *Toes densely long-feathered.* Feathers long in comparison to size of bird, tending to conceal part of claws. Examples: Richardson's Owl (*Cryptoglaux funerea richardsoni*), Great Gray Owl (*Scotiaptex nebulosa*).

The systems of life zones used in this paper are those used by the majority of naturalists. It is realized that all do not agree on what names they should bear or on their exact delimitations.

The system used here for North America is that of Merriam, Bailey, Nelson and Preble,¹ for Central America, that used by Griscom,² for South America, that used by Chapman,³ ⁴ Todd and Carriker,⁵ and Hellmayr.⁶

Explanation of Table. In the accompanying table all the 192 subspecies and undivided species of American owls are tabulated according to the type of foot feathering they have and according to the life zones in which they nest. They are considered and tabulated according to only those zones in which they nest because owls may wander into any zone after the nesting season is over.

Under each zone are given the number of species and subspecies and the percentages of the owls in that zone having the various types foot feathering. Each form known to reside in each zone is included in the tabulation. To admit only those confined to one or two zones would leave out many forms entirely and make any relationship shown by the study seem of doubtful significance. The zonal limits of all forms are not known but it is believed that the percentages are approximately correct.

The numbers on the line following each type of feathering cannot add up to the totals in the last column because so many forms are found in more than one zone.

The figures concerning the bare toe and partly bare tarsus type of feath-

¹ Merriam, C. H., Bailey, V., Nelson, E. W., and Preble, E. A., Fourth Provisional Zone Map of North America, U. S. Dept. of Agriculture, Biological Survey, 1910.

² Griscom, L., The Distribution of Bird-Life in Guatemala, Bulletin of the American Museum of Natural History, Vol. LXIV, May 7, 1932, pp. 29-72.

³ Chapman, F. M., The Distribution of Bird-Life in Colombia, Bulletin of the American Museum of Natural History, Vol. XXXVI, 1917, pp. 84-169.

⁴ Chapman, F. M., The Distribution of Bird-Life in Ecuador, Bulletin of the American Museum of Natural History, Vol. LV, September, 1926, pp. 31-133.

⁵ Todd, W. E. C. and Carriker, M. A., The Birds of the Santa Marta Region of Colombia, Annals of the Carnegie Museum, Vol. XIV, October, 1922, pp. 57-106.

⁶ Hellmayr, C. E., Birds of Chile, Field Museum of Natural History, Zoological Series, Publication 308, Vol. XIX, June 13, 1932, pp. 21-23.

TABLE I

TYPES OF FOOT FEATHERING	ZONES											Total	
	Paramo and Puna	Temperate	Subtropical	Tropical	Lower Austral	Lower Sonoran	Upper Austral	Upper Sonoran	Transition	Canadian	Hudsonian		Arctic
Toes and part of tarsus bare	0	(4) 14.80	(2) 8.00	(4) 3.53	0	0	0	0	0	0	0	0	(8) 4.16
Toes bare	0	(8) 28.24	(9) 36.00	(40) 35.36	(2) 25.00	(1) 5.88	0	(1) 4.76	(1) 3.56	(1) 3.22	(1) 5.88	0	(53) 27.56
Toes sparsely feathered or bristled	0	(10) 35.60	(12) 48.00	(50) 44.32	(4) 50.00	(11) 64.72	(3) 37.50	(11) 52.40	(12) 42.88	(6) 22.54	0	0	(76) 39.68
Toes densely short-feathered	(3) 100.00	(6) 21.36	(2) 8.00	(19) 16.79	(2) 25.00	(5) 29.40	(5) 62.50	(9) 42.84	(14) 50.00	(19) 61.36	(10) 58.84	(1) 50.00	(48) 24.96
Toes densely long-feathered	0	0	0	0	0	0	0	0	(1) 3.56	(4) 12.88	(6) 35.28	(1) 50.00	(7) 3.64
Totals	(3)	(28)	(25)	(113)	(8)	(17)	(8)	(21)	(28)	(31)	(17)	(2)	(192) 100.00

ering are not included in the figures that concern the bare toe type although owls of both classes have bare toes.

