

TAXONOMIC DISTRIBUTION, ORIGIN, AND EVOLUTION OF BILATERAL SCRATCHING IN GROUND-FEEDING BIRDS

JON S. GREENLAW

Bilateral scratching (= double-scratching) is a distinctive behavior generally employed in foraging by some ground-feeding birds. It is best known in several species of the subfamily Emberizinae in which it has a discontinuous taxonomic distribution (Harrison 1967). The habit seems to be restricted to certain New World representatives of this subfamily while it is absent at least in longspurs (*Calcarius*), snow buntings (*Plectrophenax*), and Old World buntings (*Emberiza*). Harrison (1967) attempted to account for this discontinuity, but his view was recently criticized by Hailman (1973). Since Harrison's review, interest in this behavior has centered primarily on documenting its occurrence in New World emberizine taxa (Gobeil 1968, Clark 1970, Enders 1970, Taylor 1970, Hailman 1973) and in non-emberizine taxa (Greenlaw 1976) in which it was hitherto unreported. Hailman (1974) and Greenlaw (1976) also were concerned with variation in the use of double-scratching. Clark (1971, 1972) considered its relationship to bill-sweeping and to variation in foot-scutes in the subfamily. Finally, Hailman (1973) discussed the relationship between mode of terrestrial locomotion and bilateral scratching in emberizines.

Harrison's (1967) review of the bilateral-scratch in Emberizinae was incomplete when published (Hailman 1973). New information on the occurrence of the habit among emberizines and non-emberizines calls for a detailed reevaluation of the taxonomic occurrence of the behavior in birds. This paper is partly devoted to such an analysis. Also, I offer a theory of the origin and evolution of bilateral scratching in ground-feeding birds and present my views on the taxonomic significance of the behavior.

TAXONOMIC DISTRIBUTION OF BILATERAL SCRATCHING

I restrict the term "scratching," as it applies to a mode of foraging, to mean an animal's use of its legs in displacing litter or other loose material. The behavior mostly occurs on the ground, but may be employed occasionally on elevated surfaces (Davis 1957). Since birds may scratch with one leg at a time or both legs simultaneously, the term

should always be qualified by appropriate modifiers, e.g., unilateral and bilateral, respectively.

Although some authors (Wickler 1961) have interpreted simple, unqualified statements on "scratching" behavior as evidence for bilateral scratching in certain non-emberizine taxa, this is improper. Many writers in the past have not restricted the term as I do and have included bill-sweeping under its meaning.

In this study, I judged the occurrence of bilateral scratching in a genus by published and unpublished diagnostic information indicating that at least one member of the genus uses both legs together in scratching. I considered a description of the behavior necessary to document its presence in non-emberizine genera, but for emberizine genera, I accepted a simple yet explicit statement concerning its use by a species in most cases. A non-diagnostic reference to "scratching" by an emberizine species for which diagnostic information on a congener already exists is treated here as evidence of bilateral scratching. Where diagnostic evidence for bilateral scratching in an emberizine genus is lacking, a non-diagnostic record of scratching by a species of that genus is queried in Table 1; I accept it only tentatively as bilateral scratching pending additional information.

The species presently known to scratch bilaterally and a few that may do so are listed in Table 1. In well-studied species, only selected references are cited in the table. Many of the species listed scratch regularly while others do so only occasionally (Greenlaw 1976).

EMBERIZINAE

The bilateral-scratch is widespread in the New World Emberizinae (Table 1), but even in this subfamily, its occurrence is still poorly known, especially in neotropical genera. It is known to occur in 46 species in the genera *Passerella* (includes *Melospiza*), *Zonotrichia*, *Junco*, *Ammodramus*, *Ammospiza*, *Spizella*, *Poocetes*, *Amphispiza*, *Aimophila*, *Geospiza*, *Camarhynchus*, *Pinaroloxias*, *Pipilo*, *Melozona*, *Arremonops*, and *Pezopetes*.

The record for *Amphispiza bilineata* may

TABLE 1. Taxonomic distribution of bilateral scratching behavior.^a

Taxa	Type of evidence ^b	Selected references
FURNARIIDAE		
? <i>Furnarius rufus</i>	see text	Friedmann 1927
PARADOXORNITHINAE		
<i>Panurus biarmicus</i>	D	Koenig 1951
EMBERIZINAE		
<i>Passerella iliaca</i>	D	Nice 1943, Terrill 1968, Hailman 1973, this study
<i>P. (Melospiza) melodia</i>	D	Nice 1943, Hailman 1973, this study
<i>P. (M.) lincolni</i>	D	Nice 1943, Wetmore 1944, Speirs and Speirs 1968, this study
<i>P. (M.) georgiana</i>	D	Hailman 1973, this study
<i>Zonotrichia capensis</i>	D	Slud 1964, Miller and Miller 1968
<i>Z. querula</i>	D	Semple & Sutton 1932, Nice 1943, Baumgartner 1968
<i>Z. leucophrys</i>	D	Nice 1943, Wheeler <i>vide</i> Clement 1968, Hailman 1973, this study
<i>Z. albicollis</i>	D	Nice 1943, Skinner <i>in</i> Lowther & Falls 1968, Hailman 1973, 1974, this study
<i>Z. atricapilla</i>	ND	Davis 1957
<i>Junco hyemalis</i> ^c	ND, D	Bailey 1928, Allen <i>in</i> Eaton 1968, Hailman 1973, 1974, this study
<i>J. phaeonotus</i>	D	Marshall 1957
<i>Ammodramus (Passerculus) sandwichensis</i>	D, ND ^d	Nice 1943, Elliott 1968, Gobeil 1968, Hailman 1973, this study
<i>A. savannarum</i>	D	J. P. Tramontano, pers. comm.
<i>Ammospiza maritima</i>	D	Enders 1970
<i>Spizella arborea</i>	D	Nice 1943, Clark 1970, this study
<i>S. pusilla</i>	D (see text)	D. B. Heckenlively, pers. comm.
<i>S. passerina</i>	ND (see text)	Skinner 1928:192
<i>Poocetes gramineus</i>	D	Phillips, Marshall & Monson 1964, Taylor 1970, this study
<i>Amphispiza bilineata</i>	ND (see text)	Harrison 1967
<i>A. belli</i>	ND, D	Dixon <i>vide</i> Miller 1968, Hailman 1973
<i>Aimophila botterii</i>	D	J. P. Tramontano, pers. comm.
<i>A. cassin'i</i>	D	J. P. Tramontano, pers. comm.
<i>A. ruficeps</i>	D	Nice 1943, J. P. Tramontano, pers. comm.
<i>A. rufescens</i>	D	Smith 1909, Wolf 1977
? <i>Loxigilla portoricensis</i>	ND	Wetmore 1927
<i>Geospiza magnirostris</i>	ND, D	Bowman 1961, pers. comm., Hundley 1963
<i>G. fortis</i>	ND, D	Bowman 1961, pers. comm.
<i>G. fuliginosa</i>	ND, D	Bowman 1961, pers. comm.
<i>G. difficilis</i>	ND, D	Bowman 1961, pers. comm.
<i>G. scandens</i>	D	Bowman, pers. comm.
<i>G. conirostris</i>	D	Bowman, pers. comm.
<i>Camarhynchus crassirostris</i>	D	Bowman, pers. comm.
<i>C. psittacula</i>	ND, D	Bowman 1961, pers. comm.
<i>C. pauper</i>	D	Bowman, pers. comm.
<i>C. parvulus</i>	D	Bowman, pers. comm.
<i>C. pallidus</i>	D	Bowman, pers. comm.
<i>Pinaroloxias inornata</i>	D	Bowman, pers. comm.
<i>Pipilo (Chlorura) chlorurus</i>	D	Bailey 1939:31, Phillips, Marshall and Monson 1964, Marshall & Johnson 1968
<i>P. ocai</i>	ND	Cody & Brown 1970, Edwards 1972
<i>P. erythrophthalmus</i>	D	Woodbury 1933, Nice 1943, Davis 1957, Marshall 1957, Hailman 1973, this study
<i>P. fuscus</i>	D	Davis 1957, Marshall 1957, Marshall & Johnson 1968
<i>P. aberti</i>	D	Marshall & Johnson 1968
<i>P. albicollis</i>	D	Marshall 1964
<i>Melospiza kieneri</i>	D	Wolf <i>in</i> Marshall 1964
<i>M. leucotis</i>	D	Slud 1964
? <i>Arremon aurantirostris</i>	ND	Slud 1964
<i>Arremonops rufivirgatus</i>	D	Sutton 1951

