

TAXONOMIC DIFFERENCES IN HEAD MOVEMENTS OF VOCALIZING PASSERINES

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An improved understanding of evolutionary relationships among the many passerine taxa is likely to depend in part on the recognition of additional systematic characters of all kinds, structural, behavioral, and molecular. Undoubtedly many characters exhibit evolutionary convergence (Clark, 1973b), but by using larger numbers of diverse characters systematists may be able to avoid the interpretative pitfalls posed by convergences in individual characters. Comparative studies of behavior may be expected to be a fruitful source of additional systematic characters as indicated by numerous previous studies (see, for examples, Barlow, 1972; Cullen, 1959; Ficken and Ficken, 1966; Hinde, 1970; Johnsgard, 1960).

Despite the considerable attention that has been given to avian vocalizations, head movements of vocalizing birds have been relatively neglected. On the possibility that such movements might constitute systematic characters, I have noted their occurrence in passerines. The present report summarizes my observations and reviews the literature. Although much additional investigation will be necessary to provide a comprehensive treatment of the subject, I present my findings here in the hope of stimulating others to record pertinent data.

METHODS

During spring and summer over several years I observed singing or calling by wild birds perched or standing but not close to conspecific individuals. The following categories and details summarize my results.

RAISING THE BILL COINCIDENT WITH VOCALIZATION

Many passerine species frequently raise the bill at the start of singing and lower the bill at or near the end. I have seen this behavior in the Willow Flycatcher (*Empidonax traillii*), Alder Flycatcher (*E. alnorum*), Wood Pewee (*Contopus virens*), Blue-winged Warbler (*Vermivora pinus*), Nashville Warbler (*V. ruficapilla*), Yellow Warbler (*Dendroica petechia*), Chestnut-sided Warbler (*D. pensylvanica*), Prairie Warbler (*D. discolor*), Ovenbird (*Seiurus aurocapillus*), Northern Waterthrush (*S. noveboracensis*), Common Yellowthroat (*Geothlypis trichas*), American Redstart (*Setophaga ruticilla*; see also Ficken, 1962), Eastern Meadowlark (*Sturnella magna*), Scarlet Tanager (*Piranga olivacea*), Rose-breasted Grosbeak (*Pheucticus ludovicianus*), Indigo Bunting (*Passerina cyanea*; see also Thompson, 1972), Rufous-sided Towhee (*Pipilo erythrophthalmus*), Savannah Sparrow (*Passerculus sandwichensis*), Chipping Sparrow (*Spizella passerina*), Clay-colored Sparrow (*S. pallida*; see also Root in Bent, 1968), Field Sparrow

(*S. pusilla*; see also Allen in Bent, 1968), and Song Sparrow (*Melospiza melodia*). Raising of the bill coincident with calling or singing is also reported for the Eastern Phoebe (*Sayornis phoebe*; Bent, 1942), Swainson's Warbler (*Limnothlypis swainsonii*; Meanley, 1968), Green-tailed Towhee (*Chlorura chlorura*; Barnes in Bent, 1968), and Seaside Sparrow (*Ammospiza maritima*; Trost in Bent, 1968; Post and Greenlaw, 1975). Other records of possibly similar behavior are for the antbird *Phacellodomus rufifrons* (Skutch, 1969), the cotingid *Lipaugus cinerascens* (Snow, 1961), and the tyrannid *Pseudocolaptes (= Myiosympotes) flaviventris* (Wetmore, 1926). The Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) is unusual in raising the bill upward and backward over the left shoulder during song (Orians and Christman, 1968).

At least some of the species exhibiting a raised bill during vocalizations can also vocalize without a noticeable lifting of the bill as I have seen for the singing Common Yellowthroat, Eastern Meadowlark, Scarlet Tanager, Rose-breasted Grosbeak, Rufous-sided Towhee, and Chipping Sparrow. Meanley (1968) noted that the Swainson's Warbler does not tilt its head upward for whisper or subsongs in contrast to the upward movement for primary songs. Thompson (1972) reported that the backward tilt of the head during song is less pronounced in foraging than in nonforaging Indigo Buntings. The degree of tilting during vocalization may also vary taxonomically. For example, I have not yet seen singing Chipping Sparrows tilt the bill as far upward as the congeneric Field and Clay-colored sparrows sometimes do.

