

ADDITIONAL RECORDS OF PASSERINE TERRESTRIAL GAITS

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The varied methods of locomotion in birds pose significant problems in behavior, ecology, adaptation, and evolution. On the ground birds progress with their legs moving either synchronously (hopping) or asynchronously (walking, running) as the extreme conditions. Relatively terrestrial species often have asynchronous gaits, whereas primarily arboreal species are typically synchronous on the ground. Particularly important earlier studies on passerines are Kunkel's (1962) comparative behavioral survey and Rüggeberg's (1960) analysis of the morphological correlates of gaits. Over several years I have noted gaits for 47 passerine species in the U.S., England, and Kenya, and have examined many references. I here summarize behavioral records for families not mentioned by Kunkel (1962) and also for species with gaits markedly unlike those of confamilial species discussed by him. My supplementary review is selective rather than exhaustive with the aim of indicating more fully the distribution of gaits among the passerine families. Regional handbooks, life history studies, and other publications contain numerous additional records, but I know of none that negate the conclusions presented here. J. S. Greenlaw (in prep.) has reviewed elsewhere the passerine double-scratch foraging behavior that has at times previously been discussed in connection with gaits (e.g., in Hailman 1973).

VARIATION WITHIN SPECIES

Gaits often vary within a species (Kunkel 1962, Hailman 1973, Schwartz 1964, Gobeil 1968, Eliot *in* Bent 1968:669-670, this study). As an additional example, I have seen Common Grackles (*Quiscalus quiscula*) hop in contrast to their usual walk. Such intraspecific variation is possibly related to both substrate and speed of locomotion (Hailman 1973), but further studies will be necessary to clarify the possible relationships.

Ontogenetic changes can result in intraspecific variation in gaits (Nice 1943, Kunkel 1962). Recent records are summarized in Table 1. Some species change little, if at all, ontogenetically as I have noted for the House Sparrow (*Passer domesticus*) in which both fledglings and adults hop. Another source of variation within species is difference between foraging and display gaits (see, for example, Delius 1969, Miller 1951, Rowley 1962, Schwartz 1964). Injuries or malformations also contribute to intraspecific

TABLE I
EXAMPLES OF ONTOGENETIC CHANGES IN GAIT

| Species | Juvenile gait | Adult gait | Reference |
|----------------------------------|---------------|------------|------------------------------------|
| <i>Gymnorhinus cyanocephalus</i> | hop | walk | Ligon 1974 |
| <i>Mimus polyglottos</i> | hop | walk | Horwich 1969 |
| <i>Cossypha natalensis</i> | step and hop | hop | Farkas 1969 |
| <i>Oenanthe oenanthe</i> | walk | hop | N. Smith in Ficken and Ficken 1966 |

variation. As examples, I have seen Starlings (*Sturnus vulgaris*), a Red-winged Blackbird (*Agelaius phoeniceus*), Common Grackle, and Dark-eyed Junco (*Junco hyemalis*) jump along on only one functioning leg; the first 3 of these typically walk. In addition, Nickell (1965) observed such jumping by a one-legged American Robin (*Turdus migratorius*). As Short (1971) noted, birds with a capability for asynchronous leg movements and a concomitant ability to balance on one leg appear more likely to survive if a leg is lost or injured than do birds that hop and cannot balance on one leg.

Observation and reporting of gaits can contribute artifactual variation. Details are not easily seen for rapid movements. Description is particularly difficult for gaits intermediate between walking and hopping as seen in the Philippine Glossy Starling (*Aplonis panayensis*, Restall 1969) and the African White-browed Sparrow Weaver (*Plocepasser mahali*, this study). Finally, caution should be used regarding published reports, for Harrison (1969) mentions that some authors have used "running" as a synonym for "moving rapidly" without implying an asynchronous gait.

VARIATION AMONG SPECIES

Despite variation within species and the lack of detail in many reports, existing data indicate major differences among certain taxa.

Furnariidae.—Walking or running apparently typify the Furnariinae (*Geositta*, *Upucerthia*, *Eremobius*, *Cinclodes*, *Furnarius*; Wetmore 1926, Feduccia 1970). In contrast, Buff-throated Foliage-gleaners (*Automolus ochrolaemus*) of the more arboreal Philydorinae hop over the ground (Skutch 1969a). In the Synallaxinae the Slaty Spinetail (*Synallaxis brachyura*, Skutch 1969a) and Rufous-fronted Thornbird (*Phacelodopus rufifrons*, Skutch 1969b) hop, but Wetmore (1926) reported walking or

running for canasteros (*Asthenes dorbignyi*, *A. patagonica*) and Lark-like Brush-runners (*Coryphistera alaudina*). Sharp-tailed Streamcreepers (*Lochmias nematura*) of the subfamily Sclerurinae walk (Mitchell 1957), whereas leafscrapers (*Sclerurus*) hop (Skutch 1969a) or run (Slud 1964).

Formicariidae.—Members of this family hop except for the walking of the terrestrial anthruses (*Formicarius*; Skutch 1969a, Slud 1964, Wetmore 1926, Willis 1967, 1969).

Cotingidae.—I have seen a caged Andean Cock-of-the-rock (*Rupicola peruviana*) hopping.