TABLE 1. (continued).

Taxa	Type of evidence ^b	Selected references
<i>Pezopetes capitalis</i>	D	Skutch 1967
? <i>Oreothraupis arremonops</i>	ND	Carriker in Meyer de Schauensee 1966
ICTERIDAE		
<i>Agelaius phoeniceus</i>	ND, D	Skinner 1928, Greenlaw 1976
<i>Molothrus bonariensis</i>	D	Wetmore 1926
<i>M. ater</i>	D	Greenlaw 1976
VIDUINAE		
	D (see text)	
<i>Vidua chalybeata</i>		Poulsen 1953, Payne, pers. comm.
<i>V. junerea</i> (includes <i>V. "wilsoni"</i>)		Payne, pers. comm.
<i>V. purpurascens</i>		Payne, pers. comm.
<i>V. regia</i>		Poulsen 1953, Payne, pers. comm.
<i>V. fischeri</i>		Cunningham-van Someren 1974
<i>V. macroura</i>		Poulsen 1953, Payne, pers. comm., Fry 1975
<i>V. hypocherina</i>		Cunningham-van Someren 1974
<i>V. paradisaea</i>		Poulsen 1953, Payne, pers. comm., Fry 1975
<i>V. obtusa</i>		Payne, pers. comm.

^a Nomenclature and sequence of taxa in Emberizinae follow Paynter (1970) except for North American emberizines north of Mexico where I prefer the generic treatment of Mayr and Short (1970). Because the generic limits of *Aimophila* may require revision, I maintain *Amphispiza* as a distinct genus. Where appropriate, the alternate generic allocation used in the A.O.U. Check-list (1957) is given in (). Nomenclature of the Viduinae is that of Traylor (1968) except for the indigo-birds, and *Vidua paradisaea* and *V. obtusa*, where Payne's judgements (1971, 1973) on species limits are followed.

^b D = Diagnostic; refers to a description or comment in the literature, or an unpublished observation, which directly or indirectly specifies that a particular species uses both feet simultaneously in scratching. ND = Non-diagnostic; indicates a reference to scratching behavior in a particular species which does not specify how the scratching is accomplished. See text for additional comment.

^c *J. hyemalis* includes *J. "caniceps"* which the thirty-second supplement of the A.O.U. Check-list (1973) retains as a separate species. Bailey (1928) provided non-diagnostic records of scratching for *caniceps*.

^d Non-diagnostic reference is Elliott (1968) who mentioned scratching in the Ipswich Sparrow (*Ammodramus sandwichensis princeps*), a form that some consider to be a distinct species.

be suspect. I have not found a reference in the primary literature to support Harrison's (1967) statement that this sparrow scratches bilaterally (as it probably does). Hailman (1973) reported the behavior in *A. belli*.

Twelve of the fourteen species of Galápagos finches scratch bilaterally in overturning large stones (Table 1. R. Bowman, pers. comm.). At least ten species also scratch while foraging in litter on the ground. Only *Camarhynchus heliobates*, a poorly-known inhabitant of mangrove swamps, and *Certhidea olivacea*, a warbler-like finch, are not yet known to scratch bilaterally, although Bowman (pers. comm.) suspects that they may occasionally do so.

Harrison's (1967) view that bilateral scratching is truly absent in *Calcarius*, *Plectrophenax*, and *Emberiza* is probably correct. But the same cannot yet be said with certainty for any other emberizine genus. In species that scratch only occasionally, cursory observations on foraging behavior that fail to document its presence cannot prove its absence. This problem is illustrated by the genus *Spizella*. Bilateral scratching has long been known in *S. arborea* (Table 1), but field observations by Clark (1970) and by Greenlaw (unpubl. data) on *S. pusilla* and *S. passerina*, and those by Nice (1943:42) and by Skinner (1928:195) on *pusilla*, have failed

to supply positive evidence of scratching in either of these species. D. B. Heckenlively (pers. comm.) saw a captive *pusilla* scratch bilaterally only once during two years of close observations. He has not seen *pusilla* use the behavior in the field, nor has he observed it at all in *passerina*. Skinner (1928:192), who described and commented on the behavior in other emberizines known to use it, remarked concerning *passerina* that "Most seeds are picked up as the birds hop across the ground, but sometimes they stop and scratch."