In contrast are species in which raising of the bill coincident with calls or songs is apparently either absent or occurs significantly less frequently. Two apparent examples of such species for which I have repeatedly observed singing are the Gray Catbird (*Dumetella carolinensis*) and American Robin (*Turdus migratorius*). The latter commonly perches with the bill tilted slightly above the horizontal, but I have detected no further raising when singing begins. Other species for which in limited observations I have thus far failed to detect raising of the bill coincident with vocalizations are the Black-capped Chickadee (*Parus atricapillus*), Tufted Titmouse (*P. bicolor*), White-breasted Nuthatch (*Sitta carolinensis*), Brown Creeper (*Certhia familiaris*), House Wren (*Troglodytes aedon*), Brown Thrasher (*Toxostoma rufum*), Curve-billed Thrasher (*T. curvirostre*), Wood Thrush (*Hylocichla mustelina*), Eastern Bluebird (*Sialia sialis*), White-eyed Vireo (*Vireo griseus*), Red-eyed Vireo (*V. olivaceus*), Warbling Vireo (*V. gilvus*), House Sparrow (*Passer domesticus*), Red-winged Blackbird (*Agelaius phoeniceus*; see also Orians and Christman, 1968), Purple Finch (*Carpodacus purpureus*), and American Goldfinch (*Spinus tristis*). Certain of these species do sing at times with the bill tilted upwards (e.g., in vireos), but I have not detected a special raising coincident with song. The Brown Creeper can sing on a tree trunk while body and bill are oriented vertically, but I have detected no shift in head angle at the start of singing. In my limited observations, Northern Orioles (*Icterus galbula*) extend the neck coincident with song, thus raising

the head higher and forward, but do not raise the bill upward. A similar movement during song is reported for the Green-backed Sparrow (*Arremonops conirostris*; Moynihan, 1963). Another emberizine that does not raise the bill for song is the Lark Bunting (*Calamospiza melanocorys*; Keyser cited by Baumgarten in Bent, 1968).

Anderson and Anderson (1957) report that the Cactus Wren (*Campylorhynchus brunneicapillus*) elevates its bill only slightly above the horizontal while singing; they also state that most published drawings of the species singing depict the bill far too close to the vertical. According to Bent (1948), Leconte's Thrasher (*Toxostoma lecontei*) sings with the head thrown back, but I have not yet noted this for either Brown or Curve-billed thrashers. Further observations are needed for nearly all species that I have failed to see raise the bill coincident with vocalizations. For most of these species my lack of records might be due to either insufficient observations or failure to detect slight upward movements of the bill. However, the extensive study of Orians and Christman (1968) indicates a genuine absence of bill-raising coincident with song in the Tricolored (*Agelaius tricolor*) and Red-winged blackbirds.

OTHER HEAD MOVEMENTS

My primary interest has been to determine the taxonomic occurrence of raising of the bill coincident with vocalizations, but I have also noted other head movements. In singing passerines the mandibles are commonly opened, and the lower mandible and throat often move noticeably. In many if not all species the head may turn laterally from side to side during vocalizations. Such side-to-side head turning in a relatively horizontal plane is common also in silent passerines when perched either on or off the ground, as I have noted for 53 passerine species representing 18 families of Wetmore (1960).

