ORAL FLANGES OF JUVENILE BIRDS

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IN the pre- and posthatching development of birds a number of structural features are present for only a relatively short time. Such traits, particularly prominent externally, may have significance in aging birds, as taxonomic characters, and as subjects for the study of adaptation. Examples of transitory structures which have recently been studied are natal plumages (cf. Clark, 1964) and egg teeth (Parkes and Clark, 1964).

In this paper I review the occurrence, variations, and possible taxonomic significance of the transitory enlarged flanges of the bill bordering the mouth in juveniles of nidicolous birds. This inquiry was undertaken to determine whether or not the marked differences in form of flanges might be of taxonomic significance. A summary of this topic is believed of potential value, particularly to call attention to the many major gaps in available information.

A problem in studying transitory characteristics is obtaining a suitable series of developmental stages of living juveniles or preserved specimens. Many of the available records for flanges are based unfortunately on study of only one or a few stages, not necessarily those most informative. Interpretations based on samples covering only a limited range of ages should be made cautiously as illustrated below in the discussion of flanges in the Mockingbird (*Mimus polyglottos*).

SOURCES OF DATA

Selected specimens were examined in the collections of the United States National Museum (Washington, D. C.), the American Museum of Natural History (New York), and the University of Connecticut (Storrs). In addition, a number of live juveniles have been observed, and a few of these photographed. Furthermore, numerous books and journal articles were checked for information on flanges. No attempt has been made, however, to cite all references mentioning or figuring flanges.

GENERAL COMMENTS

At least two rather distinct kinds of enlarged flanges are known to occur in juveniles. In the form found in woodpeckers and wrynecks, the major enlargement of the flanges is primarily on the lower jaw instead of being distributed around the corner of the gape as in passerines (see Fig. 1). In both woodpeckers and passerines, the flange is probably detectable before hatching, reaches its maximal relative development during early posthatching growth, and then regresses during the latter part of the nestling period. Presence of a flange is thus generally indicative of a young bird, although adult birds of a relatively few species have various kinds

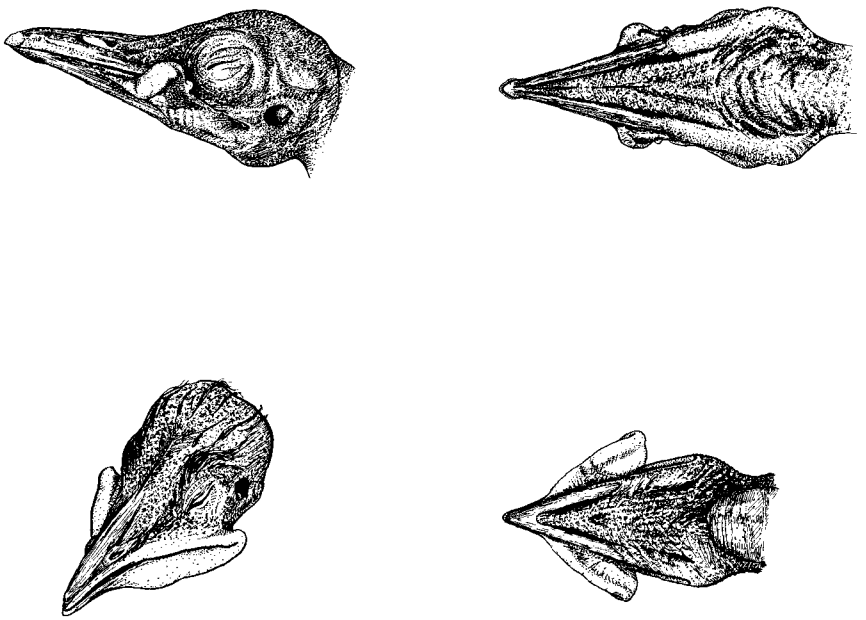

FIG. 1. Juvenile oral flanges of a flicker (*Colaptes* sp.; top) and a Starling (*Sturnus vulgaris*; bottom.)

of flaps along the gape (see Wackernagel, 1954, for some examples, and also the discussion below under Callaeidae).