Records are also uncertain for *Aimophila ruficeps*, a member of a genus not listed by Harrison (1967) as bilateral scratchers. Marshall (1957) stated that he had not seen *ruficeps* scratch while foraging on the ground. Wolf (1977) in his detailed discussion of the foraging behavior of this species did not mention scratching at all. But J. P. Tramontano (pers. comm.) noted that *ruficeps*, and *botterii* and *cassinii* as well, regularly scratch bilaterally when foraging in the breeding season in southeastern Arizona grasslands.

Since *Pipilo* and *Atlapetes* are considered to be closely related (e.g., Paynter 1970:168), it is surprising that bilateral scratching, as characteristic as it is of *Pipilo*, has not yet been reported unequivocally in *Atlapetes*.

The evidence for the behavior in the genus is, at best, contradictory. Carriker (*in* Todd and Carriker 1922:524) noted that *Buarremon basilicus* (= *A. torquatus basilicus*, Paynter 1970) in Colombia spends much of its time "scratching about among the leaves and rubbish, like the Towhee [*Pipilo erythrophthalmus*] of the eastern United States." This comparison clearly implies that the bird scratches bilaterally. Yet Skutch (1954, 1967), who observed the foraging of *A. torquatus* in Central America, reported only bill-sweeping in this and other species of *Atlapetes*, a behavior unknown in *Pipilo*. Similarly, Cody and Brown (1970), in discussing the feeding behavior of *Pipilo ocai*, *P. erythrophthalmus*, and *Atlapetes brunneinucha* in Oaxaca, Mexico, commented that all three birds "feed exclusively on the ground by scratching in leaf litter." Although this implies that like the towhees, *A. brunneinucha* also scratches bilaterally, this must be provisionally rejected because Skutch (1967) and Slud (1964) reported only bill-sweeping in this species. Because of the uncertainty about the presence of the behavior in the group, I do not accept unqualified records of "scratching" behavior in *Atlapetes* (e.g., Sutton 1951, Edwards 1972) a priori as evidence of bilateral scratching.

The records of scratching in Table 1 for *Arremon*, *Oreothraupis*, and *Loxigilla* are non-diagnostic and thus may or may not concern bilateral scratching. *Arremon aurantirostris* apparently does not use its bill in flicking the leaves aside after the manner of *Atlapetes* (Skutch 1954). Yet some technique is employed in displacing litter on the forest floor (Slud 1964), suggesting that the bird may scratch bilaterally.

The reference to scratching in *Oreothraupis* (Carriker, quoted by Meyer de Schauensee 1966) may concern bill-sweeping and not bilateral scratching. Meyer de Schauensee (1966) and Paynter (1970) considered *Oreothraupis* to be related to *Atlapetes* (others place it in the Thraupidae). In *Pselliophorus*, also closely allied to *Atlapetes*, apparently only bill-sweeping is now known (Slud 1964, *P. tibialis*).

NON-EMBERIZINE TAXA

Bilateral scratching has been documented in the non-emberizine taxa, Icteridae (Wetmore 1926, Greenlaw 1976) and Paradoxornithinae. Among icterids, it has been recorded in *Molothrus* (two species) and in *Agelaius* (one species). In the Paradoxornithinae, the be-

havior is known only in *Panurus biarmicus* from a description by Koenig (1951:254-255).

The occurrence of the bilateral-scratch in the Viduinae seems to be established although unilateral scratching movements may also be employed. Poulsen (1953:37-38) indicated that viduines make small hopping movements on both legs during scratching, thereby scattering soil and pieces of litter when their spread feet touch the ground. In a letter to Sibley (*vide* Sibley 1970:89), Poulsen reiterated his observation, noting that the scratching of viduines resembles that of *Junco*. Payne (pers. comm.) and Fry (1975) have confirmed that viduines use both feet together in scratching. Cunningham-van Someren (1974), however, reported that they scratch "with either a rapid movement of one leg, in the manner of a domestic fowl, or a rapid shuffling of both feet alternated." In view of the evidence from other observers documenting synchronous leg movements, I am skeptical of this report.

Bilateral scratching may also be used by certain ground-feeding furnariids. Friedmann (1927:190), referring to *Furnarius rufus* in Argentina, stated that "on one occasion I saw an Hornero scratching among some dead leaves and stems with both feet simultaneously like a Fox Sparrow (*Passerella iliaca*)." Because this report of bilateral scratching is based on a single observation, I have queried it in Table 1.

The Cardinal (*Cardinalis cardinalis*) is also said to scratch bilaterally. Skinner (1928:216) noted that it obtains seeds in winter "by picking them directly from the weed stems, by foraging on the ground, and by scratching the ground in the same manner as Fox Sparrows and Towhees." I have not included this record in Table 1 because although the Cardinal is well-known, to my knowledge no one since Skinner has reported seeing it use the behavior.

Harrison (1967) commented that some thrushes and babblers scratch bilaterally but he provided no documentation. Wickler (1961:323) listed bilateral scratching ("Hupfscharren") in eight groups: emberizines, viduines, tapaculos, *Panurus*, *Turdus*, *Orthonyx*, *Menura*, and *Brachypteracias*. I have attempted to confirm the presence of bilateral scratching in the taxa on Wickler's list not already discussed here. In addition, I have sought to evaluate many casual reports of "scratching" behavior that have come to my attention concerning thrushes and babblers not mentioned by Wickler, and concerning bulbuls, pittas, and members of several other

groups. In every case where specific information on modes of ground-foraging was available, I discovered that the purported bilateral scratching or "scratching" behavior concerned bill-sweeping or bill-tossing (e.g., *Turdus*, bulbuls, pittas) or some form of unilateral scratching (e.g., *Turdus merula*, *Orthonyx*, *Menura*). Thus, I cannot confirm the presence of bilateral scratching in any birds other than those listed in Table 1.

ORIGIN AND EVOLUTION OF BILATERAL SCRATCHING

Ground-feeding is a behavior that has originated and diversified many times in birds. Yet, as a method of finding food on the ground, bilateral scratching seems surprisingly restricted, occurring in only a few of the major taxa that include ground-feeders. My ideas on the importance of certain preadaptations and ecological conditions for the origin of bilateral scratching have been developed from current knowledge of the behavior in mainland emberizines. Although generic limits and intergeneric relationships within the Emberizinae as a whole are poorly understood, the group is generally considered monophyletic. The occurrence of the behavior in non-emberizine taxa, with the possible exception of the Icteridae, should provide an opportunity to independently evaluate the generality of some of these ideas. I will discuss bilateral scratching by the Galápagos finches separately.

