PASSERINE FOOT-SCUTES

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THE Order Passeriformes continues to pose challenging problems in avian systematics. Passerines are not only superficially uniform in many aspects of structure, but also have apparently evolved repeatedly in convergent and parallel directions. A verifiable phylogenetic or cladistic arrangement may thus be difficult to attain even within restricted groups of passerines.

I started the present study to determine whether scutellation of the feet might provide useful characters in passerine systematics. Although a number of authors (e.g., Bock and Miller, 1959; Storer, 1960; Rylander and Bolen, 1970) have discussed the external structure of the feet of birds, few have undertaken detailed examination.

MATERIALS AND METHODS

Specimens included over 3,000 study skins, more than 120 birds kept in 70 percent ethanol, a few frozen specimens, and several living birds. I examined over 2,400 specimens with a binocular dissecting microscope and studied others with a low power hand lens. The preserved specimens are in the collections of the Field Museum, Yale Peabody Museum of Natural History, and the University of Connecticut.

One can usually discern major features of the upper (dorsal) scutes of toes on study skins, but alcoholic specimens are necessary for detailed examination of lateral, medial, and ventral aspects of the toes. Large samples of alcoholic specimens representing a variety of species were not available; hence for quantitative comparison within and between species, I chose to study the number of upper scutes on study skins. Samples for my counts ranged from 13 to 133 birds per species with a combined total of 2,310 study skins representing 65 passerine species. I counted twice the row of upper scutes along the dorsal midline of each of the three forward toes (digits II, III, IV) from the claw proximally to that basal scute not constituting a continuation of the row. Where the corresponding right and left toes of a bird differed in counts, I noted whether the source of this bilateral difference was proximal or distal along the toes. It was occasionally difficult to decide whether to count a particular minor protuberance as a distinct scute, but such arbitrary assignment usually involved only one scute higher or lower in count, a level of possible error not affecting my general conclusions. Counts were sometimes impossible because of damage, injury, or loss of part or all of a toe.

The familial classification follows Wetmore (1960). For nomenclature within families I used the following sources: Mimidae after Davis and Miller (1960), Ploceidae after Moreau and Greenway (1962) and Traylor (1968), and Fringillidae after Mayr (1968), Howell et al. (1968), and Paynter (1970).

RESULTS

General arrangement of scutes and papillae on the toes.—On typical avian feet, large upper scutes cover the dorsal surface of each toe, and

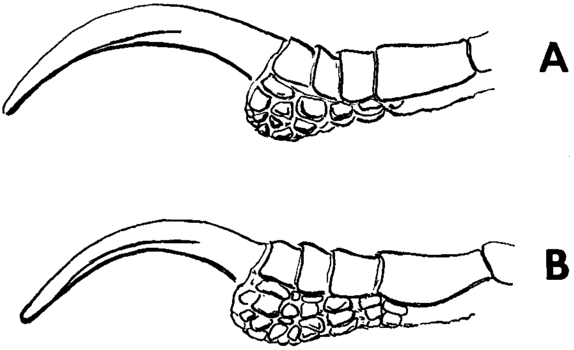

Figure 1. Medial views of the hind toes of two male Rufous-sided Towhees (A and B).

the plantar region bears relatively small papillae clustered in toe pads. In many species structures appearing intermediate between scutes and papillae occur along the sides of the toes between the upper scutes and papillae.

Individuality and bilateral asymmetry of toes.—Using a binocular dissecting microscope I examined both feet of each bird in four samples of alcoholic specimens: 25 Semipalmated Sandpipers (*Ereunetes pusillus*), 26 Catbirds (*Dumetella carolinensis*), 40 House Sparrows (*Passer domesticus*), and 10 Rufous-sided Towhees (*Pipilo erythrophthalmus*). For each of these four samples I compared each foot directly with every other foot, with right and left feet placed together as though in a mirror image relationship. Had I not seen differences between two feet in alignment of scutes or papillae, I would have judged the feet to be alike, but in every case, at least some, and often many, scutes or papillae differed conspicuously in alignment. Thus in a combined total of 5,901 qualitative comparisons, each foot appeared unique in details of pattern.