Pipridae.—Skutch (1969a) reported a Blue-crowned Manakin (*Pipra coronata*) hopping on boards off the ground.

Tyrannidae.—Asynchronous gaits occur commonly in the genera *Corythopis*, *Agriornis*, *Xolmis*, *Muscisaxicola*, *Lessonia*, *Muscigralla*, *Myiotheretes*, *Hymenops*, *Fluicola*, *Machetornis*, and *Serpophaga* (Haverschmidt 1968, Wetmore 1926, Short and Morony 1969, Hudson 1920, Smith 1971a, b). At least Negrito Flycatchers (*Lessonia rufa*, Wetmore 1926) and ground tyrants (*Muscisaxicola*, Smith 1971a) both hop and run. More arboreal flycatchers such as kingbirds (*Tyrannus* spp., Youngworth 1937) and Vermillion-crowned Flycatchers (*Myiozetetes similis*, Skutch 1960) hop occasionally when on the ground.

Dicruridae.—I have seen the African drongo *Dicrurus adsimilis* hop.

Corvidae.—Kunkel (1962) did not mention the walking characteristic of the adult Piñon Jay (*Gymnorhinus cyanocephalus*, Ligon 1974).

Craetidae.—Within this heterogeneous family the walking of the Australian Magpie (*Gymnorhina tibicen*, Kramer cited in Kunkel 1962) contrasts with the hopping of the Pied Currawong (*Strepera graculina*, Frith 1969).

Grallinidae.—Torrent Larks (*Grallina bruijni*) walk (Diamond 1972) unlike the hopping of Apostlebirds (*Struthidea cinerea*, Austin 1967).

Timaliidae.—In the subfamily Orthonychinae, Spine-tailed Logrunners (*Orthonyx temminckii*) and 2 species of Scrub-robins (*Ptilorrhoa*) have asynchronous gaits (Rand and Gilliard 1968, Diamond 1972), whereas Lesser Melampittas (*Melampitta lugubris*) hop (Rand and Gilliard 1968).

Numerous species of the subfamily Timaliinae hop (Kunkel 1962), but Black-capped Babblers (*Pellorneum capistratum*, Smythies 1968) and Gray-crowned Babblers (*Pomatostomus temporalis*, Frith 1969) have asynchronous gaits.

Campephagidae.—Ali and Ripley (1971) report hopping by Black-headed Cuckoo-shrikes (*Coracina melanoptera*). In contrast, Ground Cuckoo-shrikes (*Pteropodocys maxima*) run (Serventy and Whittell 1962).

Muscicapidae.—The running gait of Silverbirds (*Empidonis semipartitus*, Mackworth-Praed and Grant 1960) is apparently unusual for this family.

Laniidae.—Unlike other shrikes, Bush-shrikes (*Tchagra*) run over the ground (G. G. Olivier in Thomson 1964:735).

Parulidae.—Kunkel (1962) cited the typically asynchronous gaits of *Seiurus* (cf. Schwartz 1964), but probably many New World warblers hop when on the ground, as seen by me for the Yellow-rumped Warbler (*Dendroica coronata*) and by Ficken (1962) for redstarts (*Setophaga ruticilla*).

Icteridae.—Contrary to Kunkel (1962), orioles (*Icterus*) probably typically hop when on the ground as both Youngworth (1937) and I have observed for the Northern Oriole (*I. g. galbula*).

DISCUSSION

Kunkel (1962) reported conspicuous differences in gait (predominantly synchronous versus mainly asynchronous) between species within the Corvidae, Turdidae, Sylviidae, Sturnidae, Ploceidae, Icteridae, Carduelinae, and Emberizinae. From my review 11 other families or subfamilies may be added to his list: Furnariidae, Formicariidae, Tyrannidae, Cisticolidae, Grallinidae, Orthonychinae, Timaliinae, Campephagidae, Muscicapidae, Laniidae, and Parulidae. Thus at least 19 higher taxa of passerines reportedly contain both species with chiefly asynchronous gaits and species that are mainly synchronous. The presence of 2 alternative species-specific phenotypes in each of these higher taxa indicates considerable evolutionary convergence in gaits (Clark 1973).

I know of no simple measurements that will enable predictions of gait from structure alone. Species with similar gaits but belonging to different families sometimes differ considerably in structure of the pelvic appendage, e.g., in relative leg length or limb proportions (Rüggeberg 1960).

Marked variation in terrestrial gaits within a species and within individuals raises the possibility that differences in gaits among species might not be due to inherited specifications for behavior per se. However, the structural differences associated with species differences in gaits (Rüggeberg 1960) are likely to be inherited and could influence the relative frequency of gaits. An analogous situation occurs in foraging in which inherited structure can facilitate eating certain foods, but birds, being behaviorally somewhat flexible, often can use unusual foods.

SUMMARY

Extremes in avian terrestrial gaits are hopping (synchronous leg movements) as opposed to walking or running (asynchronous). This review summarizes newer records for gaits of passerine families and subfamilies. At least 19 of these higher taxa include both species that are largely synchronous and species that are chiefly asynchronous. Variation within many species indicates that gait behavior per se might not be directly inherited. Presumably inherited structural differences between species contribute to the ontogenetic development of taxonomic differences in gait.

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