# HOLDING FOOD WITH THE FEET IN PASSERINES

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Evolutionary affinities of families, genera, and species remain undetermined in numerous cases within the Order Passeriformes. Although behavior is undoubtedly useful in clarifying evolutionary relationships (Ficken and Ficken, 1966), application of many behavioral features suffers from the lack of comprehensive surveys. I review here one such feature, the use of the feet in manipulating food. Although Finn (1922) and Wickler (1961) have partially summarized this behavior, here for brevity termed "holding," the present survey is the first comprehensive one for passerines. A subsidiary goal is to provide a behavioral summary useful in interpreting species differences in foot scutellation (Clark, 1972).

For several years I have watched holding by both wild and captive passerines. In addition, I have examined hundreds of publications, but undoubtedly have missed some records. Furthermore, I have omitted numerous references duplicating information given in the cited sources. My nomenclature follows Wetmore (1960) for families and Peters' "Check-list of Birds of the World" for most lower taxa.

## VARIATIONS IN HOLDING

*Occurrence.*—Records for the presence or absence of holding are available for more than 145 species (Table 1). Negative findings are difficult to interpret, for holding might occur rarely in some of

TABLE 1. Presence (+) and absence (−) of holding in passerines.

Dendrocolaptidae: *Dendrocincla fuliginosa* (−; Willis, 1967), *Dendrocolaptes certhia* (−; Willis, 1967); Furnariidae: *Automolus ochrolaemus* (+; Skutch, 1969); Formicariidae: *Gymnopithys salvini* (−; Willis, 1968), *G. lunulata* (−; Willis, 1968), *G. leucaspis* (−; Willis, 1967); Tyrannidae: *Xolmis* spp. (+; Hudson, 1920), *Empidonax* sp. (+; La Rivers, 1941), *E. difficilis* (+; Pearse *in* Bent, 1942); Hirundinidae: *Tachycineta bicolor* (−; this study); Dicruridae: *Dicrurus adsimilis* (+; Ali, 1961), *D. caerulescens* (+; Kramer, 1930), *D. paradiseus* (+; Simmons, 1963); Corvidae: *Cyanocitta cristata* (+; this study), *C. stelleri* (+; Skutch, 1967,) *Aphelocoma ultramarina* (+; Swarth, 1904; this study), *Cyanolyca pumilo* (+; Skutch, 1967: 107), *Cyanocorax cyanomelas* (+; Wetmore, 1926), *Psilorhinus morio* (+; Skutch, 1960), *Calocitta formosa* (+; captive bird; this study), *Perisoreus canadensis* (+; Ouellet, 1970), *Pica nuttallii* (+; Linsdale, 1937), *Nucifraga caryocatactes* (+; Witherby et al., 1943), *Corvus frugilegus* (+; captive, bird, this study), *C. brachyrhynchos* (+; Bent, 1946), *C. corone* (+; Finn, 1922), *Corvus* sp. (+; captive raven; this study), *C. albicollis* (+; captive bird; this study); Cracticidae: *Gymnorhina tibicen* (+; Kramer, 1930); Grallinidae: *Corcorax melanorhamphus* (+; Hobbs, 1971); Ptilonorhynchidae: *Chalamydera* sp. (−; Kramer, 1930); Paradisaeidae: *Seleucidis melanoleuca* (+; Rand and Gilliard, 1967), *Diphyllodes magnificus* (+; Simmons, 1963), other species (+; Kramer, 1930); Paridae: *Aegithalos caudatus* (+; Simmons, 1963), *Remiz pendulinus* (+; Hampel, 1966), *Anthoscopus minutus* (+; Skead, 1959), *Auriparus flaviceps* (+; Taylor, 1971), *Parus lugubris* (+; Löhrl, 1966), *P. atricapillus* (+; Brewer, 1963; this study), *P. carolinensis* (+; Brewer, 1963), *P. gambeli* (+; this study), *P. wollweberi* (+; this study), *P. ater* (+; Vince, 1964), *P. afer* (+; Rowan, 1967b), *P. niger* (+; Steyn, 1966), *P. major* (+; Vince, 1964), *P. caeruleus* (+; Vince, 1964), *P. inornatus* (+; Root, 1967), *P. bicolor* (+; this study); Sittidae: *Sitta* spp. (−; Norris, 1958); Chamaeidae: *Chamaea fasciata* (+; Erickson, 1938);

