

THE OCCURRENCE OF BILL-SWEEPING IN THE TERRESTRIAL FORAGING OF BIRDS

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BROAD taxonomic surveys of particular behavioral traits provide an important background for systematic decisions as well as interpretations on the evolution of behavior. I here review one kind of behavior, discuss aspects of its evolution, and assess its potential as a taxonomic character. In seeking food hidden on the ground some avian species often use characteristic lateral sweeps of the bill to move aside twigs, leaves, dry soil, or snow. In view of its descriptive appropriateness the term "bill-sweeping" has been chosen to designate this foraging behavior. Kilham (1968) used the same term for similar movements used by nuthatches (*Sitta*) on a trunk or branch apparently to create spurious olfactory trails which may serve to mislead squirrels seeking nuthatch nests.

My observations have been made over several years in the field, at a feeding station, and in aviaries. Although the ornithological literature is too voluminous to search exhaustively for records of bill-sweeping, an extensive literature search has been made with examination of studies on hundreds of species. I have listed a citation for each genus for which I have found a record of sweeping but have not attempted to cite every published comment on the subject. Much remains to be learned about bill-sweeping, and I hope that this first review of the subject will also indicate areas needing further investigation. The present report is an extension of an earlier study on bill-wiping which involves similar movements (Clark, 1970*b*).

Bill-sweeping ordinarily results in the movement of a conspicuous quantity of material on a substrate and is thus unlike typical bill-wiping. The sideward motions of the bill used by some aquatic foragers (e.g., *Platalea*) also resembles sweeping but are not reviewed here. In addition, the common cases in which items are lifted between the mandibles and then dropped without a consistent and detectable lateral movement of the bill are also excluded from detailed consideration. At a feeding station I have seen such raising and dropping of items without sweeping by *Cyanocitta cristata*, *Parus atricapillus*, *P. bicolor*, *Sitta carolinensis*, *Quiscalus quiscula*, *Molothrus ater*, *Spinus pinus*, *S. tristis*, *Junco hyemalis*, *Spizella arborea*, and *Passerella iliaca*.

RECORDS OF BILL-SWEEPING

Species reported to bill-sweep are listed in Table 1. Variable features in sweeping include 1) the substrate, 2) the conspicuousness of the sweeps, and 3) the way in which the mandibles are used.

TABLE I
RECORDS OF BILL-SWEEPING IN FORAGING

Taxa	Source of Data
Tinamidae	
<i>Crypturellus boucardi</i>	Lancaster, 1964a
<i>Nothoprocta cinerascens</i>	Lancaster, 1964b
Pteroclididae	
<i>Pterocles orientalis</i>	This study
Columbidae	
<i>Columba livia</i>	Johnston, 1960
<i>Zenaidura macroura</i>	" "
<i>Geopelia cuneata</i>	" " ; this study
<i>Scardafella inca</i>	" "
<i>Columbigallina passerina</i>	" "
Momotidae	
<i>Momotus momota</i>	Skutch, 1964
Upupidae	
<i>Upupa epops</i>	Skead, 1950
Furnariidae	
<i>Automolus ochrolaemus</i>	Skutch, 1969
<i>Sclerurus albigularis</i>	Slud, 1964
<i>S. guatemalensis</i>	Skutch, 1969
Formicariidae	
<i>Myrmeciza exsul</i>	Skutch, 1969
<i>Formicarius analis</i>	Skutch, 1945
<i>Gymnopithys bicolor</i>	" " ; Willis, 1967
<i>Grallaria perspicillata</i>	Skutch, 1969
Corvidae	
<i>Cyanocitta cristata</i>	This study
<i>C. stelleri</i>	Brown, 1963, 1964
<i>Aphelocoma coerulescens</i>	" "
<i>A. ultramarina</i>	" "
<i>Pica pica</i>	Linsdale, 1937
Sittidae	
<i>Sitta carolinensis</i>	This study
Timaliidae	
<i>Eupetes leucostictus</i>	Rand and Gilliard, 1968
<i>Garrulax rufogularis</i>	Harrison, 1962
Troglodytidae	
<i>Campylorhynchus griseus</i>	Selander, 1964
Mimidae	
<i>Dumetella carolinensis</i>	Allen cited by Gross in Bent, 1948
<i>Melanotis hypoleucus</i>	Skutch, 1950
<i>Toxostoma rufum</i>	Engels, 1940; Klopfer and Hailman, 1967: 184; this study
<i>T. curvirostre</i>	Engels, 1940

