GEOGRAPHICAL VARIATION IN THE NESTLING COLORATION OF PARASITIC COWBIRDS

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ABSTRACT.—Cowbird nestlings show significant geographical variation in rictal flange color. Twenty-four cowbirds from the Southwest, where the race *Molothrus ater obscurus* breeds, had yellow flanges whereas 73 from the remainder of the United States and Canada, where the races *artemisiae* and *ater* breed, had white flanges. There is little or no intralocality variation. Nestling cowbirds with yellow and white flanges apparently are accepted and fed by hosts regardless of the color of the rictal flanges of the host's own young, but I hypothesize that the quality of host care received by a nestling cowbird is influenced by its rictal flange color and that host responses are the selective pressure responsible for the geographical variation. Character displacement in nestling coloration is suggested by the fact that *M. a. obscurus* is the only race of *Molothrus ater* that has yellow flanges and it is also the only race that is sympatric with another cowbird, *Molothrus aeneus*, a species that apparently has white flanges. Character displacement could be caused by competition for host species and is further indicated by other lines of evidence. *Received 18 February 1976, accepted 19 February 1977.*

INTRASPECIFIC variation in egg appearance occurs in many parasitic birds and is most plausibly explained by the selective pressures arising from host responses to parasitic eggs (Payne 1967, Rothstein 1971, Southern 1954). In contrast, the appearance of parasitic nestlings has little known effect on the great majority of hosts (Hamilton and Orians 1965). However, variation in parasitic nestlings could imply that some aspects of the hosts exert a selective pressure on the parasite's nestlings. Indeed, the few known cases of within-taxon variation in parasitic nestlings have been explained in this manner. Lack (1968: 88–89) accounted for intraspecific variation in the juvenal plumage of a parasitic cuckoo by relating each plumage variant to different hosts. Similarly, intrageneric variation in the nestling gape of parasitic finches may represent adaption to different hosts (Payne 1967, 1973: 61). In this paper, I show that nestlings of the parasitic Brown-headed Cowbird (*Molothrus ater*) have either yellow or white rictal flanges. I also discuss the possible significance of this variation. The nestling variation is especially notable because it correlates with recognized subspecies of the cowbird and the cowbird does not show as strong variation in its eggs or adults.

RESULTS

Data on 97 cowbird nestlings and fledglings (Table 1, Fig. 1) are based on observations of live birds or analyses of colored photographs. Except for locality 5 (see below), no difficulty resulted from categorizing a cowbird's rictal flanges as white or yellow. Previous studies of passerine mouth colors also reported that most nestlings can be easily categorized as having one of a small number of colors (Ficken 1965) and my inspection of photographs of nestlings of various species (in Phillips et al. 1964, Porter 1972, and Wetmore 1964) shows most have rictal flanges easily categorized as white or yellow, although some do have yellowish-white flanges. In all cases in Table 1 for which data for the rictal flanges and tomia exist, both were the same color; in some cases data exist only for the flanges. In every case for which data exist, the inside of the mouth was red or pink; there is no evidence that this character is strongly variable.

Photographs from locality 5 show yellow flanges and tomia for three cowbirds, but the yellow appears to be lighter than that on cowbirds from localities 1–4 (Table 1). Also at locality 5, L. Baptista (pers. comm.) recorded that a cowbird in a White-crowned Sparrow (*Zonotrichia leucophrys*) nest studied in 1976 had white flanges. But Baptista believes his designation of white may have been a relative one due to the fact that sparrow nestlings, with which he was more familiar, have very bright yellow flanges. Taken together, these data show that yellow-flanged cowbirds occur at locality 5 and raise the question of whether white-flanged ones also occur.