Timaliidae: *Pomatorhinus schisticeps* (+; Kramer, 1930), *Chrysomma sinense* (+; Kramer, 1930), *Turdoides affinis* (+; Ali and Ripley, 1971), *Garrulax albogularis* (+; Kramer, 1930), *G. leucolophus* (+; Kramer, 1930), *G. striatus* (+; Kramer, 1930), *G. canorus* (+; Kramer, 1930), *Leiothrix lutea* (+; Kramer, 1930), *Minla* sp. (+; Simmons, 1963), *Heterophasia* sp. (+; Simmons, 1963), *Panurus biarmicus* (+; Koenig, 1952); Mimidae: *Toxostoma rediviyum* (+; this study); Sylviidae: *Polioptila caerulea* (−; Root, 1967); Muscicapidae: *Monarcha melanopsis* (+; Harrison, 1969), *Rhipidura fuliginosa* (+; Harrison, 1969), *R. leucophrys* (+; Harrison, 1969); Artamidae: *Artamus leucorhynchus* (+; Immelmann 1966), *A. cinereus* (+; Immelmann, 1966); Laniidae: *Lanius collurio* (+; Ash, 1970; Ullrich, 1971), *L. minor* (+; Ullrich, 1971), *L. ludovicianus* (+; Miller, 1931), *L. excubitor* (+; Cade, 1967; Ullrich, 1971); *L. collaris* (+; Cooper, 1971), *L. senator* (+; Ullrich, 1971); Cyclarhidae: *Cyclarhis gujanensis* (+; Skutch, 1967: 124); Vireolaniidae: *Vireolanius melitophrys* (+; Skutch, 1967: 124); Callaeidae: *Heteralocha acutirostris* (+; Buller cited in Phillipps, 1963); Sturnidae: *Sturnus vulgaris* (−; this study); Meliphagidae: *Myzantha* sp. (+; Finn, 1922); Vireonidae: *Vireo griseus* (+; Nolan, 1960; Nolan and Wooldridge, 1962; Williamson, 1971), *V. bellii* (+; Nolan, 1960), *V. solitarius* (+; Skutch *in* Bent, 1950); Parulidae: *Icteria virens* (+; N. Smith cited in Ficken and Ficken, 1962), other species (−; Ficken and Ficken, 1962); Ploceidae: Estrildinae: *Spermophaga haematina* (+; Harrison, 1966), *Lagonosticta rufopicta* (−; Harrison, 1956), *L. senegala* (−; Harrison, 1962), *L. rubricata* (−; Harrison, 1962), *Uraeginthus angolensis* (−; Goodwin, 1959), *U. granatina* (−; Harrison, 1962), *Estrilda caerulescens* (+; Harrison, 1962), *E. troglodytes* (+; Harrison, 1962), *E. astrild* (+; Immelmann and Immelmann, 1967), *E. nonnula* (+; Goodwin, 1963), *Amandava amandava* (−; Harrison, 1962), *Aegintha temporalis* (−; Harrison, 1962), *Emblema oculata* (+; Immelmann, 1965), *Poephila guttata* (−; Immelmann, 1965), *Lonchura malabarica* (+; Immelmann and Immelmann, 1967), *L. cucullata* (+; Immelmann and Immelmann, 1967), *L. castaneothorax* (+; Immelmann, 1965); Passerinae: *Passer domesticus* (±; Kunkel, 1961; Summers-Smith, 1963), *P. luteus* (−; Kunkel, 1961); Icteridae: *Cacicus holosericeus* (+; Skutch, 1967), *Icterus* spp. (+; Skutch, 1967), *I. galbula* (+; Wellman, 1928), *Dives dives* (+; Skutch, 1954), *Quiscalus mexicanus* (+; this study), *Q. major* (+; Snyder and Snyder, 1969), *Q. quiscula* (+; Roberts, 1932; this study), *Euphagus cyanocephalus* (+; La Rivers, 1941), *Molothrus ater* (+: Brackbill *in* Bent, 1958); Thraupidae: *Habia cristata* (−; Willis, 1966); Fringillidae: Cardinalinae: *Cardinalis cardinalis* (−; this study), *Passerina amoena* (+; Miller, 1939); Fringillinae: *Fringilla coelebs* (±; Marler, 1956; Kear, 1962), *F. montifringilla* (−; Newton, 1967); Carduelinae: *Serinus* spp. (+; Kear, 1962; Kunkel, 1966), *Carduelis chloris* (+; Newton, 1967), *C. spinus* (+; Newton, 1967), *C. pinus* (+; this study), *C. tristis* (+; Coutlee, 1963; this study), *C. carduelis* (+; Newton, 1967), *Acanthis flammea* (+; Newton, 1967), *A. flavirostris* (−; Kear, 1962), *A. cannabina* (+; Newton, 1967), *Carpodacus purpureus* (−; this study), *C. mexicanus* (−; this study), *Loxia curvirostra* (+; Newton, 1967), *L. leucoptera* (+; Allen *in* Bent, 1968), *Pyrrhula pyrrhula* (−; Newton, 1967), *Coccothraustes coccothraustes* (−; Newton, 1967), *C. vespertinus* (−; this study); Emberizinae: *Emberiza citrinella* (−; Kear, 1962), *Zonotrichia* (= *Melospiza*) *melodia* (−; this study), *Junco hyemalis* (−; this study), *Spizella arborea* (−; this study), *S. passerina* (−; this study), *S. pusilla* (−; this study), *Geospiza fortis* (+; Bowman, 1961), *Camarhynchus psittacula* (+; Bowman, 1961), *C. parvulus* (+; Bowman, 1961), *C. pallidus* (+; Millikan and Bowman, 1967), *C. heliobates* (+; Curio and Kramer, 1964), *Certhidea olivacea* (+; Bowman, 1961).