The structural difference between the passerine and woodpecker flanges is perhaps correlated with a functional difference. Blume (1961) has noted for the Black Woodpecker (*Dryocopus martius*) that the stimulus for the young juvenile to accept regurgitated food is the parental touching of the bill pad or flange. Kilham (1962:131) mentioned for young Downy Woodpeckers (*Dendrocopos pubescens*) that "one method of feeding these nestlings was to approach from the side, brushing the fleshy knob at the base of the bill with a bit of food impaled on a toothpick. The young would open their bills and swallow the food readily." However, as pointed out by Schifter (1967), Hoyt (1944) observed that begging occurs in very young Pileated Woodpeckers (*Dryocopus pileatus*) without tactile stimulation. Possibly these apparently contradictory findings can be resolved by considering tactile stimulation as only one of the means by which young woodpeckers may be induced to open their bills. It is possible that the flanges of woodpeckers do have greater tactile sensitivity than those of passerines, for Dewar (1908) found that touching the flanges of a six-day old Sky

Lark (*Alauda arvensis*) elicited no response. Similarly I noted that rubbing the flanges with a plant stem failed to produce gaping in two Traill's Flycatchers (*Empidonax traillii*) held in my hand on their second or third day after hatching.

Wackernagel (1954) studied the histology of both woodpecker and passerine flanges and found, in general, a relatively low concentration of sensory Herbst corpuscles. He suggested that any differences in sensitivities should be based on differences in the finer nerve endings which have not yet been critically studied. As Wackernagel pointed out, definitive conclusions on the function of flanges must await experimental evidence. Statements attributing great tactile sensitivity to passerine flanges (cf. Welty, 1962: captions of Figs. 17.9 and 17.21) are at best questionable in the absence of experimental evidence.

In another kind of functional interpretation Dewar (1908) proposed that the passerine flanges help to keep food from slipping outside the nestling's mouth during feeding by an adult.

More common has been the suggestion that the lightly colored flanges serve as outlines of the opened juvenile mouth to guide the adult in feeding young (Butler, 1916; Swynnerton, 1916; Wackernagel, 1954; Armstrong, 1965). This idea is supported by the tendency for hole-nesting species to develop relatively larger flanges, as Ingram (1907) and Wackernagel (1954) have found for European passerines and as is apparently also the case for North American species (see below). To the human observer looking into a darkened nest hole, such as that of the Tree Swallow (*Iridoprocne bicolor*), the juvenile flanges may appear as one of the most conspicuous objects. By analogy, an adult bird moving rapidly from the bright exterior into the darkened nest chamber without time for dark adaptation might be significantly aided in feeding the young by the bright outline of flanges.

The greatly enlarged flanges of the kind found in hole-nesting passerines can probably be considered as another example in the list of special adaptations often associated with hole-nesting in birds (von Haartman, 1957). It appears probable that there has been much convergent evolution in the development of flanges, but present information is too limited to determine which similarities of different taxa are due to convergence.

SYSTEMATIC ACCOUNT

The ordinal and familial classification followed here is that of Wetmore (1960). There are apparently no records of conspicuously developed oral flanges in orders Sphenisciformes through Psittaciformes of Wetmore's checklist; however, juveniles of a number of species included within these orders do show a fold of skin at the corner of the mouth, perhaps homologous

to the oral flanges of passerines. I have observed such folds on juveniles of the genera *Ciconia, Buteo, Circus, Falco, Actitis,* and *Rynchops* (see also Wackernagel, 1954, on *Vanellus*).

Detailed data on nestlings are needed especially for Psittacidae, Trochilidae, Trogonidae, Momotidae, Bucerotidae, Galbulidae, Bucconidae, Capitonidae, and Ramphastidae.