I visited Hooded Oriole (*Icterus cucullatus*) nests at locality 1 regularly and noted no change in rictal flange color as nestling cowbirds and orioles developed. Similarly, J. M. White (pers. comm.) noted no change in flange color as cowbirds at locality 8 developed (Table 1). I reared two yellow-flanged cowbirds in captivity to determine how long they retained their flange colors. One bird, a male removed from a Brewer's Blackbird (*Euphagus cyanocephalus*) nest at locality 2, lost all traces of yellow on its flanges between 21 ± 1 and 23 ± 1 days of age. The other bird, a male removed from a Hooded Oriole nest at locality 1, still had yellow on its flanges at 62 ± 1 days of age. Both birds still had traces of yellow on their tomia when their ages were 71 ± 1 and 62 ± 1 days, respectively. When the birds were next checked, at ages of 210 ± 1 and 201 ± 1 days, no yellow was on the tomia or flanges. Based on these individuals, I estimate that the flange color of fledged cowbirds can be determined reliably for at least 1–2 weeks after the birds have left the nest. Preserved specimens appear to have little value in studying flange color. A yellow-flanged cowbird from a Hooded Oriole nest showed considerable fading of the flanges after only 4 months in formalin.

Close analysis of a cowbird from a Hooded Oriole nest at locality 1 showed that the yellow on the anterior part of the rictal flanges was brighter than that on the posterior part at the corner of the mouth. Also, the edges of the eyelids of the 1–2 day-old cowbird were of the same yellow color as the flanges. Eyelids of the orioles in the nest were white. Eyelid color in cowbird nestlings does not seem to vary concordantly with flange color. Yellowish eyelids are detectable in photographs of yellow-flanged cowbirds form localities 1, 2, 4 and 5 and in photographs of white-flanged cowbirds from localities 7, 20 and 21. Also, Friedmann (1929: 262) reported that a white-flanged cowbird at locality 19 had "green-yellow" eyelids. However, there may be some variation in eyelids as the color on two nestlings appears to be dark gray in a photograph from locality 16.

Information for 13 of 22 localities (Table 1) is based on two or more specimens. Only one of these 13 localities, number 5, shows possible individual variation in rictal flange color. Thus, it seems likely that at most and possibly all localities, nestling cowbirds have a single flange color. It will be of great interest to determine the flange colors in areas where a transition exists from yellow to white. Data from locality 5 suggest that the transition is clinal along the West Coast.

The distribution of nestlings with yellow flanges corresponds to that of the southwestern race of the cowbird (*M. a. obscurus*). Excluding locality 5 from consideration, each of 21 specimens from 4 localities within the range of *obscurus* (Fig. 1) had yellow flanges. By contrast, each of 18 specimens from 7 localities within the range of *M. a. artemisiae* had white flanges as did each of 55 from 10 localities within the range of *M. a. ater*. The probability, under random expectation, that 4 of 4 *obscurus* localities would have yellow-flanged cowbirds while 17 of 17 *artemisiae-ater* localities would have white ones is $<.01$ (hypergeometric distribution in Owen 1962).