these species but not have been seen. I have accepted negative records only for species that have been watched extensively. Positive records might also be deceptive because individual variation might occur. For example, in the House Sparrow (*Passer domesticus*; Kunkel, 1961; Summers-Smith, 1963: 37) and the Chaffinch (*Fringilla coelebs*; Marler, 1956; Kear, 1962), occasional individuals hold food with a foot, but such behavior is atypical. For many species only scattered observations are available. For example, I once saw a California Thrasher (*Toxostoma reduvivum*)

holding an unidentified food item against the ground with one foot, but additional observations are necessary to determine whether such behavior is typical.

I exclude one special kind of behavior from the category of "holding." Nelson J. Moore (pers. comm.) has watched Mexican Juncos (*Junco phaeonotus*) obtain seeds by landing on the middle portion of a bent stem. The junco then sidles along the stem, pushing it closer to the ground, until finally the bill can reach the seeds. Although the feet aid in obtaining this food, this behavior seemingly requires less dexterity than most actions ordinarily termed "holding."

For those species that do hold food, certain variations that might conceivably be of systematic significance are emphasized in the following discussion. As many published descriptions of holding are incomplete, a full characterization of this behavior is not possible for many species.

*Two feet versus one.*—Certain Corvidae and Paridae often hold with both feet as certain other taxa do occasionally (e.g., *Chamaea* [Erickson, 1938], *Lanius* [Ash, 1970], *Quiscalus* [Snyder and Snyder, 1969], *Loxia* [Newton, 1967]). This behavior is taxonomically less widespread than the use of one foot. Apparently all species that can hold with both feet at once might also hold with a single foot. Hardness and size of food might determine in part whether it is held by one or both feet. A secure grip with both feet presumably aids in stabilizing large items or in pounding or tearing hard objects. Holding small items with both feet apparently requires greater dexterity than the use of a single foot.

*Attached versus detached food.*—Food that is held might be either free or attached to a plant. Many birds momentarily perch on one leg while reaching out with the other foot to pull a food-bearing stem or twig closer; examples are the Verdin (*Auriparus*; Taylor, 1971), *Panurus* (Koenig, 1952), some icterids (*Icterus* [Wellman, 1928]; *Molothrus* [Brackbill *in* Bent, 1958: 443]), and certain estrildine, cardinaline, and carduelinе finches (Immelmann, 1965; Immelmann and Immelmann, 1967; Kear, 1962; Kunkel, 1966, Miller, 1939). At least the Verdins (Taylor, 1971) and certain carduelines (Kear, 1962; Kunkel, 1966) can also hold detached food. Newton (1967) noted that Red Crossbills (*Loxia curvirostra*) feed on large cones attached to the tree but carry small cones to a perch to extract the seeds. Newton commented that pulling a resisting stem might require a stronger grasp than does the holding of detached items. However, manipulating small detached objects might require greater skill in coordinating bill and feet.