ORIGIN AND EVOLUTION IN EMBERIZINES

Two related questions may be asked regarding the origin of bilateral scratching in Emberizinae: (1) What were the probable behavioral preadaptations for it? (2) Is it likely that special ecological conditions favored its origin, and, if so, what were they? The problem of postadaptive modification of the behavior raises an additional question (3): What was the probable ancestral form of bilateral scratching in the subfamily and what conditions, if any, might have promoted evolutionary modification, or even loss, of the behavior?

Variation in form and use. In all emberizines that scratch bilaterally, the behavior is characterized by a double hop, first forward and then backward. During the forward hop, the bird's body is shifted to the front and the head raised somewhat; the rearward hop follows immediately, propelling the bird to approximately its original position and lowering

its head close to the substrate. The backward hop forcefully ejects debris to the rear with both feet.

Frequency of the behavior, scratching stance, and the apparent strength of scratching (as indicated by the amount of forward-rearward displacement of the body and by the vigor of the leg movements) vary within and among species. Some differences in scratching between species may be obligate, related to hind limb morphology (or gait) (Davis 1957) or to differences in body size. Other differences are probably facultative, resulting perhaps from variation in the feeding substrate or in availability of alternate foods. Grassland species (e.g., Savannah Sparrow [*Ammodramus (Passerculus) sandwichensis*] and Vesper Sparrow [*Poocetes gramineus*]) tend to scratch infrequently using a crouched stance and short, weak movements. In contrast, shrub and woodland species (e.g., Fox Sparrow and Rufous-sided Towhee) tend to scratch more regularly, assuming a more erect posture and employing more vigorous movements.

Emberizines scratch bilaterally on diverse substrates including broad-leaved litter, fibrous grass-forb litter, loose soil, snow, and soft mud.

Ecological distribution of bilateral-scratchers. The habitats of living emberizines that scratch bilaterally may indicate some of the ecological factors that favored the origin and spread of the behavior in their ancestors. The ecological distribution of most emberizine genera that include bilateral scratchers (see Table 1) is summarized in Table 2. My assumptions are: (1) the adaptive value of the behavior is related to substrate and has not changed substantially since it appeared in the subfamily, and (2) the ecological distribution of modern emberizine genera reflects to some extent the habitat relationships of their ancestral stocks.

This analysis is based on descriptions of the breeding habitats of emberizines, and includes information on all mainland species in each genus treated except those endemic to South America. I have excluded the latter because, as a group, they are poorly known ecologically and behaviorally and because the generic relationship of several of them is unclear. Under Paynter's (1970) classification, only two species of *Ammodramus* and two of *Aimophila* are not considered here. I have also excluded the Galápagos finches from this analysis because they are probably derived from mainland stock and their scratch-

TABLE 2. The number of North and Central American emberizines in genera that contain bilateral-scratchers found breeding in different habitat categories along an ecological gradient.^a A given species may be placed in more than one category.

Genera	No. species ^b	Grassland	Mixed grassland-shrub-tree	Scrub-open woodland-forest border	Forest-dense woodland interior ^c
<i>Passerella</i>	4	0	3	3	0
<i>Zonotrichia</i>	5	0	1	5	0 (2)
<i>Junco</i>	3	0	1	3	0 (2)
<i>Ammodramus</i>	5	5	3	0	0
<i>Ammospiza</i>	3	3	2	0	0
<i>Spizella</i>	6	0	5	6	0
<i>Pooecetes</i>	1	1	1	0	0
<i>Amphispiza</i>	2	0	2	2	0
<i>Aimophila</i>	12	4	10	9	0 (2)
<i>Pipilo</i>	6	0	3	6	1 (2)
<i>Melospiza</i>	3	0	1	3	1 (1)
<i>Arremonops</i>	3	0	1	3	0
<i>Pezopetes</i>	1	0	0	1	0
Total species	54	13	33	41	2 (9)

^a Data on habitat distribution were collected from many sources. The most important of these are Miller (1941), Pough (1951), Slud (1964), Skutch (1967), Austin (1968), Peterson and Chalif (1973), Wolf (1977), and my field notes on certain species.

^b Generic limits are based on Paynter (1970) and Mayr and Short (1970), as in Table 1. The number of species and their ranges are taken from Paynter (1970).

^c Includes continuous forest-dense woodland and interior edge (small openings, blowdowns, roadcuts, etc.). The number of species sometimes found in continuous, unbroken arboreal cover is shown without parentheses and the number generally associated with interior edge is shown in parentheses.

ing behavior may have been derived from that source.

Four habitat categories were delineated, grading from herbaceous to woody vegetation as follows: (1) grassland, (2) mixed grassland-shrub-small tree associations, (3) scrub, open woodland, and woodland-forest border, and (4) forest and dense woodland interior (including interior edge formed by small openings, roadcuts, etc.). Woody plant density and the stature of the plant communities increase, while the prevalence of herbaceous plants decreases along the gradient.

The most important distinction between these habitat categories is the frequency of different types of substrate. Grasslands have a litter of grass-forb stems and leaves, and usually areas of bare soil. The type, amount, and distribution of the litter varies among grassland associations. Habitats in the second and third categories typically have a mosaic-like substrate with patches of grass-forb litter, broad-leaved litter, and bare soil. Herbaceous litter prevails in category 2. In category 3, either herbaceous and broad-leaved litter are equally extensive, or the latter prevails. In habitats of category 4, the ground is more or less covered by a carpet of fallen broad leaves or needles and twigs from woody plants. Unless the canopy is open in these habitats, herbaceous litter is mostly confined to the edge.

Most emberizines in genera containing bilateral-scratchers typically breed in relatively

open, non-forest habitats with varying amounts of woody vegetation mixed with or adjacent to grass-forb areas (Table 2). *Ammodramus* (including *Passerculus*), *Ammospiza*, and *Pooecetes* are grassland genera.

Of the 54 species included in this analysis, 33 (61%) live primarily in grassland habitats with some woody vegetation (category 2), and 41 (76%) occur in open woods with some herbaceous cover (category 3). The few emberizines that enter forest-dense woodland interior (9 species) are generally restricted to internal openings and other breaks in the overstory cover. None of them may be characterized as true forest species.