The interrelated features of area, shape, alignment, and often number of integumental units (scutes and papillae) differ between feet. Such differences occur regularly on the ventral, lateral, and medial sides of the toes and less commonly among the upper scutes. As an example, Figure 1 shows the medial sides of the hind toes of alcoholic specimens of two male Rufous-sided Towhees that differ conspicuously in the scutes on the side of the toe and in the papillae below. I frequently saw differences in color and amount of protuberance of papillae and scutes, but excluded these in concluding that each foot is unique.

The external structure of avian feet is complex. The foot of a House

TABLE 1
INTRASPECIFIC RANGE OF SCUTE COUNTS FOR TOE III AND PERCENT DISTRIBUTION OF BILATERAL DIFFERENCES IN THESE COUNTS

Species	Number of birds in sample	Range of sample	Difference between count of right and left side			
			0	1	2	3
Cyanocitta cristata	18	4	72	28		
Corvus brachyrhynchos	35	4	46	46	6	3
Parus atricapillus	45	2	62	38		
Sitta carolinensis	24	4	83	17		
S. canadensis	34	4	80	18	3	
Certhia familiaris	16	5	63	19	13	6
Dumetella carolinensis	28	3	68	29	4	
Toxostoma rufum	16	2	81	19		
Zonotrichia melodia	31	2	87	13		
Z. lincolnii	24	2	88	12		
Z. georgiana	74	3	85	15		

Sparrow, for example, has several hundred papillae; hence for convenience I usually studied only limited, but equivalent, parts of the entire foot. On the 40 alcoholic specimens of House Sparrows I examined primarily the medial side of the hind toe. Although I often compared only the medial or lateral side of the corresponding toes, even this limited part was unique for each foot. A small, uncounted number of comparisons revealed no case in which right and left sides of one toe were identical. Furthermore in no case was one toe like any of the seven others on the same bird. Thus the details of pattern appear to be unique not only for each foot but also for each toe.

Ontogeny of patterns.—I examined alcoholic specimens of nestlings of Robins (*Turdus migratorius*), Starlings (*Sturnus vulgaris*), and Baltimore Orioles (*Icterus galbula*). For each of these species I qualitatively inspected three nestlings from a single nest. Each individual was bilaterally asymmetrical, and each foot was unique in the maximal 15 intraspecific comparisons. In such young juveniles the patterns are less conspicuous than on older birds.

Bilateral differences within individuals compared with intraspecific differences.—Both my qualitative observations and my counts of upper scutes support the expected interpretation that the range of bilateral difference within most individuals is less than the range of intraspecific variation (Table 1). In the quantitative study of asymmetry I used only those specimens for which I could make clear counts bilaterally; hence the number of birds per species listed in Table 1 is less than the total number examined for that species. In all species of Table 1, the range of the sample is greater than the bilateral difference in any

TABLE 2
PERCENT DISTRIBUTION OF SCUTE COUNTS FOR TOE III

Species	Number of toes in sample	Number of scutes per toe									
		8	9	10	11	12	13	14	15	16	17
Cyanocitta cristata	39				13	44	23	18	3		
Corvus brachyrhynchos	73			7	21	48	15	10			
Parus atricapillus	96			34	49	17					
Sitta carolinensis	75						7	65	19	4	5
S. canadensis	74				9	37	28	20	5		
Certhia familiaris	33					3	3	21	52	18	3
Dumetella carolinensis	60				12	65	17	7			
Toxostoma rufum	34			21	77	3					
Zonotrichia melodia	68		6	87	7						
Z. lincolnii	51		10	71	20						
Z. georgiana	153	3	20	73	4						

individual. However in some other species I found that occasional individuals differ bilaterally as much as the range among individuals, especially where the latter range is small. As an example, in counts of the upper scutes on the three forward toes of 29 study skins of House Sparrows, one exceptional individual had a bilateral difference as great as the intraspecific range for one of the three toes (9–11 scutes on toe III).