Cuculidae.—Murphy and Amadon (1953: Fig. 41) published a photograph which may be interpreted as showing a slight degree of flange enlargement in juvenile *Coccyzus americanus.* The presence of passerine-like flanges in *Cuculus micropterus* is indicated by the lower photograph in Plate 1 of Neufeldt (1966).

Strigidae.—On a downy *Otus asio,* I noted a weakly developed fold about the base of the mouth opening. There is no evidence known to me for special enlargement of flanges in this family.

Steatornithidae.—Ingram (1958) reported no conspicuous enlargement of the gape in *Steatornis* nestlings.

Apodidae.—I have seen moderately developed flanges on a study skin of juvenile *Apus apus.* Moreau (1942) and Wetherbee (1961*a*) have noted the absence of such flanges at hatching in *Micropus* (*Apus*) *caffer* and *Chaetura pelagica* respectively. Flanges probably occur on older specimens, for these appear to be shown in a photograph of juvenile *Chaetura pelagica* published by Fischer (1958: Fig. 19).

Coliidae.—Schifter (1967) has studied in detail the external development of three species of this family. In *Colius macrourus* and *C. indicus* he found flanges which at least superficially resemble those of woodpeckers; however, the enlargements on the lower mandible are, as he noted, longer and less spherical in outline in the colies. It is curious that such enlargements of the lower mandible do not occur in *C. striatus* (Schifter, 1967).

Todidae.—No flanges were detected by me on three young specimens of *Todus subulatus.* This family needs additional study.

Meropidae.—Witherby et al. (1938:265) have reported that the flanges of juvenile *Merops apiaster* are very small and inconspicuous.

Coraciidae.—Wackernagel (1954) has reported that flanges generally resembling those of passerines occur in *Coracius garrulus* and this interpretation is well supported by photographs published by von Frisch (1966:46).

Upupidae.—Witherby et al. (1938:268) stated for juvenile *Upupa epops* that the flanges are large, thick, and conspicuous. Wackernagel (1954) has noted in addition that these flanges are structurally like those of passerines.

Indicatoridae.—There is little available information on the status of flanges in honeyguides. I noted a weakly developed fold on very young *Indicator indicator.* Friedmann (1955:209–210) cited Ranger to the effect that in *I. minor* there is some enlargement of the colored corners of the gape from the 26th to the 35th days posthatching and that this enlargement is absent at hatching.

Schifter (1967) has apparently interpreted the photographs in Friedmann (1955) as showing that honeyguides have woodpecker-like flanges; however, in these published photographs I have been unable to convince myself that Schifter's interpretation is necessarily correct.

Picidae.—This family, containing the woodpeckers and wrynecks, is the only one placed by Wetmore (1960) in his suborder Pici. As already noted, the woodpeckers

TABLE 1

SOME RECORDS OF ORAL FLANGES OF PICIDAE

Species	Sources of record
Jynx torquilla	Barruel, 1954:133 (photographs).
Colaptes auratus	Brewster, 1893; Burns cited by Bent, 1939:276; Wetherbee and Wetherbee, 1961.
Chrysoptilus melanochloros	This study.
Picus viridis	Witherby et al., 1938:280, after Gurney; Blume, 1961.
Picus canus	Wackernagel, 1954.
Dryocopus martius	Blume, 1961.
Dryocopus pileatus	Hoyt, 1944:377, 380.
Centurus carolinus	Kilham, 1961.
Dendrocopos major	Blume, 1961.
Dendrocopos villosus	Bendire cited by Bent, 1939:16.
Dendrocopos pubescens	Kilham, 1962.
Picoides tridactylus	This study.
Picoides arcticus	Bates cited by Forbush, 1927:272.

and wrynecks have an unusual form of mouth flange thus far unreported for any other group except possibly the colies. It would be of great interest to know definitely whether this kind of bill "knob" occurs in any additional groups outside the suborder Pici.

