MOUTH COLOR OF NESTLING PASSERINES AND ITS USE IN TAXONOMY

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MOUTH color has received little attention as a taxonomic character although tongue and palatal markings of nestlings have proved useful in determining relationships in the estrildines (Delacour, 1943; Steiner, 1960). I use the term mouth color in the restricted sense and exclude the flanges, mandibles, tongue, or associated structures which may also be brightly colored or patterned in nestlings. Recently Skutch (1954, 1960) has shown that mouth colors of nestling passerines are conservative, often delimiting families. However, his descriptions of the mouth color of the young of certain Central American parulids (Skutch, 1954) differed from my observations on North American species. This led me to review the distribution of mouth colors in nestling passerines, to assess their function and the probable selective pressures affecting them, and finally to evaluate their use in taxonomy. Since relatively little published information on mouth colors is available, I hope that this brief survey will stimulate the acquisition of additional information.

There are several problems encountered in comparing descriptions of mouth color by different workers. First, the exact age of the birds at the time of examination is not always stated, although this may be important because of changes which take place. For example, the mouths of newly hatched Tree Pipits (*Anthus trivialis*) are deep orange, turning crimson at 4 days (Ticehurst, 1910). In many species the color of the nestling differs from that of the adult. A second problem is the lack of standardization of color terminology, and where specimens were used, this is further complicated because of the rapid fading which takes place after death. Despite these variables, the mouth colors of almost all nestling passerines are either red or yellow, although in one group (corvids) they are described as "mauve" or "reddish purple" and in others (Witherby et al., 1938) as being "pinkish-orange" or "orange-yellow."

Wetherbee (1961) studied the mouth colors of many North American neonatal birds hatched in incubators and suggested that mouth coloration is due to at least three different factors: (1): "a horny yellow covering sheathing the bones of the bill" giving yellow color to young wrens, titmice, starlings, swallows, flycatchers, and thrushes; (2) "a transitory red or orange coloring of the epidermis by pigments from the yolk, probably carotinoids." For example, the Red-winged Blackbird (*Agelaius phoeniceus*) and Rose-breasted Grosbeak (*Pheucticus ludovicianus*) feed on phytophagous insects rich in carotenoids and since xanthophyll is selectively deposited in the egg, the food of the

parents probably determines the color of the nestlings' mouths; (3) differences in the extent of capillary vascularization. According to Wetherbee, this is responsible for the red coloration of the mouths of sparrows. There is certainly a need for further investigation of the biochemical and physiological factors underlying mouth color in young birds. Wetherbee's conclusion concerning the effect of diet on pigments of the young is questionable because many insectivorous species have young with red linings, others with yellow (Table 1).

The bright mouth linings of the young serve to direct and stimulate feeding by the adult, and conspicuousness is thus to be expected (Armstrong, 1947). The type of nest may be correlated with mouth lining color in some cases, since elaborate and conspicuous markings and globular projections are found in and around the mouths of young of certain species which nest in cavities or have covered nests (Ticehurst, 1910; Swynnerton, 1916). Another interesting adaptation occurs in parasitic cuckoos. The mouth-lining colors of cuckoos which eject nestmates do not resemble the hosts' mouth colors but in cases where the cuckoo young do not eject the young they are similar. Moreover, the mouth lining of the young cuckoo is yellow for the first few days, resembling the colors of the most common host species and then gradually changes to red in 9 days (Armstrong, 1947). Another brood parasite, the Brown-headed Cowbird (*Molothrus ater*), resembles nonparasitic icterids in having a red mouth lining. However, 15 of the 50 most commonly parasitized species (Friedmann, 1963) have yellow mouth linings, and there is no evidence that fewer young cowbirds are raised successfully by these hosts. The higher incidence of parasitism of species with red mouth linings probably reflects their numerical preponderance in North America.

Although most passerine mouth linings are various shades of red or yellow, the linings of adults include, in addition, black, white, and bright green (Armstrong, 1947). Particularly distinctive colors are often associated with opening of the mouth during displays, especially those involved in courtship, such as courtship feeding, and to a lesser degree, threat. For example, those birds of paradise which open their bills during their elaborate courtship displays have mouth linings of various shades of green or more rarely yellow or white (Armstrong, 1947). In some cases there is obviously selection for maximum contrast with the plumage, e.g., a white gullet in the Magnificent Riflebird (*Craspedophora magnifica*) and black in the Gannet (*Morus bassanus*) (Armstrong, 1947). In a few species there is sexual dimorphism, the color of the male usually being more striking (Armstrong, 1947). The greater divergence of mouth-lining color in adults of closely related species than in young is probably related to their frequent incorporation into displays involved in reproductive isolation. In the case of the young, there is evidently little if