*Clamping versus grasping.*—Birds might clamp food against a perch or substrate or, alternatively, grasp the food in a foot held off the perch in a parrot-like fashion. Birds that grasp include *Dicrurus* (Kramer, 1930; Simmons, 1963), *Remiz* (Hampel, 1966), some Timaliidae (Simmons, 1963), *Artamus* (Immelmann, 1966), and *Lanius* (Miller, 1931). *Remiz* (Löhrl in an appendix to Hampel,

1966), the timaliids, and at least one species of *Lanius* (Ash, 1970) can also clamp, as do most passerine species that hold food with a foot.

*Frequency of holding.*—Miller (1931) commented that individual Loggerhead Shrikes (*Lanius ludovicianus*) differ in the extent of holding. Differences between relatively closely related species in amount of holding are reported for shrikes and cardueline finches. Ullrich (1971) found holding to be more common in *Lanius excubitor* than in three other congeneric species. Kunkel (1966) reported that holding is better developed in *Serinus citrellinoides* than in other closely related carduelines. Newton (1967) noted that, among those European carduelines known to hold food with a foot, holding is less frequent in Greenfinches (*Carduelis chloris*).

*Footedness.*—For Red Crossbills Newton (1967) noted a correlation between use of the right or left foot in holding detached cones and the direction of crossing of the mandibles. If the lower mandible turns to the right, the right foot usually holds the cone, and vice versa.

Vince (1964) reported that individuals of three species of *Parus* exhibited footedness, i.e., a tendency to use predominantly the right or left foot in clamping mealworms. Footedness also occurs in grasping by parrots (Smith, 1972).

*Approach of the bill with respect to the foot.*—In Pine Siskins (*Carduelis pinus*) and American Goldfinches (*C. tristis*) at a feeding station I have noted variations in the manipulation of sunflower seeds or fragments thereof. Frequently in these birds the approach of the bill to a seed held with the foot is on the lateral side of the foot, in contrast to the medial approach typical for corvids (*Corvidae*), titmice (*Parus*), and grackles (*Quiscalus*). However, at least some individuals of *C. pinus* and *C. tristis* use a medial approach. Possibly individual *Carduelis* use both medial and lateral approaches, but observations on individually recognizable birds will be necessary to confirm this suggestion.

*Holding in flight.*—Crows (*Corvus*; Bent, 1946), Gray Jays (*Perisoreus*; Ouellet, 1970), and certain shrikes (*Lanius*; Ash, 1970; Cade, 1967) regularly carry objects in the feet while flying. A captive Wren-tit (*Chamaea*) also once flew with food in its feet, but this was exceptional (Erickson, 1938).

## ONTOGENY OF HOLDING

Vince (1964) observed that imperfect use of the feet in manipulating food begins at 17 days after hatching in *Parus major* and *P. caerulescens*. Cooper (1971) reported that captive *Lanius collaris* first held mealworms with a foot during the sixth week after hatching. Ullrich (1971) found that holding tends to develop earlier in ontogeny in *L. senator* than in *L. excubitor*.

Vince's extensive experiments on titmice (*Parus*) indicate that holding is partially inherited but perfected through learning; juveniles prevented from manipulating objects with their feet

during early development are capable of holding items imperfectly as soon as given suitable items (Vince, 1964). Hybridization studies on cardueline finches (Hinde, 1956) also indicate genetic inheritance of holding. *Carduelis carduelis* frequently uses the feet in holding; *Serinus canarius* sometimes does; but *Carduelis chloris* does so relatively rarely. Crosses of *C. carduelis* with either of the other two species often held food with their feet, but none of the hybrids between *Serinus* and *C. chloris* regularly did so.

Where the occurrence of holding is individually variable, as in the House Sparrow and Chaffinch, learning is apparently of great importance in the ontogeny of holding. Learning apparently also contributes significantly when captive birds (e.g., *Parus*) develop the ability to use their feet to pull up a string bearing food at the lower end (Thorpe, 1963; Millikan and Bowman, 1967). Similar behavior might occur in wild birds as in the case of a Tufted Titmouse (*P. bicolor*) using its feet to pull up a caterpillar hanging on a thread (Dickinson, 1969).