TABLE 1 Continued

Taxa	Source of Data
<i>T. redivivum</i>	" "
<i>Cinlocerthia ruficauda</i>	Zusi, 1969
Turdidae	
<i>Catharus</i> sp.	Dilger, 1956
<i>Hylocichla mustelina</i>	Dilger, 1956; this study
<i>Turdus merula</i>	Snow, 1958; this study
<i>T. albicollis</i> (= <i>T. assimilis</i>)	Skutch, 1960
<i>T. migratorius</i>	This study
Parulidae	
<i>Seiurus noveboracensis</i>	Schwartz, 1964
<i>S. motacilla</i>	Slud, 1964
Ploceidae	
<i>Passer domesticus</i>	This study
<i>Lagonosticta rubricata</i>	Goodwin, 1964
<i>Uraeginthus</i> sp.	Goodwin, 1965
Icteridae	
<i>Quiscalus quiscula</i>	This study
Thraupidae	
<i>Rhodinocichla rosea</i>	Skutch, 1962
Fringillidae	
<i>Atlapetes brunneinucha</i>	Slud, 1964; Skutch, 1967
<i>A. torquatus</i>	Skutch, 1954

Birds may sweep in vegetational litter, dry soil, or snow. The kinds of substrates on which sweeping occurs obviously depend on the habitats utilized by particular species. Pigeons commonly sweep in dry soil (cf. Johnston, 1960), and perhaps sandgrouse do also, for at a zoo I observed both a pigeon *Geopelia cuneata* and a sandgrouse *Pterocles orientalis* engaged in a similar type of bill-sweeping at their shared food bowl. Apparently neither pigeons nor sandgrouse have been reported to sweep in leaf litter. Among other species listed in Table 1, jays (*Cyanocitta*, *Aphelocoma*; Brown, 1963), timaliids (*Garrulax*; Harrison, 1962), thrashers (*Toxostoma*; Engels, 1940), and estrildines (e.g., *Lagonosticta*; Goodwin, 1964) sweep in soil.

The majority of the species of Table 1 reportedly sweep in vegetational litter, and I have seen this activity engaged in by *Cyanocitta cristata*, *Toxostoma rufum*, *Hylocichla mustelina*, *Turdus merula*, *T. migratorius*, and *Quiscalus quiscula*. Certain species of jays (Brown, 1963), timaliids (Harrison, 1962), and thrashers (Bent, 1948; Engels, 1940) are sufficiently versatile to sweep in vegetational litter as well as dry soil. *Cyanocitta cristata* and *Passer domesticus* were seen during this study to sweep in snow.

Most species that I have observed sweeping do so conspicuously. However, the ploceid *Passer domesticus* makes relatively inconspicuous lateral movements which were most readily detected when birds sought food beneath a thin layer of powdery snow. Their movements produced momentary small clouds of flying snow near their heads, whereas the foraging of nearby emberizines, *Junco hyemalis* and *Spizella arborea*, had no such effect.

Whether swept items are lifted between the mandibles or are simply pushed aside is often difficult to determine in the field. Although more data are desirable, it appears that use of only one or both of these methods may be a species-specific trait. Gross (after Allen in Bent, 1948: 333) reports that both methods are used by the Catbird (*Dumetella carolinensis*) as does Bent (1948: 364) for the Brown Thrasher (*Toxostoma rufum*). In London, England, I observed European Blackbirds (*Turdus merula*) using both methods (see also Snow, 1958: 28). Bicolored Antbirds (*Gymnopithys bicolor*; Willis, 1967), Tremblers (*Cinlocerthia ruficauda*; Zusi, 1969), and Northern Waterthrushes (*Seiurus noveboracensis*; Schwartz, 1964) lift pieces between the mandibles during sweeping, but apparently do not simply push items aside. In addition, I have seen a White-breasted Nuthatch (*Sitta carolinensis*) grasp leaves between the mandibles and lift them aside to uncover sunflower seeds at a feeding platform, but I have not observed sweeping by "pushing aside" in this species. By contrast, Skutch (1969: 276) reports that the furnariid *Sclerurus guatemalensis* flicks aside leaves with a closed bill; this genus has not been reported to lift items between the mandibles during sweeping.