Certain slight adjustments in the highest percentages were necessary because of discrepancies caused by the process of division.

Discussion of table. It will be noted in the table that none of the types of foot feathering in American Owls are confined to any one zone, nor are all types represented in any one zone.

The barest and most heavily feathered types of foot feathering are restricted to the more warm and humid and the more frigid zones, respectively. The 8 forms with the toes and part of the tarsus bare are associated with the warm and humid Tropical, Subtropical, and Temperate Zones of regions near the equator. Furthermore, they are found in only the humid portions of these zones. The 7 forms with tarsus and toes densely long-feathered, being residents of only the Transition (to a limited extent), Canadian, Hudsonian, and Arctic Zones, are associated with a cold environment.

The 53 forms with bare toes are represented in all except 3 of the 13 zones. They are more frequently associated, however, with the humid Temperate, Tropical and Subtropical Zones. In so far as known, all but one of the bare-toed forms of these zones are found resident in only the humid divisions, and not in the dry or desert divisions, of these zones.

The 76 forms with toes sparsely feathered or bristled are found in all but the 4 zones that have environment of lower temperature, the Paramo and Puna, Hudsonian, and Arctic Zones. They constitute 28 per cent or more of the Owl fauna of the zones in which they are represented, and have the highest percentage in 6 of the zones as well as in the totals for all the zones. Their highest percentages are in the arid Sonoran Zones. The 50 Owls of the Tropical Zone that have this type of feathering have a strong tendency to occupy a different type of environment than that occupied by the bare-toed group. We find that about 30 of these 50 are confined to the arid parts of the Tropical Zone. The remaining 20 are present in both the humid and arid parts of the Tropical Zone.

Of the 12 forms with sparsely feathered or bristled toes residing in the Subtropical Zone, 6 occupy the arid and 6 the humid parts of the zone.

The 48 forms with the toes densely short-feathered constitute the most widely distributed group. One or more of these forms are found in each of the 13 zones. The forms with this type of feathering constitute a larger percentage of the Owl family in the 4 colder zones than in the warmer zones. Therefore the dense and short type of feathering is associated with an environment which, in regard to temperature, is the antithesis of that occupied by the bare-toed forms. *Bubo virginianus*, which has the toes densely short-feathered, is represented by one or more of its subspecies in all the zones except the Arctic and the Puna. It may occasionally breed in

those. The length of the feathers of the feet varies from zone to zone. The Arctic Horned Owl (*Bubo v. subarcticus*) and St. Michael's Horned Owl (*Bubo v. algistus*) of the Hudsonian Zone have the foot feathers slightly longer. On some specimens the feathering is almost long enough to place them in a class with the toes densely long-feathered. The Montana Horned Owl (*Bubo v. pallascens*) chiefly of the Sonoran Zones and Oaxaca Horned Owl (*Bubo v. melancerus*) and Yucatan Horned Owl (*Bubo v. mayensis*) chiefly of the Tropical Zone have the toe feathers somewhat shorter.

The Long-eared Owl (*Asio wilsonianus*) of North America is found breeding from the Hudsonian to the Lower Sonoran Zone but is partial to the colder zones. Its toes are of the densely short-feathered type. This also is true of the closely related *Asio otus* of boreal Europe and Asia.

Their close neotropical relative, the Stygian Owl (*Asio stygius*) of the Tropical rain forests of Cuba, and southern Mexico to northern Argentina, has the toes bare, except in southern Mexico and Central America, where it has the toes very sparsely short-feathered.

Another owl of the short-feathered toe group that shows variation from zone to zone is *Asio flammeus*. The typical race of the Short-eared Owl has the toes densely feathered while the Colombian Short-eared Owl (*Asio f. bogotensis*) and the equatorial Short-eared Owl (*Asio f. aequatorialis*) of the humid Temperate and Paramo Zones near the equator, have the feathering more thinly distributed. Also, the Hispaniolan Short-eared Owl (*Asio d. domingensis*) and the Porto Rican Short-eared Owl (*Asio d. portoricensis*) of the Tropical Zone have the feathering of the toes thinner still. Beyond the equator in southern South America, where colder and less humid conditions prevail, we find the South American Short-eared Owl, *Asio f. swindus*, which has the toes as densely feathered as the boreal representative, which it resembles except for larger size and less black on the primary coverts.