DISCUSSION

Potential systematic significance. In my observations, species raising the bill coincident with vocalization represent the taxa Tyrannidae (3 species), Parulidae (9), Icteridae (1), Thraupidae (1), Cardinalinae (2), and Emberizinae (6), but I have failed so far in limited observations to detect such behavior in other species of the Paridae (2), Sittidae (1), Certhiidae (1), Troglodytidae (1), Mimidae (3), Turdidae (3), Vireonidae (3), Ploceidae (1), Icteridae (2), and Carduelinae (2). However, certain species for which I have failed to see bill-raising coincident with vocalization may in fact exhibit such behavior, and much more observation will be necessary to determine more fully the taxonomic distribution and details of the behavior. Nevertheless, certain tentative conclusions may be offered. Certain groups of species generally considered to be relatively closely related, e.g., in the Parulidae and in the Emberizinae, share the feature of bill-raising coincident with song. This suggests that variation in the feature might in some cases

serve as a systematic character. However, caution should be used in systematic interpretations, for the apparent taxonomic distribution of this behavior also indicates at least some evolutionary convergence. The bill-raising coincident with vocalization has presumably either originated or been lost more than once independently as judged by (1) its occurrence in certain tyrannids and distantly related oscines and (2) apparent variation within the Icteridae. Despite the likely convergences, further data on the taxonomic distribution and details of this behavior might provide additional evidence for evolutionary relationships among certain species or genera of passerines.

A major complication is that many, perhaps all, species raising the bill coincident with vocalizations can also sing without bill-raising. I lack detailed data concerning the conditions associated with such bill-raising, but in the United States this behavior is commonly seen in singing males during the reproductive period of spring and summer.

Negative records, i.e., failure to see bill-raising coincident with vocalization, must be viewed skeptically unless based on many hours of observation throughout the breeding season. In view of the time required for verifying the lack of bill-raising coincident with vocalization in any species, the presence or absence of this attribute probably cannot soon be used broadly as a systematic character. Equivalent difficulties arise in the case of many other potential behavioral characters that are either present or absent, e. g., holding food with the feet (Clark, 1973a) and double-scratch foraging behavior (Clark, 1970; J. S. Greenlaw, in prep.). If extended study of a single species fails to reveal a particular kind of behavior that is readily seen in another species, then we may assume at least a quantitative difference between the species in the frequency of the behavior. Such differences may be potentially useful in systematics.

Functional hypotheses. Raising the bill coincident with vocalization presumably requires energy that might be saved by vocalizing without raising the head. Therefore, assuming selection favoring energetic efficiency, raising of the bill presumably serves some useful function(s). Possibly bill-raising changes the characteristics of the vocalization such as loudness, but I know of no direct evidence supporting this hypothesis.

As another possible function raising of the bill for vocalization might be a visual signal. In watching Willow and Alder flycatchers I have been impressed by the conspicuous flash of the yellow lower mandible as the singing birds raise their bills; conceivably such movements could convey information to other birds. Bill-up postures are common in a variety of passerine displays associated with courtship and reproductive fighting (Andrew, 1961) and undoubtedly there serve in signaling.

Other head movements during vocalizations are perhaps related to the nature of the vocalizations, e. g., opening of the mandibles and movements of the lower mandible and throat. In view of the taxonomic specificity of many vocalizations, head movements

affecting sound production might also exhibit taxonomic differences, but I know of no actual examples. Side-to-side turning of the head occurs in both silent and vocalizing birds and presumably serves at least in watching for potential food items, predators, and conspecific individuals.

SUMMARY

New observations of 41 passerine species reveal possible taxonomic differences in the occurrence of raising of the bill coincident with vocalizations. Such conspicuous bill-raising occurs in certain species in the Tyrannidae, Parulidae, Icteridae, Thraupidae, Cardinalinae, and Emberizinae, but is apparently absent in certain other icterids and emberizines and perhaps in numerous other taxa. Closely related taxa among the parulids and among the emberizines share the bill-raising, and this behavior might constitute a useful systematic character, but many additional data are needed. The apparently scattered taxonomic distribution of bill-raising coincident with vocalization indicates that convergent evolutionary gain or loss of the behavior may have occurred at least occasionally. Raising of the bill might serve to modify the vocalization and/or as a visual display.

Other head movements, not known to vary taxonomically, are discussed briefly.

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