European Blackbirds (Snow, 1958: 28) and Wood Thrushes (*Hylocichla mustelina*; Dilger, 1956; Klopfer and Hailman, 1967: 184) may scratch with a foot as well as bill-sweep in clearing the substrate. These are the only records known to me of species using both of these techniques in foraging.

In a few additional cases, bill-sweeping is not directly involved in foraging. Brown (1963) reports the use of digging (sweeping) motions in the burying of hoarded food by the Mexican Jay (*Aphelocoma ultramarina*) and also (Brown, 1964) comments on "digging" as a displacement activity of both this species and the Steller's Jay (*Cyanocitta stelleri*).

American Goldfinches (*Spinus tristis*) often make sideward sweeps with the bill in a pile of seeds (Coutlee, 1963; this study). The function of this activity is unknown, but conceivably these movements might serve to uncover food in dry soil, although such behavior has apparently never been recorded.

Many species apparently do not sweep. I have been able to make ex-

tended observations on the following species and have never observed bill-sweeping: *Charadrius melodus*, *Pluvialis dominica*, *Sterna hirundo*, *Parus atricapillus*, *Agelaius phoeniceus*, *Molothrus ater*, *Richmondia cardinalis*, *Hesperiphona vespertina*, *Pipilo erythrophthalmus*, *Junco hyemalis*, *Spizella arborea*, *S. passerina*, *S. pusilla*, *Zonotrichia albicollis*, and *Melospiza melodia*. In addition, Dunham (1966) implies that the Rose-breasted Grosbeak (*Pheucticus ludovicianus*) does not sweep.

DISCUSSION

In many of the species known to sweep, this behavior occurs only under restricted conditions. For example, in the Robin (*Turdus migratorius*), I have observed that sweeping is unlikely to occur if food can be found without sweeping. Skutch (1969: 237) reports that the antbird *Myrmeciza exsul* flicks leaves aside apparently only when in pursuit of fleeing prey. Sweeping may thus be highly restricted and, although characteristic of a species, may not be a preeminent kind of behavior.

Sweeping can be relatively readily seen only for birds that forage regularly on the ground. Thus it is difficult to estimate the potentiality for sweeping in the numerous species that are primarily arboreal. Although sweeping is commonly an adaptation for terrestrial feeding, it is not necessarily confined to extensively terrestrial species as exemplified by its occurrence in the White-breasted Nuthatch, a specialized arboreal species. Sweeping in the foraging of nuthatches might possibly be correlated with the regular use of similar movements in apparent nest defense (Kilham, 1968).

Among species known to sweep there is an impressive diversity in size and shape of bills. Apparently no morphological adaptations for sweeping have thus far been described. Specializations in bill structure have ordinarily been discussed in relation to commonly used feeding methods, and little attention has been given to possible morphological correlates of less frequent kinds of feeding behavior.

If the apparently widely scattered taxonomic distribution of sweeping reflects the general situation, considerable evolutionary convergence has occurred through either independent origins or losses of the trait. An extreme interpretation would be that bill-sweeping occurred in the common ancestors of extant birds and has subsequently been lost in many lineages. At the opposite extreme would be an hypothesis that the present distribution can be explained entirely by independent origins. Direct evidence on the evolutionary history of sweeping is not available, but presumably such a simple behavioral trait as sweeping might be evolutionarily gained or lost more readily than a more complex kind of behavior. The most con-

servative hypothesis appears to be that the present taxonomic distribution is a result of both repeated origins and independent losses.