## EVOLUTION OF HOLDING

Holding potentially extends the range of possible foods by enabling consumption of items too hard or too large to be handled by the bill alone. Even for items edible by the bill alone, holding might increase efficiency in feeding. Hypothetically holding might evolve where it results in consuming food more rapidly or at less energetic cost. Conversely, holding, if inefficient, might secondarily be lost during evolution. Selection should favor individuals with more efficient behavior, and such behavior might become increasingly genetically determined. However, the sequence of behavioral changes in the evolutionary gain or loss of holding is unknown in any actual case.

A variety of hypothetical initial stages of evolutionary changes leading to holding are conceivable. Birds that accidentally stand on food, whether on the ground or arboreally, might represent an initial stage; use of the bill in moving such food might lead to regular holding of food. Alternatively, use of the feet developed in connection with manipulation of nest materials might lead to food holding. As still another possibility, while standing with each foot on adjacent perches, a bird might pull one of these closer with one foot and thereby obtain food more efficiently. A hypothetical sequence leading to grasping would originate with the use of the foot in scratching to dislodge food items from the bill, as occurs in shrikes (Miller, 1931). More extensive studies of variation in holding within a species (e.g., the House Sparrow or the Chaffinch) or between closely related species (e.g., in shrikes, estrildines, or carduelines) might suggest the kinds of evolutionary sequence most likely in the origin or loss of holding in particular groups.

Analyses of food habits and body proportions might eventually help to explain why holding occurs in some species but not in other closely related ones. For example, *Pyrrhula* and *Coccothraustes* do not hold, but some related smaller-billed carduelines do (Table 1 and Newton, 1967). Perhaps the relatively massive bills

of *Pyrrhula* and *Coccothraustes* are so efficient in food manipulation as to eliminate possible advantages in holding with a foot.

The scattered taxonomic distribution of holding (Table 1) indicates multiple evolutionary origins and/or losses for this behavior. Nonpasserines also show such convergence; holding occurs in representatives of many taxa including the following: Falconiformes, Megapodiidae (Finn, 1922), Rallidae (Finn, 1922; Wickler, 1968), Columbidae (Gifford, 1925), Psittacidae (Brereton, Watters, and Pidgeon, 1967; Smith, 1971), Cuculidae (Finn, 1922), Strigiformes, Coliidae (Rowan, 1967a), Trogonidae (Skutch, 1971). Among nonpasserines, as in passerines, the details of holding vary taxonomically.

The repeated convergences in holding plus its relative simplicity limit its usefulness as a systematic character in cases of unresolved relationships between passerine families. In general, holding is probably a derived, rather than ancestral, character in view of its relative rarity among avian taxa. The details of holding vary taxonomically, and more intensive study of these differences might enable further systematic applications, particularly below the family level.

Holding has already been used as a systematic character in several cases. Mayr and Amadon (1951) noted the superficial resemblance and similarities of food holding between some jays (e.g., *Perisoreus*) and titmice (*Parus*); however, the internal anatomy and less conspicuous features of external structure differ considerably. They also concluded that holding in this case has no phylogenetic significance, i.e., the similarities are convergent. For the western North American Wren-tit (*Chamaea*), holding is one of the traits suggesting affinity with the Old World Timaliidae (Simmons, 1963). Harrison (1969) has proposed that holding might be useful for characterizing the Monarchini and Rhipidurini among the Old World flycatchers (Muscicapidae). Harrison (1962) has also applied holding as a systematic character delimiting the genus *Estrilda* in the Estrildinae.

Holding might prove useful in the systematics of other groups. Among the Paridae apparently holding by bushtits (*Psaltriparus*) is unknown; conceivably the occurrence of holding might be systematically significant within the family. The carduelines vary considerably in holding, and the differences here also might be systematically useful. Among the Emberizinae at least six species of Galápagos Finches hold, but this behavior is apparently thus far unrecorded for any mainland species. However, in the emberizines as in many other passerine taxa, knowledge of comparative behavior is still extremely scant.