Differences between species.—Closely related species are often relatively similar in counts of upper scutes, as, for example, on the middle toe of the Song (*Zonotrichia melodia*) and Lincoln's Sparrow (*Z. lincolnii*; see Table 2). However in other cases related species show notable differences ($P < 0.01$ in a Chi-square test). Thus, for example, the White-breasted Nuthatch (*Sitta carolinensis*) is quite different from the Red-breasted Nuthatch (*S. canadensis*) in counts for the middle toe (Table 2).

My data indicate that species often differ with respect to numbers of upper scutes in passerines, as seen in Table 2. As the 65 species for which I made counts represent 21 Wetmorian families, the number of species per family is far too low to draw specific taxonomic conclusions. Furthermore I have not studied possible functional correlates of differences between species. For these reasons I present only a small sample (Table 2) of the extensive data from my counts.

Scutellation at the base of the two outer toes.—While making the counts discussed in previous sections, I noted conspicuous qualitative differences among a few species in both the Mimidae and Emberizinae, and I therefore undertook a broader taxonomic survey for these taxa.

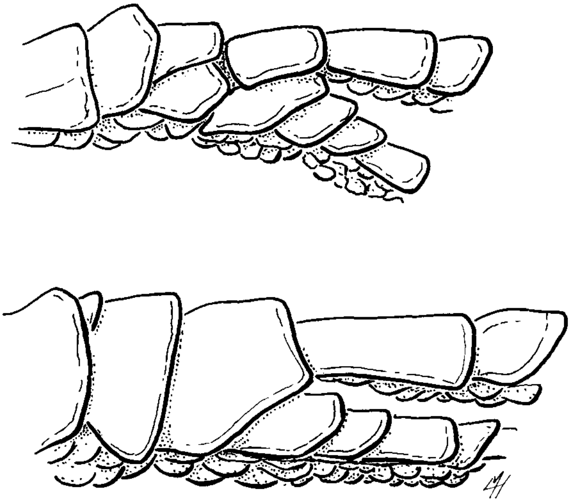

Figure 2. Divided scute at the base of the two outer toes of a Catbird (*Dumetella carolinensis*; top) in contrast to the single scute of a Brown Thrasher (*Toxostoma rufum*; bottom).

Mockingbirds (two species of *Mimus* plus *Nesomimus*) and thrashers (*Oreoscoptes* plus seven species of *Toxostoma*) typically have a large single scute at the base of the two outer toes (digits III and IV; Figure 2). In contrast, divided scutes generally occur at the base of these toes in *Dumetella* (Figure 2), *Melanoptila*, *Melanotis* (both species), *Cinclocerthia*, *Ramphocinclus*, *Donacobius*, *Allenia*, and *Margarops*. Variation within a species and bilaterally within individuals necessitates studying at least a small series to determine the condition of a substantial majority of individuals of each species. I examined five or more specimens for each of the indicated mimid species.

Analogous variation occurs within the Emberizinae. Genera with typically a single scute at the base of the two outer toes are as follows (where more than one species was examined, the number is given in parentheses): *Calamospiza*, *Zonotrichia* (including *Passerella*, *Melospiza*, 7), *Junco*, *Ammodramus* (7), *Spizella* (3), *Pooecetes*, *Chondestes*, *Amphispiza* (2), *Aimophila*, *Torreornis*, *Oriturus*, *Incaspiza*, *Emberizoides*, *Embernagra*, *Pipilo* (2), *Melozone* (2), *Arremon* (3), *Arremonops* (2), *Atlapetes* (8), *Pezopetes*, *Pselliophorus*, *Lysurus*, *Saltatricula*. In contrast, the following genera typically have divided scutes at the base of the two outer toes: *Melophus*, *Emberiza* (4), *Calcarius* (3), *Plectrophenax*, *Phrygilus* (3), *Melanodera*, *Haplospiza*, *Lophospingus*, *Rowettia, Nesospiza, Diuca, Idiopsar, Xenospingus, Poospiza* (7), *Sicalis, Volatinia, Sporophila* (2), *Amaurospiza, Melopyrrha, Catamenia, Tiaris, Loxipasser, Loxigilla, Geospiza, Camarhynchus, Certhidea, Pinaroloxias, Urothraupis, Gubernatrix, Coryphospingus* (2), *Paroaria.* For the indicated emberizine species I examined a minimum of three specimens and usually six or more.