Sweeping for food has presumably evolved from other kinds of behavior. For example, a feeding bird might with its bill accidentally push aside some of the ground cover and thereby obtain additional food; given a genetic basis for this tendency, selection might favor the gradual evolution of sweeping as a regular method of foraging. Alternatively, the accidental uncovering of food through bill-wiping on the ground might be a first stage in an evolutionary series leading to sweeping. As bill-wiping occurs widely among birds (Clark, 1970*b*), its potential as an evolutionary source for sweeping is great. Indeed, the bill-wiping characteristic for so many species may be a kind of preadaptation for sweeping. In another possibility, the lifting and dropping of unpalatable items without sweeping movements, as apparently occurs in many birds, might develop a lateral component and evolutionarily give rise to sweeping. The first two suggested possibilities might potentially account for sweeping without lifting, and the third would be a conceivable origin for sweeping that involves holding objects between the mandibles. Other possibilities can be envisioned, and in no case is the evolutionary origin of bill-sweeping clearly indicated.

Bill-sweeping may have limited value as a taxonomic character in view of its probable history of repeated evolutionary origins and losses. Although bill-sweeping is presumably generally homologous within a genus (e. g., *Turdus*) or between closely related genera (e. g., *Turdus* and *Hylocichla*), the sweeping of birds in different orders is probably not homologous. The question of possible homologies between remotely related genera or between families remains open.

Despite the care that must be exercised in applying bill-sweeping as a taxonomic character, there are three specific cases in which sweeping is possibly relevant to taxonomic decisions. (1) The question as to whether sandgrouse are more closely related to pigeons or plovers has recently been extensively debated (cf. Maclean, 1967; Stegmann, 1969; George, 1969). My finding of sweeping in sandgrouse and pigeons, in contrast to the lack of this behavior in plovers, is at least suggestive. (2) The sweeping of *Rhodinocichla rosea* is one of a number of features suggesting its possible affinities with the Mimidae (Skutch, 1962), but other, apparently evolutionarily more conservative, characters indicate a relationship with the Thraupidae (Eisenmann, 1962). (3) The bill-sweeping of the brush-finches (*Atlapetes*) is of interest in view of the problem of the relationship of this genus to the towhees (*Pipilo*; Parkes, 1957). *Pipilo erythrophthalmus*, in apparent contrast to *Atlapetes*, scratches with both feet in foraging and does not bill-sweep (Clark, 1970*a*; this study). This foraging difference,

if characteristic of each genus, would lend support to the idea that similarities in appearance of adults in certain species of *Pipilo* and *Atlapetes* are a result of evolutionary convergence.

SUMMARY

Records of the use of sideward bill movements in terrestrial feeding are summarized and analyzed for more than 45 species of birds. Variable features in sweeping include the nature of the substrate, conspicuousness of the movements, and the method of use of the mandibles; at least some of these aspects appear to be species-specific. The scattered taxonomic distribution of bill-sweeping indicates that considerable evolutionary convergence has occurred, but bill-sweeping may in some cases be used along with other evidence as indicative of phylogenetic relationships.

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LITERATURE CITED

- BENT, A. C. 1948. Life histories of North American nuthatches, wrens, thrashers and their allies. U. S. Natl. Mus. Bull., 195.
- BROWN, J. L. 1963. Social organization and behavior of the Mexican Jay. *Condor*, 65:126-153.
- BROWN, J. L. 1964. The integration of agonistic behavior in the Steller's Jay *Cyanocitta stelleri* (Gmelin). *Univ. California Publ. Zool.*, 60:223-328.
- CLARK, G. A., JR. 1970a. Apparent lack of the double-scratch in two species of *Spizella*. *Condor*, 72:370.
- CLARK, G. A., JR. 1970b. Avian bill-wiping. *Wilson Bull.*, 82:279-288.
- COUTLEE, E. L. 1963. Maintenance behavior of the American Goldfinch. *Wilson Bull.*, 75:342-357.
- DILGER, W. C. 1956. Adaptive modifications and ecological isolating mechanisms in the thrush genera *Catharus* and *Hylocichla*. *Wilson Bull.*, 68:171-199.
- DUNHAM, D. W. 1966. Maintenance activities of the Rose-breasted Grosbeak. *Wilson Bull.*, 78:68-78.
- EISENMANN, E. 1962. On the systematic position of *Rhodinocichla rosea*. *Auk*, 79:640-648.
- ENGELS, W. L. 1940. Structural adaptations in thrashers (Mimidae: Genus *Toxostoma*) with comments on interspecific relationships. *Univ. California Publ. Zool.*, 42:341-400.
- GEORGE, U. 1969. Über das Tränken der Jungen und andere Lebensäusserungen des Senegal-Flughuhns, *Pterocles senegallus*, in Marokko. *J. Ornithol.*, 110:181-191.
- GOODWIN, D. 1964. Observations on the Dark Firefinch, with some comparisons with Jameson's Firefinch. *Avicult. Mag.*, 70:80-105.
- GOODWIN, D. 1965. A comparative study of captive Blue Waxbills (Estrildidae). *Ibis*, 107:285-315.
- HARRISON, C. J. O. 1962. Observations on Rufous-chinned Jay-thrushes (*Garrulax rufogularis*). *Avicult. Mag.*, 68:188-197.