Behavioral preadaptations. It seems clear to me that bilateral scratching is derived from hopping. The forward hop of the scratch resembles an ordinary hop used in locomotion, although in some species it may be shorter than the typical locomotory hop. The rearward power-hop in scratching is a special, derived component. I have seen Rufous-sided Towhees perform modified hops when ground-feeding, leaping straight up at foliage overhead or even jumping backward from a standing position when startled by something ahead. The power-hop of bilateral scratching might be derived from such movements.

Koenig (1951), Wickler (1961), and Harrison (1967) argued that birds who scratch by hopping evolved from hopping ancestors. Harrison implied that obligate coupling be-

tween bilateral scratching and hopping locomotion continues once the former appears in a phyletic line, but Hailman (1973) showed that this is not necessarily so. Hopping is widespread in Emberizinae and is probably the ancestral condition. Many emberizines, including those that scratch bilaterally, also perform asynchronous gaits (Hailman 1973; pers. observ.). Thus, once evolved, bilateral scratching might be retained independently of subsequent evolution of the locomotory behavior (Wickler 1961).

Whether a bird scratches generally depends also on where it forages. Ground-feeders with a hopping gait seeking food covered by litter are more apt to scratch bilaterally than are arboreal feeders with a hopping gait that glean food from foliage and branches (e.g., most wood warblers, vireos, and tanagers). Emberizines illustrate well the significance of foraging on debris-covered ground as a preadaptation for bilateral scratching. These birds typically find their food on ground largely or partly obscured by litter, yet most of them are not highly terrestrial. Many emberizines that scratch spend much of their time in vegetation well above the ground, singing, resting, and occasionally feeding. In contrast, certain other highly terrestrial species, such as larks, wagtails, and pipits, that usually forage in relatively open areas with little or no accumulation of litter or on patches of short, dense grass may not exhibit any debris-displacing behavior while foraging.

The apparent correlation between feeding on a debris-littered substrate and the use of bilateral scratching is not absolute. Old World buntings (*Emberiza*) often feed on the ground in places where litter is prevalent, but they do not scratch (Harrison 1967). I have seen the Lapland Longspur (*Calcarius lapponicus*), a non-scratcher related to *Emberiza*, bill-tossing debris while ground-feeding. Among New World emberizines, *Atlapetes* are not definitely known to scratch bilaterally in leaf litter, yet several use their bills in pushing leaves aside. Such exceptions suggest that foraging on litter and a hopping gait are not sufficient to account for the distribution of bilateral scratching in ground-feeding birds, even though both may be prerequisites for the origin of the behavior.

To complicate matters, foraging in litter can be preadaptive for two basic modes of displacing litter known among modern ground-feeders: sweeping or tossing debris aside with the bill or scratching it aside with the feet. These two methods have different taxo-

nomic distributions (Clark 1971), which could be explained as an outcome of multiple pathways of evolution (Bock 1959, Bock and Miller 1959). This explanation implies that the two modes of displacing litter are different adaptive responses in different organisms to a common selection force associated with uncovering hidden food on the ground. Since this theory requires that the same selection force(s) be responsible for each of the evolutionary "answers," the differences in behavior are not adaptive.

I reject this explanation for two reasons. First, the apparent difference in the ecological distributions of the two behaviors implies that they are not equally suitable alternatives for displacing every type of litter. If so, then each behavior may be favored by somewhat different selection forces related to different classes of litter. Second, the theory does not account for the occurrence of both behaviors in the same species. For example, *Turdus merula* uses bill-sweeping and the unilateral-scratch in foraging (Snow 1958); several species of Galápagos finches employ bill-sweeping and the bilateral scratch (Bowman 1963). In such species the two methods may be used in somewhat different circumstances.

Ecological factors. It is likely that certain ecological conditions, presumably related to the nature of the foraging substrate, must be present to favor the origin of bilateral scratching. The major classes of substrate encountered by most ground-foraging emberizines are broad-leaved litter, grass-forb litter and bare soil. Broad-leaved litter tends to be heavy and coarse while grass-forb litter is light and fibrous. Seeds are more common under grass-forb litter than under broad-leaved litter. Different emberizines find different proportions of these substrates as they forage (see Table 2).

Many emberizines scratch readily in both broad-leaved and grass-forb litters. Since grassland sparrows that scratch bilaterally rarely encounter broad-leaved litter in their habitats, they are limited to scratching in the grass-forb type (Table 3). My observations suggest that emberizines scratch only infrequently on bare mineral soil. Instead, they generally inspect the surface of the soil briefly between short bouts of hopping or running. Often I have watched Song Sparrows (*Passerella [Melospiza] melodia*), White-throated Sparrows (*Zonotrichia albicollis*), and other emberizines cease scratching when they moved from a patch of litter to bare soil, only to im-

TABLE 3. Use of bilateral scratching on different substrates by certain emberizines. The information in this table comes from the author's field notes.

Species	Substrate		
	Broad-leaved	Herbaceous	Other
<i>Passerella iliaca</i>	++	+	snow
<i>P. (Melospiza) melodia</i>	+	++	snow, wood chips
<i>P. (M.) lincolni</i>	+	++	-
<i>P. (M.) georgiana</i>	+	+	-
<i>Zonotrichia leucophrys</i>	+	+	-
<i>Z. albicollis</i>	++	+	snow, wood chips, needle litter
<i>Junco hyemalis</i>	+	+	snow
<i>Ammodramus</i> (<i>Passerculus</i>) <i>sandwichensis</i>	-	+	-
<i>Spizella arborea</i>	+	+	snow, wood chips
<i>Poocetes gramineus</i>	-	+	-
<i>Pipilo erythrophthalmus</i>	++	+	sand, needle litter

KEY: ++: scratches frequently (many observations); +: scratches infrequently (few observations); -: no observations.

mediately resume scratching when they entered another area of litter.

Grass-forb litter seems to be the only major type of substrate on which all mainland emberizines listed in Table 1 scratch regularly. Grassland species encounter it year round, while certain woodland species (e.g., Rufous-sided Towhee and White-throated Sparrow) may do so only during the non-breeding period when they occupy more open areas (pers. observ.). In fact, all emberizine scratchers may scratch more during the non-breeding season when food becomes scarce and seeds comprise the bulk of their diet than during the breeding season when foods other than seeds are plentiful (Greenlaw 1976).