TABLE 1
MOUTH-LINING COLORS OF NESTLING PASSERINES

		Y yellow or orange-yellow R red or pink
Tyrannidae	Y	Skutch, 1960; Wetherbee, 1961
Alaudidae	Y	Witherby et al., 1938
Hirundinidae	Y	Witherby et al., 1938; Wetherbee, 1961
Oriolidae	R	Witherby et al., 1938
Corvidae	R	Witherby et al., 1938; Skutch, 1960
Paridae	Y	Witherby et al., 1938; Wetherbee, 1961
Certhiidae	Y	Witherby, et al., 1938
Pycnonotidae	R	Swynnerton, 1916
Cinclidae	Y	Witherby et al., 1938
Troglodytidae	Y	Witherby et al., 1938; Skutch, 1960
Mimidae	Y	Engels, 1940; pers. obs.
Turdidae	Y	Witherby et al., 1938; Skutch, 1960; Wetherbee, 1961
Sylviidae	Y, R	Witherby et al., 1938; Swynnerton, 1916
Muscicapidae	Y	Witherby et al., 1938
Prunellidae	R	Gilliard, 1958
Motacillidae	Y, R	Witherby et al., 1938
Bombycillidae	R	Wetherbee, 1961
Laniidae	Y	Swynnerton, 1916; Witherby et al., 1938
Sturnidae	Y	Witherby et al., 1938; Wetherbee, 1961
Vireonidae	Y	Skutch, 1960
Coerebidae	R	Skutch, 1954; Skutch, 1962
Parulidae	R, Y	Skutch, 1954; pers. obs.
Ploceidae	R, Y	Swynnerton, 1916
Icteridae	R	Skutch, 1954
Thraupidae	R	Skutch, 1954
Fringillidae	R	Witherby et al., 1938; Skutch, 1954; Wetherbee, 1961

any selective pressure for species specificity, as would be expected if its function is primarily stimulation and orientation of the adult's feeding response. In this case any conspicuous coloration would be about equally effective.

It is apparent from the data (Table 1) that nestling mouth-lining color is usually a good family character. There are a few exceptions. Several cardueline species (but so far as is known, no other higher passerines) have two colors, e.g., red and blue in Hawfinches (*Coccothraustes coccothraustes*) and pink and yellow in Crossbills (*Loxia curvirostra*) (Witherby et al., 1938). Groups having intrafamilial variation are Sylviidae, Ploceidae, Motacillidae, and Parulidae. In the first three groups some members have open nests, others covered, and there are special adaptations such as tongue spots in some sylviids and motacillids, and even more elaborate structures in certain ploceids, indicating selection for conspicuousness.

There are no apparent adaptive reasons for the presence of red mouth linings in some parulids and yellow in others. Central American representatives of other groups (e.g., emberizines) do not differ in mouth-lining color from North American species, although the type of nest is different (domed nests being more common in tropical forms). All North American parulids examined (17 species of 8 genera) had red linings. However, certain primarily Central American species have yellow linings: Buff-rumped Warbler (*Basileuterus fulvicauda*), Black-cheeked Warbler (*B. melanogenys*), Slate-throated Redstart (*Myioborus miniatus*), and Collared Redstart (*M. torquatus*) (Skutch, pers. comm.). Mr. Eliot Porter (pers. comm.) reports that his Kodachromes of nestling Red-faced Warblers (*Cardellina rubrifrons*) and Painted Redstarts (*Setophaga picta*) show deep orange-yellow mouths which were definitely not red. Central American species with red linings include the Flame-throated Warbler (*Vermivora gutturalis*) (Skutch, pers. comm.), and judging from published Kodachromes, the Olive Warbler (*Peucedramus taeniatus*) and Pink-headed Warbler (*Ergaticus versicolor*) as well. These warblers are the only nine-primaried oscines for which information is available which have yellow mouth linings. This probably indicates that *Myioborus, Basileuterus, Cardellina rubrifrons*, and *Setophaga picta* are a closely related assemblage. They are probably not very closely related to the wood warblers and their morphological resemblances may be the result of adaptations to similar feeding habits. Parkes (1961) has suggested that *Setophaga picta* is more closely related to *Myioborus* than to the supposedly congeneric American Redstart (*Setophaga ruticilla*). This is supported by the data on nestling mouth-lining colors.

Skutch (1962) questions the validity of placing the Bananaquit (*Coereba flaveola*), which has a red mouth lining, with the wood warblers since his observations showed Central American warblers have yellow linings. Since other warblers have red linings, there is no reason to doubt the relationship of *Coereba* to the parulids on the basis of this character.

It certainly does not follow that all forms with the same mouth-lining color are closely related, especially since the number of nestling mouth-lining colors is so limited. Convergence is probable in the case of certain unrelated families (Table 1). However, yellow is probably the more primitive nestling mouth color in passerines, judging from its distribution in the various families. Mouth-lining color bears out certain proposed relationships among the various "families" of nine-primaried oscines and also the "Muscicapidae" of Mayr and Amadon (1951) (including Mimidae, Troglodytidae, Muscicapidae, Cinclidae, Turdidae, Sylviidae in Table 1).

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