In a partial survey of passerine species of the world, I found the predominantly single scute condition only in the genus *Vidua* (two species examined) and *Bubalornis* in addition to the indicated mimids and emberizines. Even the genus *Dinemellia* in the same subfamily as *Bubalornis* has a predominantly divided condition. Other taxa for which I have examined series of one or more representative species with the predominantly divided scute condition are the following: Tryannidae, Alaudidae, Hirundinidae, Dicruridae, Corvidae, Paridae, Sittidae, Certhiidae, Pycnonotidae, Cinclidae, Troglodytidae, Turdidae, Regulidae, Motacillidae, Bombycillidae, Laniidae, Sturnidae, Vireonidae, Parulidae, *Uraeginthus, Estrilda, Lonchura, Plocepasser, Histurgops, Philetairus, Passer, Montifringilla, Amblyospiza, Quelea, Foudia, Euplectes,* Icteridae, Thraupidae, Catamblyrhynchidae, *Spiza, Pheucticus, Saltator, Passerina, Fringilla, Serinus, Linurgus, Carduelis, Leucosticte, Rhodopechys, Uragus, Carpodacus, Pinicola, Haematospiza, Pyrrhula, Coccothraustes.*

My counts of upper scutes terminated proximally at the end of the row of scutes extending along the toe. Thus where a single scute lay at the base of the two outer toes, the counts for those toes were relatively low, as in the Brown Thrasher (*Toxostoma rufum*) and species of emberizines with the predominantly single scute condition (e. g. *Zonotrichia*, cf. Table 2). Furthermore the occurrence of the single scute condition eliminates the possibility of bilateral asymmetry in counts in the region at the base of these toes. Thus both low counts and low asymmetry in the basal region may be correlates of the single scute condition.

DISCUSSION

Variations within individuals and within species.—Bilateral asymmetry of individuals and individual uniqueness of details of patterns of foot-scutes are apparently characteristic for many bird species. The extent of individual variation is reminiscent of the well-known ones for human fingerprints, palms, soles, and toes (Cummins and Midlo, 1961; Holt, 1968), although the avian foot scutellation differs considerably in appearance from the ridged skin of the plantar surfaces of human hands and feet. Similarities in the avian and human variation include individuality for each digit, bilateral asymmetry in each individual, and the lesser conspicuousness of patterns in young individuals. In human fingerprints the range of variation among individuals exceeds the bilateral difference in any one individual, and bird feet are probably similar in this respect.

Details of human fingerprints normally persist throughout life (Holt, 1968) despite the presumably considerable wear on the fingers. I lack direct evidence that the avian variations are as permanent. Both the bilateral asymmetry and individuality appear in young birds before they use their feet extensively in landing and locomotion. Although subsequent wear might possibly modify details of pattern, the avian foot structure is compatible with the idea that at least some of these details are relatively fixed. The papillae are resilient and after indentation by weak pressures tend to regain their original shapes, as I have seen on thawed carcasses. Furthermore the firm attachment of papillae and scutes seemingly tends to prevent changes in their alignment, though presumably severe injuries or diseases might alter the appearance considerably.

Little is known about the molting of either tarsal scutes or those on the feet. Jeffries (1883) reported such molting, but apparently the most detailed observations are the brief remarks of Gullion (1953) on the American Coot (*Fulica americana*). Neither these accounts nor my observations indicate that molting modifies the arrangement in scutellation.