Figure 1 illustrates the condition of this flange in *Colaptes* sp. Table 1 presents a list of woodpecker species for which a similar flange has been reported or illustrated. In general, it appears that the flange of woodpeckers is much reduced by the time the young leave the nest as observed by me for *Colaptes auratus* and reported in the literature for *Picoides arcticus* (Forbush, 1927:272, after Bates) and *Dryocopus pileatus* (Hoyt, 1944).

Wetherbee and Wetherbee (1961:148) observed the form of the bill flange in *Colaptes auratus* and suggested that the presence of maximal enlargement of the flange on the lower jaw might be developmentally associated with the prognathus condition of the lower jaw. However, protruding lower mandibles have also been reported for newly hatched young of a number of other avian families (kingfishers, jacamars, toucans, barbets, hoopoes; cf. Skutch, 1944*a*, *b*; Skead, 1950) for which there is no report of a woodpecker-like flange. Indeed, Hoopoes (*Upupa*) are reported to have a passerine-like flange (Wackernagel, 1954).

Passeriformes.—Table 2 lists those passerine species for which I have seen flanges. These represent 17 of the 70 passerine families listed by Wetmore (1960). In addition, there are numerous literature reports and illustrations indicating the presence of these flanges in other species and families (cf. Swynnerton, 1916; Wackernagel, 1954). It appears likely that flanges occur throughout the passerines; any exception to this generalization would be quite unexpected.

Ficken (1965) surveyed the color of the mouth linings and found inter-

TABLE 2

PASSERINE SPECIES FOR WHICH THE AUTHOR HAS SEEN FLANGES ON LIVING (*) OR PRESERVED SPECIMENS

Tyrannidae
Muscivora forficata
Sayornis phoebe *
Empidonax traillii *

Hirundinidae
Iridoprocne bicolor *
Riparia riparia
Stelgidopteryx ruficollis
Progne subis

Corvidae
Cyanocitta cristata *
Corvus corax
Corvus brachyrhynchos
Corvus ossifragus

Grallinidae
Corcorax melanorhamphus *

Paridae
Parus atricristatus

Cinclidae
Cinclus mexicanus

Troglodytidae
Troglodytes aedon *
Telmatodytes palustris

Mimidae
Dumetella carolinensis
Toxostoma rufum

Turdidae
Turdus migratorius *
Hylocichla mustelina
Sialia sialis

Muscicapidae
Colluricincla harmonica
Myiagra freycineti
Panurus biarmicus

Bombycillidae
Bombycilla cedrorum

Sturnidae
Sturnus vulgaris *

Vireonidae
Vireo olivaceus
Vireo gilvus

Parulidae
Limnothlypis swainsonii
Vermivora sp.
Dendroica petechia
Seiurus motacilla
Wilsonia canadensis

Ploceidae
Passer domesticus

Icteridae
Sturnella neglecta
Agelaius phoeniceus *
Icterus galbula

Fringillidae
Pheucticus ludovicianus
Pipilo erythrophthalmus
Spizella passerina *

esting correlations with commonly recognized taxonomic groupings in the passerines. It is perhaps significant that, according to Ficken's data, yellow mouth linings occur in those families which are commonly hole or cavity nesters, e.g., Hirundinidae, Paridae, Certhiidae, Cinclidae, Troglodytidae, and Sturnidae. Presumably a yellow mouth lining would appear brighter than a red one in a darkened cavity. In addition, it may be noted that at least two species of hole-nesting Sittidae, not listed by Ficken, also have yellow mouth linings (Norris, 1958:227).

Variations in the color of the passerine flanges are not reviewed in detail here, but, in general, the flanges have a light color, often yellow, white, or cream-colored. However, in *Prunella modularis* the flanges are pink (Romanoff, 1960). In those groups having young with red mouth linings, there is apparently typically a marked contrast between the lighter flange color and the interior of the mouth as seen, for example, in nestling Red-winged Blackbirds (*Agelaius phoeniceus*).