## SUMMARY

Holding of food with the feet occurs in representatives of more than 20 passerine families. Variable features in holding include the use of one versus two feet, the nature of the food, the details of the way in which the food is held, and the frequency of holding. This behavior is probably usually inherited with its perfection dependent

on learning, but in a few species in which the occurrence of holding is individually variable, its development apparently depends substantially on learning. Despite repeated convergent or parallel evolution in holding within passerines, this behavior might be potentially useful as a systematic character in Timaliidae, Muscicapidae, Estrildinae, and perhaps other taxa.

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LITERATURE CITED

Ali, S. 1961. The book of Indian birds. 6th ed. Bombay, Bombay Nat. Hist. Soc.
Ali, S., and S. D. Ripley. 1971. Handbook of the birds of India and Pakistan. Vol. 6. Bombay, Oxford Univ. Press.
Ash, J. 1970. Observations on a decreasing population of Red-backed Shrikes. *Brit. Birds.*, **63:** 185-205.
Bent, A. C. 1942. Life histories of North American flycatchers, larks, swallows, and their allies. *U. S. Natl. Mus., Bull.*, 179.
— 1946. Life histories of North American jays, crows, and titmice. *U. S. Natl. Mus., Bull.*, 191.
— 1950. Life histories of North American wagtails, shrikes, vireos, and their allies. *U. S. Natl. Mus., Bull.*, 197.
— 1958. Life histories of North American blackbirds, orioles, tanagers, and allies. *U. S. Natl. Mus., Bull.*, 211.
— 1968. Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows and allies. Order Passeriformes: family Fringillidae. (O. L Austin, Jr , ed.) *U. S. Natl. Mus., Bull.*, 237, Pt. 1.
Bowman, R. I. 1961. Morphological differentiation and adaptation in the Galápagos Finches. *Univ. Calif. Publ. Zool.*, **58:** *vii* + 326p.
Brereton, J. L., P. Watters, and R. Pidgeon. 1967. Behavioural characters of use in the taxonomy of parrots. *Avic. Mag.*, **73:** 77-78.
Brewer, R. 1963. Ecological and reproductive relationships of Black-capped and Carolina Chickadees. *Auk*, **80:** 9-47.
Cade, T. J. 1967. Ecological and behavioral aspects of predation by the Northern Shrike. *Living Bird*, **6:** 43-86.
Clark, G. A., Jr. 1972. Passerine foot-scutes. *Auk*, **89:** 549-558.
Cooper, J. 1971. Post-nestling development in the Fiscal Shrike. *Ostrich*, **42:** 175-178.
Coutlee, E. L. 1963. Maintenance behavior of the American Goldfinch. *Wilson Bull.*, **75:** 342-357.
Curio, E., and P. Kramer. 1964. Vom Mangrovefinken (*Cactospiza heliobates* Snodgrass und Heller). *Zeits. f. Tierpsychol.*, **21:** 223-234.
Dickinson, J. C., Jr. 1969. A string-pulling Tufted Titmouse. *Auk*, **86:** 559.
Erickson, M. M. 1938. Territory, annual cycle, and numbers in a population of wren-tits (Chamaea fasciata). *Univ. Calif. Publ. Zool.*, **42:** 247-334.
Ficken, M. S., and R. W. Ficken. 1962. Some aberrant characters of the Yellow-breasted Chat, *Icteria virens*. *Auk*, **79:** 718-719.
Ficken, R. W., and M. S. Ficken. 1966. A review of some aspects of avian field ethology. *Auk*, **83:** 637-661.
Finn, F. 1922. Bird behaviour. London, Hutchinson.
Gifford, E. W. 1925. The Gray-hooded Quail Dove (*Gallicolumba rubescens*) of the Marquesas Islands, in captivity. *Auk*, **42:** 388-396.
Goodwin, D. 1959. Observations on Blue-breasted Waxbills. *Avic. Mag.*, **65:** 149-169.
— 1963. Some notes on Black-capped Waxbills. *Avic. Mag.*, **69:** 149-157.
Hampel, F. 1966. Überwinterung und Verhaltensweisen der Beutelmeise (*Remiz pendulinus*) am Seeburger See. *J. f. Ornithol.*, **107:** 359.