Ecological conditions that favored the origin of bilateral scratching in Emberizinae probably were provided only by grass-forb litter. If the behavior arose on broad-leaved litter, one would expect it to be widespread in forest-interior and forest-edge non-emberizines and absent or greatly restricted among emberizines. The reverse seems to be the case. At present, no true forest species in any group is known to scratch bilaterally. Bill-sweeping and bill-tossing appear to be the characteristic means for displacing broad-

leaved litter among forest ground-feeders, regardless of gait (Clark 1971, Table 1). It may be significant that only bill-sweeping has been documented unequivocally in those species of *Atlapetes* which inhabit forest edges and interiors.

The importance of grass-forb litter in the origin of bilateral scratching is easy to understand. The long, thin stems and leaves of dead grasses and small forbs form an interlaced, network of litter around the bases of living plants. Bill-sweeping in this material can be ineffective and dangerous. The thin, fibrous material offers little surface for efficient sweeping and the ends of long, stiff stems could easily poke and damage the eyes of a bill-sweeper, especially if it were short-billed. Bill-tossing the many bits of debris at a single foraging site could consume much time and energy. The bilateral-scratch, using the toes as a rake, is a simple and effective method for pulling litter out of the way and quickly uncovering food. Using both legs together avoids the potential difficulty in unilateral scratching of standing on some long-stemmed material with the supporting foot.

Bilateral scratching by emberizines might have evolved in several types of American grasslands. It seems likely, however, that it originated in open grasslands with only a moderate density of herbaceous cover interrupted by many avenues and spaces between grass stems or grass clumps offering room for effective scratching. In dense grassy areas, litter becomes wedged among the crowded stems and is difficult to move by scratching.

Conditions favoring the origin and early spread of scratching among emberizines probably occurred in dry or semiarid grasslands, characterized by a mixture of exposed ground, herbaceous plants, scattered shrubs, and small trees. Here, the scarcity of food, reinforced by seasonal declines in productivity, may have favored those variants in the pre-scratching stock that could effectively find seeds hidden under the patches of litter.

Postadaptive modification and loss. Once evolved, scratching is preadapted for uses other than the one associated with its origin. If "new" selection forces arise, postadaptive modifications of the behavior may occur (Bock and Wahlert 1965).

The earliest form of bilateral scratching probably was characterized by weak hopping movements and infrequent use (with regular use of other modes of foraging on or near the

ground). Unless a walking or running gait was common along with hopping, it is unlikely that the legs were often moved asynchronously in early bilateral scratching. Such asynchrony now seems to be rare in the scratching of emberizines, even in grassland species, although two instances are known (Hailman 1973, Greenlaw 1976). The initial form of the scratch may have been simply a backward jump from a standing position, using the toes to rake debris toward the rear. The innovation of a forward preparatory hop added power and leverage to the scratch and enabled a bird to uncover a larger area and displace heavier material in a single set of movements.

I do not know of any cases of emberizines scratching by simply jumping backwards from a standing position. But I have seen Red-winged Blackbirds (*Agelaius phoeniceus*) do so, especially in a heavy litter of wood chips where the jump seemed ineffective.

Although bilateral scratching seems to have originated as a means of moving grass-forb litter, it can be used to displace broad-leaved litter and other loose material as well. In addition, it can be used in non-foraging contexts; for example, a ground-nester can scratch a depression in litter and duff and make its nest flush with the substrate (Veghte in Austin 1968:1129). This generalized benefit probably accounts for the spread of the behavior in Emberizinae.

The role that broad-leaved litter may have played in the origin of bilateral scratching is unclear but it was important in the subsequent evolution of the habit. I hypothesize that as the ancestral scratchers in open habitats diversified, some of their descendents entered woodlands and foraged in leaf litter from deciduous trees and shrubs. Selection favored the evolution of vigorous, large-amplitude scratching movements in these birds, like those of the Rufous-sided Towhee and Fox Sparrow. Since the litter is nearly continuous and thick in woodlands, emberizines occupying them would increasingly rely on scratching when foraging on the ground.

The comparatively weak and infrequent scratching of modern grassland sparrows does not necessarily mean that bilateral scratching in these birds is undergoing evolutionary degeneration and loss. Instead, it appears likely that their use of the bilateral scratch resembles the ancestral form of the behavior more closely than does the vigorous and frequent scratching of certain scrub and woodland species. In the grassland species, little postadaptive modification of their scratching has occurred.

The wide taxonomic and habitat distributions of the bilateral scratch among New World emberizines, and its occurrence in the Galápagos finches, suggest that the behavior is quite old in the subfamily. The habit may have been lost independently several times in the group, but to determine this, one must be able to identify instances where it has been or is being lost in a phyletic line. This is not easy to do from current evidence.

One approach is to examine genera that contain some species that scratch regularly and others that do so infrequently or not at all. Clark (1970) noted that *Spizella* provides just such an example. He reported that *S. arborea* often scratches bilaterally in foraging, but that *S. passerina* and *S. pusilla* apparently do not scratch at all. The records of occasional scratching in *pusilla* (one captive bird) and *passerina* (see Table 1) do not change the basic intent of Clark's argument. This pattern may indicate that the behavior is being lost in *pusilla* and *passerina*. This explanation implies that the behavior was prevalent in ancestral *pusilla*-*passerina*-*arborea* stock (assuming the group to be monophyletic) and that only modern *arborea* has retained it as an important mode of foraging. However, the opposite may have been the case. *Spizella* probably evolved from an open-habitat ancestor that used the bilateral-scratch only infrequently in patches of light, herbaceous litter. The behavior remained relatively unimportant in the *pusilla* and *passerina* lines as they tended to forage on patches of open, non-littered ground (as do modern *pusilla* and *passerina*, pers. observ.), and to pick seeds directly from the heads of standing grasses (Allaire and Fisher 1975). In contrast, scratching in ancestral *arborea* stock became more important as the birds came to occupy shrubby habitats and wooded edge where they found much leaf litter and little bare ground.