In many passerines the degree of maximal development of the flanges appears to be, at least qualitatively, related more to nest site than to taxonomic position. On the basis of present information it appears that degree of temporary enlargement of flanges will not be especially useful in the classification of passerine families.

The following comments are restricted to those families containing species with especially marked development of the flanges or for which unusually detailed observations have been reported in the literature.

Corvidae.—Ingram (1920:864 and Fig. 10) reported that *Corvus monedula*, the only British corvid which nests in holes, has flanges which are relatively larger than those of other British corvids.

Paridae.—Wackernagel (1954) has presented measurements for the growth and regression of the flanges in nestling *Parus major*.

Sittidae.—Norris (1958:226–227, 230, 291) reported that nestlings of *Sitta pygmaea* have broader and more conspicuous flanges than do the young of the similar species *S. pusilla*. This difference was presumed to be adaptive in association with the deeper and darker nest cavities of *S. pygmaea*. This case, like that reported by Schifter (1967) for colies, is particularly interesting in illustrating a substantial divergence in the early phases of ontogeny of species which are rather similar as adults.

Mimidae.—Wetherbee (1961*b*) observed that the newly hatched Mockingbird (*Mimus polyglottos*) has flanges as large as those of the newly hatched Starling (*Sturnus vulgaris*). Partly on this basis he argued against the generalization that hole-nesting birds tend to have relatively larger flanges. However, relative size of flanges at hatching apparently does not indicate the maximal degree of development, for the illustrations of Horwich (1966) indicate that maximal relative size of flanges in Mockingbirds is far less than that in the Starling (see below).

Turdidae.—Wackernagel (1954) published measurements covering flange development in *Turdus merula*.

Sylviidae.—Wackernagel (1954) has also reported measurements for young *Acrocephalus scirpaceus* in which the flanges attain maximal relative development about six days after hatching.

Callaeidae.—Falla (in Thomson, 1964:877) reported that wattles of adults of species in this family develop from a fold of skin at the base of the nestling's gape.

Sturnidae.—Figure 1 shows a very extensive development of flanges reached in the juvenile Starling (*Sturnus vulgaris*). Wackernagel (1954) and Hudec and Folk (1961) have given details on the flanges of this species. Maximal development occurs about eight days posthatching according to Wackernagel. By the 20th day posthatching regression of the flange is virtually complete. Hudec and Folk have noted the possible functional correlations between the opening of the eyes at 7–8 days after hatching and

the beginning of regression in size of the flanges at the ninth day after hatching.

Although the flange of the lower mandible in *Sturnus* is somewhat broader than the upper, as noted by Wackernagel, the appearance is not at all like that of woodpeckers.

Ploceidae.—This rather heterogeneous family contains the estrildines and viduines, members of which are unique among known birds in having transitory globules with light-reflecting properties at the corners of the nestling gape (Friedmann, 1960). The viduines are brood-parasitic on the estrildines, and there has been controversy over the extent to which similarities, including those of the reflective globules, between viduines and certain estrildines are the result of evolutionary affinity as opposed to convergent evolution (cf. Delacour, 1943; Steiner, 1960; Friedmann, 1960, 1962; Nicolai, 1964). Nicolai (p. 134) reported considerable intraspecific variation in timing of final loss of the gape and mouth markings in Estrildinae and Viduinae. If this situation occurs in other passerine families, the value of flanges as precise aging characters will be minimal.

SUMMARY

The occurrence and variations of the oral flanges in nestlings of nidicolous birds are reviewed. The taxonomic significance of these flanges remains generally unknown for apodiform, coliiform, trogoniform, coraciiform, and piciform birds. As hole-nesting passerines tend to have relatively larger flanges at maximal development than do open-nesters, the degree of enlargement of the flanges in juvenile passerines generally appears to be correlated more closely with nest site than with taxonomic position.

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