- JOHNSTON, R. F. 1960. Behavior of the Inca Dove. *Condor*, 62:7-24.
- KILHAM, L. 1968. Reproductive behavior of White-breasted Nuthatches. I. Distraction display, bill-sweeping, and nest hole defense. *Auk*, 85:477-492.
- KLOPFER, P. H., AND J. P. HAILMAN. 1967. An introduction to animal behavior. Prentice-Hall, Englewood Cliffs, New Jersey.
- LANCASTER, D. A. 1964a. Life history of the Boucard Tinamou in British Honduras. Part I: Distribution and general behavior. *Condor*, 66:165-181.
- LANCASTER, D. A. 1964b. Biology of the Brushland Tinamou, *Nothoprocta cinerascens*. *Bull. Amer. Mus. Nat. Hist.*, 127:269-314.
- LINSDALE, J. M. 1937. The natural history of magpies. *Pacific Coast Avif.*, 25.
- MACLEAN, G. L. 1967. Die systematische Stellung der Flughühner (Pteroclididae). *J. Ornithol.*, 108:203-217.
- PARKES, K. C. 1957. The juvenal plumage of the finch genera *Atlapetes* and *Pipilo*. *Auk*, 74:499-502.
- RAND, A. L., AND E. T. GILLIARD. 1968. Handbook of New Guinea birds. Natural History Press, Garden City, New York.
- SCHWARTZ, P. 1964. The Northern Waterthrush in Venezuela. *Living Bird*, 3:169-184.
- SELANDER, R. K. 1964. Speciation in wrens of the genus *Campylorhynchus*. *Univ. California Publ. Zool.*, 74:iv + 1-305.
- SKEAD, C. J. 1950. A study of the African hoopoe. *Ibis*, 92:434-461.
- SKUTCH, A. F. 1945. On the habits and nest of the ant-thrush *Formicarius analis*. *Wilson Bull.*, 57:122-128.
- SKUTCH, A. F. 1950. Life history of the White-breasted Blue Mockingbird. *Condor*, 52:220-227.
- SKUTCH, A. F. 1954. Life histories of Central American birds. *Pacific Coast Avif.*, 31.
- SKUTCH, A. F. 1960. Life histories of Central American birds. II. *Pacific Coast Avif.*, 34.
- SKUTCH, A. F. 1962. On the habits of the Queo, *Rhodinocichla rosea*. *Auk*, 79:633-639.
- SKUTCH, A. F. 1964. Life history of the Blue-diademed Motmot, *Momotus momota*. *Ibis*, 106:321-332.
- SKUTCH, A. F. 1967. Life histories of Central American highland birds. *Publ. Nuttall Ornithol. Club*, 7.
- SKUTCH, A. F. 1969. Life histories of Central American birds. III. *Pacific Coast Avif.*, 35.
- SLUD, P. 1964. The birds of Costa Rica. Distribution and ecology. *Bull. Amer. Mus. Nat. Hist.*, 128:1-430.
- SNOW, D. W. 1958. A study of blackbirds. Allen and Unwin, London.
- STEGMANN, B. 1969. Über die systematische Stellung der Tauben und Flughühner. *Zool. Jahrb. Abt. Syst. Oekol. Geogr. Tiere.*, 96:1-51.
- WILLIS, E. O. 1967. The behavior of bicolored antbirds. *Univ. California Publ. Zool.*, 79:1-132.
- ZUSI, R. L. 1969. Ecology and adaptations of the Trembler on the island of Dominica. *Living Bird*, 8:137-164.