HARRISON, C. J. O. 1956. Some fire-finches and their behavior. *Avic. Mag.*, **62:** 128-141.
—— 1962. An ethological comparison of some waxbills (Estrildini), and its relevance to their taxonomy. *Proc. Zool. Soc. London*, **139:** 261-282.
—— 1966. Some notes on the behaviour of the Red-breasted Blue-bill (*Spermophaga haematina*). *Avic. Mag.*, **72:** 16-17.
—— 1969. A behavioural character of the monarchine and fantail flycatchers. *Ostrich*, **40:** 26.
HINDE, R. A. 1956. The behaviour of certain cardueline $F_1$ interspecies hybrids. *Behaviour*, **9:** 202-213.
HOBBS, J. N. 1971. Use of tools by the White-winged Chough. *Emu*, **71:** 84-85.
HUDSON, W. H. 1920. Birds of La Plata. Vol. 1. London, Dent.
IMMELMANN, K. 1965. Australian finches in bush and aviary. Sydney, Angus & Robertson.
—— 1966. Beobachtungen an Schwalbenstaren. *J. f. Ornithol.*, **107:** 37-69.
IMMELMANN, K., and G. IMMELMANN. 1967. Verhaltensökologische Studien an afrikanischen und australischen Estrildiden. *Zool. Jahrb., Syst.*, **94:** 609-686.
KEAR, J. 1962. Food selection in finches with special reference to interspecific differences. *Proc. Zool. Soc. London*, **138:** 163-204.
KOENIG, O. 1952. Ökologie und Verhalten der Vögel des Neusiedlersee-Schilfgürtels. *J. f. Ornithol.*, **93:** 207-289.
KRAMER, G. 1930. Bewegungsstudien an Vögeln des Berliner Zoologischen Gartens. *J. f. Ornithol.*, **78:** 257-268.
KUNKEL, P. 1961. Allgemeines und soziales Verhalten des Braunrückengoldsperlings (*Passer* [*Auripasser*] *luteus* Licht.). *Zeits. f. Tierpsychol.*, **18:** 471-489.
—— 1966. Beiträge zur Biologie und Ethologie einiger zentralafrikanischer Girlitze. 1. "*Serinus*" *citrinelloides* Rüppell. *J. f. Ornithol.*, **107:** 257-277.
LA RIVERS, I. 1941. The Mormon cricket as food for birds. *Condor*, **43:** 65-69.
LINSDALE, J. M. 1937. The natural history of magpies. *Pacific Coast Avifauna*, 25.
LÖHRL, H. 1966. Zur Biologie der Trauermeise (*Parus lugubris*) (Mit Bemerkungen über die Untergattung *Poecile*). *J. f. Ornithol.*, **107:** 167-186.
MARLER, P. 1956. Behaviour of the Chaffinch *Fringilla coelebs*. *Behaviour, Suppl.* 5.
MAYR, E., and D. AMADON. 1951. A classification of recent birds. *Amer. Mus. Novit.*, 1496.
MILLER, A. H. 1931. Systematic revision and natural history of the American shrikes (Lanius). *Univ. Calif. Publ. Zool.*, **38:** 11-242.
—— 1939. Foraging dexterity of a Lazuli Bunting. *Condor*, **41:** 255-256.
MILLIKAN, G. C., and R. I. BOWMAN. 1967. Observations on Galápagos tool-using finches in captivity. *Living Bird*, **6:** 23-41.
NEWTON, I. 1967. The adaptive radiation and feeding ecology of some British finches. *Ibis.*, **109:** 33-98.
NOLAN, V., JR. 1960. Breeding behavior of the Bell Vireo in southern Indiana. *Condor*, **62:** 225-244.
NOLAN, V., JR., and D. P. WOOLDRIDGE. 1962. Food habits and feeding behavior of the White-eyed Vireo. *Wilson Bull.*, **74:** 68-73.
NORRIS, R. A. 1958. Comparative biosystematics and life history of the nuthatches Sitta pygmaea and Sitta pusilla. *Univ. Calif. Publ. Zool.*, **56:** 119-300.
OUELLET, H. 1970. Further observations on the food and predatory habits of the Gray Jay. *Can. J. Zool.*, **48:** 327-330.
PHILLIPPS, W. J. 1963. The book of the Huia. Christchurch, New Zealand, Whitcombe and Tombs.
RAND, A. L., and E. T. GILLIARD. 1967. Handbook of New Guinea birds. London, Weidenfeld and Nicolson.
ROBERTS, T. S. 1932. The birds of Minnesota. Vol. II. Minneapolis, Univ. of Minnesota Press.
ROOT, R. B. 1967. The niche exploitation pattern of the Blue-gray Gnatcatcher. *Ecol. Monogr.*, **37:** 317-350.
ROWAN, M. K. 1967a. A study of the colies of southern Africa. *Ostrich*, **38:** 63-115.
—— 1967b. Paridae: use of feet in feeding. *Ostrich*, **38:** 158.
SIMMONS, K. E. L. 1963. Some behaviour characters of the babblers (Timaliidae). *Avic. Mag.*, **69:** 183-193.