The connection between humidity and foot feathering is further shown by *Strix varia*, which has the toes mostly bare in the Lower Austral Zone of the southeastern United States, while they are densely short-feathered in the Canadian, Transition, and Upper Austral Zones of southern Canada and northern United States, and in the Temperate Zone of the mountains of Mexico. The change from bare to feathered toes occurs near the place of transition from Lower to Upper Austral Zones.

The Rocky Mountain Screech Owl (*Otus asio maxwelliae*) has somewhat longer and denser foot feathering than the subspecies on either coast.

Examples outside the Americas. The above examples of correlation are not peculiar to the Americas. In the higher mountains of northern India, *Strix indranee newarensis* has the toes densely short-feathered except near the ends. In the humid Malay Peninsula, *Strix i. maingayi* has the feathering shorter and more sparse. *Strix i. bartelsi* of Java is similar. *Strix*

leptogrammica of tropical Borneo, possibly only subspecifically distinct from the preceding, has the toes mostly bare. There are other examples.

Nearly all tropical forms of the genus *Otus* have bare toes. The following are bare-toed examples seen, with localities whence the specimens came: *Otus glabripes*, China; *japonicus*, Japan; *whiteheadi*, Philippines; *cuyensis*, Philippines; *menadensis*, Celebes; *rutilus*, Madagascar; *spilocephalus*, Malay, Borneo; *sumia*, Siam; *lempijii*, Java; *sagittatus*, Siam; *ballii*, Andamans; *rufescens*, Borneo; *bakkamoena*, India, Siam, Malay, and nearby islands.

The Fish Owls, *Ketupa* and *Scotopelia*, in keeping with their habitat and mode of life, have the toes and most of the tarsus bare.

Correlation with other characters. Along with reduction in toe feathering there is often a reduction in the size of the bird. This is true in such genera as *Bubo*, *Otus*, *Speotyto*, *Pulsatrix* and *Ciccaba*. *Strix varia* is an exception, the bare-toed *Strix v. georgica* not being appreciably smaller than the northern form. In some forms there is a corresponding reduction in the feathering of the facial rim and the facial disc. This is seen in the Vermiculated Screech Owl (*Otus vermiculatus*), Bare-legged Screech Owl (*Otus clarkii*), Crested Owl (*Lophostrix cristatus*), Burrowing Owl (*Speotyto cunicularia*), and in the Pigmy Owls (*Glaucidium*). Old world examples are *Bubo blakistoni*, *Bubo nipalensis*, *Bubo philippinensis*, *Bubo orientalis*, the forms of the genus *Ninox*, and many others.

Summary. The relationship of the feathering of the feet of American Owls to humidity and life zones indicated in the preceding table and discussion may be summarized as follows:

(a.) The bare toe and partly bare tarsus type is associated with the humid, warm environment of the Tropical, Subtropical, and Temperate Zones.

(b.) The densely long-feathered toe type is associated with the colder and less humid environment of the Arctic, Hudsonian, Canadian, and Transition Zones. Thus, extremes in foot feathering in American Owls seem to be associated with zones that have extremes of climate and humidity.

(c.) The bare-toed type is more frequently associated with the humid, warm environment of the Tropical, Subtropical and Temperate Zones.

(d.) The sparsely feathered or bristled toe type is well represented in all but the colder zones. In the Tropical, Subtropical, and Temperate Zones this type of feathering is more frequently associated with the arid parts of the zones. It constitutes the highest percentages in the Sonoran Zones and therefore tends to associate itself with aridity.

(e.) The densely short-feathered toe type is represented in all the life zones but includes a slightly higher percentage of the owl order in those zones which present a cooler environment, while in zones of greater heat and humidity it constitutes low percentages.

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