The apparent absence of bilateral scratching in the Holarctic and Old World genera *Calcarius*, *Plectrophenax* and *Emberiza* is one of the greatest puzzles of its distribution in Emberizinae. Harrison (1967) proposed that the absence of the behavior in *Emberiza* is best explained as the result of evolutionary loss in ancestral bunting stock, perhaps represented today by modern longspurs. He suggested that the loss was probably unrelated to changes in feeding requirements per se, but was associated with a transition from locomotory hopping to walking (typical gait in modern *Calcarius* and *Plectrophenax*), which occurred in pre-bunting stock before

or during the invasion of the Old World by New World emberizines. Hailman (1973) has criticized this view, I believe correctly. To the extent that bilateral scratching and gait are controlled by different selective forces, the two habits can evolve independently.

It is entirely possible that the Old World was colonized by ancestral emberizines that had already lost the bilateral-scratch in the New World for unknown ecological reasons not associated with changes in a hopping gait. However, I consider another explanation more likely for the absence of the behavior in *Emberiza* and related genera. I find no a priori reason to think that bilateral scratching is as old as the subfamily. On the contrary, it is easier to believe that the habit arose after the earliest emberizine stock had already diversified. If so, the original emberizine invasion of the Old World could have stemmed from a New World lineage, now extinct, that did not possess the bilateral scratch.

Moreover, modern longspurs may not be important for understanding the absence of the bilateral scratch in *Emberiza* (cf. Harrison 1967). I believe it likely that *Calcarius* represents a secondary colonization (perhaps two) of North America by Old World *Emberiza* followed by speciation in the New World (cf. Jehl 1968). The northern distribution (arctic, subarctic, northern plains) of *Calcarius* and the similarities in plumage color and pattern which some of them share with certain species of *Emberiza* (Jehl 1968) support this hypothesis as well as that favored by Harrison (1967). If this interpretation is correct, then the absence of bilateral scratching in living longspurs is explained by its absence in *Emberiza*, and not the converse. In this circumstance, *Calcarius* does not help to decide whether *Emberiza* is derived from scratching or non-scratching New World stock.

Place of origin. Knowledge of the geographic distribution of the bilateral-scratch among New World emberizines may indicate where the habit arose. Thanks to recent studies of the foraging behavior of neotropical emberizines, the distribution of scratchers is coming to light. I am aware that this pattern may be an artifact of incomplete and geographically biased information.

Aside from *Zonotrichia capensis*, which has Nearctic affinities, no other South American emberizine is definitely known to scratch bilaterally. In Panamá and Costa Rica there occur several genera containing bilateral

scratchers. *Pezopetes* is endemic to mountains in the area and may be related to *Atlapetes* and *Pipilo* (Paynter 1970). The other genera of scratchers in the region (*Arremonops*, *Melospiza*, *Ammodramus*, *Aimophila*, *Junco*, *Zonotrichia*) occupy highland habitats and most have clearly northern (Mexico and north) affinities. It may be significant that several recent observers have not yet seen bilateral scratching in certain emberizines endemic to the American tropics (e.g., Stiles and Hespdenheide 1972, Lill 1974, Greenlaw, unpubl. data on *Tiaris* in Puerto Rico). If this pattern of geographic occurrence proves real, it would strongly suggest a North American origin for the behavior.

Dry (open) grasslands probably were associated with the origin and early evolution of bilateral scratching among emberizines. Areas of the southwestern United States and contiguous northern Mexico are extensively covered by semiarid grassland, shrubsteppe, and shrub-tree savanna where grasses are among the dominant plants. The development of such vegetation apparently dates from at least Middle Pliocene (Axelrod 1948) and significant areas survived the Pleistocene glaciations in several refugia (Hubbard 1973). From such habitats, the original emberizine scratchers could have radiated in North America and occupied scrub, open woodland, and forest-edge habitats on the one hand, and pure, mesic grassland and salt marsh associations on the other. Representatives of this radiation could have entered the neotropics by way of the Mexican and Middle American highlands where they subsequently speciated. Some of the species may even have had time to occupy middle elevation or humid lowland tropical habitats.

ORIGIN IN NON-EMBERIZINE TAXA

The occurrence of bilateral scratching, or a modification of it, in non-emberizine taxa seems to support the notion that the habit tends to arise among hopping birds that often forage in herbaceous litter.

The Bearded Tit (*Panurus biarmicus*) inhabits reedy marshes from southern Europe to Manchuria. It feeds on small insects and seeds above the shallow water of the marshes among the reed and rush stems. It also forages on the ground (Koenig 1951) in drier places, most frequently during the non-breeding season when it eats large quantities of seeds from marsh plants (Dement'ev and Gladkov 1970). Koenig (1951:255) indicated that this species scratches bilaterally in dis-

placing the fallen leaves and stems of reeds and other marsh plants when it forages on the ground. He also emphasized the importance of the species' hopping gait as a pre-adaptation for the origin of the behavior.

Possibly the bilateral scratch did not originate in *Panurus* in marshy habitats, but in an ancestral form that inhabited open upland sites.

Parrotbills (*Paradoxornis*), probable relatives of *Panurus*, are north temperate species with short, heavy bills. They are active birds that "wander through grasslands, brushlands, hedgerows, and thickets... hunting seeds, berries, and small insects" (Austin 1961). Their diet resembles that of emberizines, and if they feed on the ground in semi-open places, they may also scratch bilaterally.

The habit in Icteridae probably arose independently from that in Emberizinae, but the possibility remains that it was inherited from pre-icterid emberizine stock that used it. Brown-headed Cowbirds (*Molothrus ater*) and Redwinged Blackbirds generally employ the behavior on light, grass-forb litter around the bases of standing plants in open places. Foraging cowbirds also scratch bilaterally in withdrawing and holding aside short, erect grass stems covering potential food (Greenlaw 1976). I believe that such scratching is derived and is not fundamental to its origin. Wetmore (1926:384) reported *Molothrus bonariensis* scratching in dust. On the ground, Brown-headed Cowbirds and Redwinged Blackbirds use a walking gait. This seems to contradict the idea that bilateral scratching is derived from hopping, but perhaps scratching need not always originate from a hopping gait. Both of these species hop occasionally (pers. observ.), so it is not necessary to suspect another behavior for its origin. Living icterids may have inherited their scratching behavior from an extinct hopping ancestor.

Viduiines are hopping ground-feeders that employ a form of the bilateral scratch while foraging. They occur widely in much of Africa south of the Sahara, generally occupying open, dry habitats containing areas of bare soil, grass-forb cover, shrubs, and trees (Payne 1973). Grass-forb litter could have played a critical role in the evolution of scratching in this seed-eating group as well.