SKEAD, C. J. 1959. A study of the Cape Penduline Tit Anthoscopus minutus minutus (Shaw & Nodder). *Ostrich, Suppl.*, **3:** 274-288.
SKUTCH, A. F. 1954. Life histories of Central American birds. *Pacific Coast Avifauna*, 31.
—— 1960. Life histories of Central American birds. II. *Pacific Coast Avifauna*, 34.
—— 1967. Life histories of Central American highland birds. *Publ. Nuttall Ornithol. Club*, 7.
—— 1969. Life histories of Central American birds. III. *Pacific Coast Avifauna*, 35.
—— 1971. Life history of the Keel-billed Toucan. *Auk*, **88:** 381-424.
SMITH, G. A. 1971. The use of the foot in feeding, with especial reference to parrots. *Avic. Mag.*, **77:** 93-100.
—— 1972. "Handedness" in parrots. *Ibis*, **114:** 109-110.
SNYDER, N. F. R., and H. A. SNYDER. 1969. A comparative study of mollusc predation by Limpkins, Everglade Kites, and Boat-tailed Grackles. *Living Bird*, **8:** 177-223.
STEYN, P. 1966. Black Tit *Parus niger* Vieillot holding food with feet. *Ostrich*, **37:** 233.
SUMMERS-SMITH, D. 1963. The house sparrow. London, Collins.
SWARTH, H. S. 1904. Birds of the Huachuca Mountains, Arizona. *Pacific Coast Avifauna*, 4.
TAYLOR, W. K. 1971. A breeding biology study of the Verdin Auriparus flaviceps (Sundevall) in Arizona. *Amer. Midl. Nat.*, **85:** 289-328.
THORPE, W. H. 1963. Learning and instinct in animals. 2nd ed. London, Methuen.
ULLRICH, B. 1971. Untersuchungen zur Ethologie und Ökologie des Rotkopfwürgers (*Lanius senator*) in Südwestdeutschland im Vergleich zu Raubwürger (*L. excubitor*), Schwarzstirnwürger (*L. minor*) und Neuntöter (*L. collurio*). *Vogelwarte*, **26:** 1-77.
VINCE, M. A. 1964. Use of the feet in feeding by the Great Tit *Parus major*. *Ibis*, **106:** 508:529.
WELLMAN, G. B. 1928. Baltimore Orioles feeding on larvae of needle miner. *Auk*, **45:** 507.
WETMORE, A. 1926. Observations on the birds of Argentina, Paraguay, Uruguay, and Chile. *U. S. Natl. Mus., Bull.*, **133.**
—— 1960. A classification for the birds of the world. *Smithson. Misc. Coll.*, **139** (11): 1-37.
WICKLER, W. 1961. Über die Stammesgeschichte und den taxonomische Wert. einiger Verhaltensweisen der Vögel. *Zeits. f. Tierpsychol.*, **18:** 320-342.
—— 1968. Über den Fussgebrauch des Purpurhuhns (*Porphyrio*). *J. f. Ornithol.*, **109:** 446-449.
WILLIAMSON, P. 1971. Feeding ecology of the Red-eyed Vireo (*Vireo olivaceus*) and associated foliage-gleaning birds. *Ecol. Monogr.*, **41:** 129-152.
WILLIS, E. O. 1966. Ecology and behavior of the Crested Ant-tanager. *Condor*, **68:** 56-71.
—— 1967. The behavior of bicolored antbirds. *Univ. Calif. Publ. Zool.*, **79:** 1-127.
—— 1968. Studies of the behavior of Lunulated and Salvin's Antbirds. *Condor*, **70:** 128-148.
WITHERBY, H. F., F. C. R. JOURDAIN, N. F. TICEHURST, and B. W TUCKER. 1943. The handbook of British birds. Vol. 1. London, Witherby.

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