Differences between species.—Significant differences between species in counts of upper scutes indicate that studies of foot-scutes might provide additional new taxonomic characters. However only within the Mimidae and Emberizinae have I studied enough species to begin assessing potential systematic applications. In these groups the occurrence of features necessarily correlated with the occurrence of a single scute condition illustrates a possible hazard of treating different aspects of a single structural feature as though independent of one another.

For conciseness in the following discussion, I omit the term "predominantly" in referring to the single as opposed to divided scute condition at the base of the two outer toes. Yet it should be noted that individual variants and asymmetrical individuals occur within perhaps every species, and the condition reported for each species is that of a substantial majority of individuals. Thus the occurrence of the single as opposed to divided scute condition cannot be determined unquestionably from a single specimen.

Although in the Mimidae the dichotomy between genera with single as opposed to divided scutes does not parallel any other character or classification known to me, scutellation warrants consideration in future revision of this family.

Distribution of the single as opposed to divided scute condition in the Emberizinae coincides partially with the distribution of double-scratch foraging behavior (Harrison, 1967; Clark, 1970). All emberizine species known to double-scratch have a single scute condition. These include *Pezopetes capitalis,* a species reported by Skutch (1967: 184) to double-scratch, but not mentioned by other writers on the subject. However at least some emberizines with the single scute condition apparently do not ordinarily double-scratch; apparent examples are some species of *Spizella* (Clark, 1970) and the brushfinches *Atlapetes* (see Clark, 1971, for a summary of evidence). Thus the single scute condition apparently has a broader taxonomic range than does the double-scratch, although the taxonomic distribution of the latter is poorly known.

Harrison (1967) pointed out that Old World buntings (*Emberiza*), longspurs (*Calcarius*), and snow buntings (*Plectrophenax*) run or walk across the substrate and lack the double-scratch and thus differ from many North American emberizines that hop over the substrate and use the double-scratch. The scutellation of these two groups also differs. It would be premature to suggest revisions in emberizine classification without a more complete survey of the group and without considering additional characters; nevertheless, the single as opposed to divided scute condition appears promising as a character in the group.

Little is known about the functional significance of differences in foot scutellation. The African viduines and a major group of New World emberizines show both the double-scratch behavior and a single scute condition. The coincidence of these two seemingly unusual characters in two apparently unrelated groups is possibly suggestive of a functional correlation between the characters. There is no absolute correlation, however, for double-scratch behavior does not occur in the mimids with the single scute condition. Many species with the single scute condition commonly forage terrestrially, but there is obviously no absolute correlation here either, for divided scutes occur in such terrestrial groups as larks (Alaudidae), pipits (Motacillidae), and longspurs (*Calcarius*).

The single scute condition is apparently considerably rarer than the divided condition among the oscine families. If this is so, then the single scute condition may be an evolutionarily derived rather than primitive state among oscines, as no evidence suggests that taxa possessing the single scute condition are especially primitive. Presumably the predominantly single scute condition has evolved at least three or four times independently.

Despite the high level of conspicuous variation within species, the scutellation of the feet appears promising in passerine systematics. Individual variation appears to be the rule, rather than the exception, in many aspects of avian structure (Berger, 1956). The occurrence of extensive intraspecific variation does not mean that a feature is without systematic value; one must be aware of such variation and make allowances for it in interpretation.

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SUMMARY

Individual differences and bilateral asymmetry are characteristic in the arrangement of scutes and papillae on the feet of many avian species. Bilateral difference within an individual is generally less than the range of variation for the species as a whole. Bilateral asymmetry and individuality arise during normal development. The degree of variation on the feet in many avian species is reminiscent of that well-known for human fingerprints, although the structural details are quite different.

Scutellation at the base of the two outer toes serves to distinguish two major groups in the family Mimidae. Analogous variation within the Emberizinae also separates two major groups, one of which is partially characterized by the occurrence of double-scratch behavior. Despite the individual variation, scutellation of the feet appears to be potentially useful in passerine systematics.

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