Payne (1971) and Fry (1975) have observed viduiines scratching on clay and sandy soils where dust or dry grass partly covered seeds. Payne pointed out that *Vidua* scratch on dry soils where herbaceous cover is not dense. Since viduiines seem to scratch fre-

quently on loose, bare soil (Payne 1971, Cunningham-van Someren 1974, Fry 1975), this substrate also may have influenced the origin and evolution of their scratching.

TAXONOMIC SIGNIFICANCE OF BILATERAL SCRATCHING

The occurrence of bilateral scratching among non-emberizine birds is poorly known, but present evidence suggests that it is restricted in ground-feeding birds. Scratching is a singular and distinct character that is probably derived only under certain circumstances. As such, it may be of value in judging taxonomic relationships in the groups where it occurs, especially in the New World emberizines. I can find no definite evidence that bilateral scratching has been lost as a mode of foraging among emberizines. Its present distribution and use in the subfamily can be adequately explained as a function of genetic spread between phyletic lines and postadaptive variation in different stocks. I assume that scratching arose in a single phyletic line in Emberizinae after the group had diversified. If my interpretation is correct, the usefulness of bilateral scratching as a taxonomic character in emberizine systematics is clear.

The possible significance of bilateral scratching in the systematics of certain passerine taxa, notably the Galápagos finches and the icterids is worth exploring. The species of Galápagos finches are believed to have arisen from a common progenitor. They are usually placed in a separate subfamily, Geospizinae, but Paynter (1970) and Sibley (1970) included them in Emberizinae. Either treatment assumes that the ancestor of these birds was finch-like, although systematists are not agreed on this. Bowman (1963) asserted that "Since only five of the 14 species of Geospizinae are clearly identifiable as 'finch' types, I see no reason a priori that a 'finch' origin of the group is any more likely than a 'warbler' origin." Harris (1972) agreed and suggested that *Coereba* may be a possible modern link between *Pinaroloxias* (and thus the other Galápagos finches) and the mainland ancestor.

I believe that the occurrence of bilateral scratching in the group can help to resolve this issue. The behavior either occurred in the founding stock when it occupied the Pacific islands or evolved independently after its arrival. If the latter was the case, and if the ancestor was warbler-like, or honeycreeper-like, then it is likely that scratching would have originated only in the ground-

finch derivatives, and not in the original arboreal form and its tree-inhabiting descendants. Under these circumstances, the behavior should be restricted to a few species in the modern group of finches (probably only in *Geospiza*). But if the ancestor was finch-like and scratched while foraging on the ground, then it is likely that its arboreal descendants would retain the behavior during their evolution as long as they continued to forage on the ground, as do most of the modern species (Bowman 1961). In this case, the behavior should be widespread today, occurring in both tree-inhabiting and ground-inhabiting species, even though it may have been lost in the most specialized of the arboreal forms (e.g., in *Certhidea*).

At least 12 species of Galápagos finches scratch on the ground, including the tree-finches *Camarhynchus parvulus*, *C. psittacula*, and *C. pallidus*. This strongly suggests that the behavior is old in the group and that the modern arboreal forms are derived from a finch-like ancestor that scratched.

The bilateral-scratch could have arisen independently in the finch-like ancestor shortly after its arrival on the islands and before any radiation had occurred. However, I believe the most parsimonious explanation for its presence in the Galápagos finches is that the founding stock of the group was derived from a bilaterally scratching emberizine on the mainland.

Island species often possess unusual modes of foraging and other unique adaptations. Characteristically these "odd" specializations are restricted to a single (or a few) island species or to a population within a species. The peculiar habits of tool-using, blood-eating, and bill-bracing in the Galápagos finches are no exception. Bilateral scratching does not fit this pattern.

The history of bilateral scratching in the Icteridae is uncertain. Since the behavior in icterids differs in several respects (e.g., scratching stance, frequency of leg asynchrony while scratching) (Greenlaw 1976) from that in emberizines, one could argue that it evolved independently in icterids. Yet an alternate explanation for its presence in Icteridae exists. Beecher (1951) concluded that these birds evolved from early emberizine finches via a molothrine-like ancestor. This view is one of the few relatively uncontroversial current ideas about relationships of the nine-primaried oscines (Short and Bock 1970). Beecher regarded *Molothrus* and *Agelaius* as modern

representatives of primitive stocks in the family, perhaps with the latter descending early from a molothrine line. If this sequence is correct, it is possible that icterids inherited bilateral scratching from an emberizine ancestor through pre-*Molothrus*. The differences in scratching behavior between modern icterids and emberizines may have arisen later during the shift to walking in the icterid line.

Finally, *Atlapetes* deserves attention. This large genus contains about 22 species (Paynter 1970). If they shared a scratching ancestor with *Pipilo* and related taxa, it is likely that some of them scratch bilaterally. But, if the behavior is entirely absent in the group, then the assumed close relationship between *Atlapetes* and *Pipilo*, *Arremonops*, *Pezopetes* and other genera in which it is present, probably should be reevaluated (Clark 1971).

SUMMARY

This paper seeks to reappraise the taxonomic distribution of bilateral scratching in ground-feeding birds and to formulate a hypothesis for its origin and evolution.

The bilateral scratch seems to have a limited occurrence among ground-feeding birds: Emberizinae, Icteridae, Paradoxornithinae, and Viduinae. In Emberizinae it is known in 45 species (16 to 19 genera). There is one report of its presence in furnariids.

Among emberizines, the behavior has a broad ecological distribution from grassland to woodland. The birds scratch bilaterally on several different types of substrate, but most frequently on herbaceous and broad-leaved litters. All emberizines that scratch do so on the former type of litter but only certain species scratch on the latter.

I hypothesize that bilateral scratching tends to originate among ground-feeding hopping birds who often seek seeds and other food under herbaceous litter in open habitats. Post-adaptive modifications that influence the frequency and vigor of scratching movements probably evolved in shrub-woodland species primarily exposed to heavy, coarse, broad-leaved litter. The use of the bilateral scratch by non-emberizines seems to support this hypothesis.

Bilateral scratching in Emberizinae may have originated in semiarid grasslands in North America. The taxonomic significance of the behavior is discussed in relation to Galápagos finches, Icteridae, and *Atlapetes*.

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Department of Biology, C.W. Post Center of Long Island University, Greenvale, N.Y. 11548. Accepted for publication 16 December 1975.