TABLE 1. Rictal flange colors of cowbirds and hosts

Locality	Cowbird N[a]	Cowbird Flange color[b]	Host Species (no. of nests)	Host Flange color[b] (authority[c])	Type[d] and source of data[e]
1. California: Goleta and Santa Barbara	13	Y	*Icterus cucullatus* (10)	W	L, P—this study
	1, (1)	Y	*Geothlypas trichas* (2)	Y	P—K. Steele p. c., L—this study
2. California: Shandon	1	Y	*Carpodacus mexicanus*	Y (pers. obs.)	L—this study
	2	Y	*Euphagus cyanocephalus* (2)	W	L, P—this study
3. Arizona: Tucson	1	Y	*Vireo bellii*	?	P—Phillips et al. 1964: 19, and E. Porter p. c.
4. Arizona: Flagstaff	2	Y	*Vermivora virginiae* (1)	Y	P—J. M. Fischer and R. P. Balda p. c.
5. California: San Francisco	3	PY	*Zonotrichia leucophrys* (3)	Y	P—L. Petrinovich p. c.
6. California: Mammoth Lakes	2	W	*Melospiza lincolnii* (1)	Y	L—this study
	1	W	*Junco hyemalis*	Y	L, P—D. F. Tomback p. c.
	(1)	W	*Euphagus cyanocephalus*	W (localities 2 and 9)	L—this study
	(1)	W	*Oporornis tolmiei*	Y (Wetmore 1964: 285)	L—this study
	(1)	W	*Empidonax* sp.	?	L—this study
7. California: Mono Lake	1	W	*Dendroica petechia*	Y (locality 21)	P—I. C. Tait p. c.
8. California: Sage Hen Creek Station (Nevada Co.)	5	W	*Junco hyemalis* (?)	Y	P—J. M. White p. c.
9. Washington: Othello	2, (1)	W	*Euphagus cyanocephalus* (3)	W	P—R. K. Furrer p. c. and 1975
10. Wyoming: Jackson	1	W	*Dendroica petechia*	Y (locality 21)	P—A. Small p. c. and 1974: 215
11. Wyoming: Dubois	1	W	*Dendroica petechia*	Y (locality 21)	P—H. C. Clarke p. c.
12. Manitoba: Delta Beach	1	W	*Agelaius phoeniceus*	W (pers. obs.)	L—this study
13. Kansas: Manhattan	37	W	*Ammodramus savannarum* (?)	W	L—P. F. Elliott p. c.
			Sturnella magna (?)	W	
			Icterus spurius (?)	W	
			Toxostoma rufum (?)	W	
			Agelaius phoeniceus (?)	W	
			Spiza americana (?)	Y	

TABLE 1. Continued

Locality	Cowbird N[a]	Cowbird Flange color[b]	Host Species (no. of nests)	Host Flange color[b] (authority[c])	Type[d] and source of data[e]
14. Kansas: Lawrence	2	W	*Spizella pusilla* (2)	Y	L—P. Lowther p. c.
15. Michigan: Oscoda Co.	1	W	*Dendroica kirtlandii*	Y (Mayfield 1960: 107, Porter 1972: 70)	P—H. F. Mayfield p. c. and 1960: pl. 7B
16. Michigan: Cheboygan Co.	2	W	*Vireo olivaceus* (1)	W (Saunders 1956)	P—O. S. Pettingill, Jr. p. c.
	1	W	*Seiurus aurocapillus*	Y (Saunders 1956, Wetherbee and Wetherbee 1961)	
17. Ohio: Hamilton Co.	2	W	*Wilsonia citrina* (1)	W (Wetmore 1964: 256)	P—E. Porter p. c. and Wetmore 1964: 287
18. Pennsylvania: Butler Co.	1	W	*Dendroica pensylvanica*	W (Saunders 1956, Porter 1972: 38)	P—H. H. Harrison p. c. and 1973: 35
19. New York: Tompkins Co.	1	W	?	?	L—H. Friedmann p. c. and 1929: 262
	2	W	*Vireo solitarius* (1)	W (Wetmore 1964: 250)	P—D. G. Allen p. c. and Wetmore 1964: 297
20. Ontario: Kingston	1	W	*Catharus mustelina*	W	P—R. F. Norman p. c.
21. Ontario: Chaffey's Locks	3	W	*Dendroica petechia* (3)	Y	P—R. J. Robertson and R. F. Norman p. c.
	1	W	*Melospiza melodia*	Y (Saunders 1956)	
22. Quebec: Montreal	1	W	*Geothlypas trichas*	Y	L—Mousley 1933

[a] Numbers not in parentheses represent nestlings. Numbers in parentheses represent fledglings.
[b] Y = yellow, PY = pale yellow, W = white.
[c] If no authority is give for the host's flange color, the color is based on host nestlings from at least one of the nests that provided data on the flange color of the cowbird(s). If an authority is given, the data on host color are not necessarily from the same locality as are the data on the cowbird.
[d] L = data based on direct observation of live birds; P = data based on colored photographs. The original colored photograph was consulted in cases in which a referenced photograph is reproduced in black and white in the literature.
[e] p. c. = personal communication.

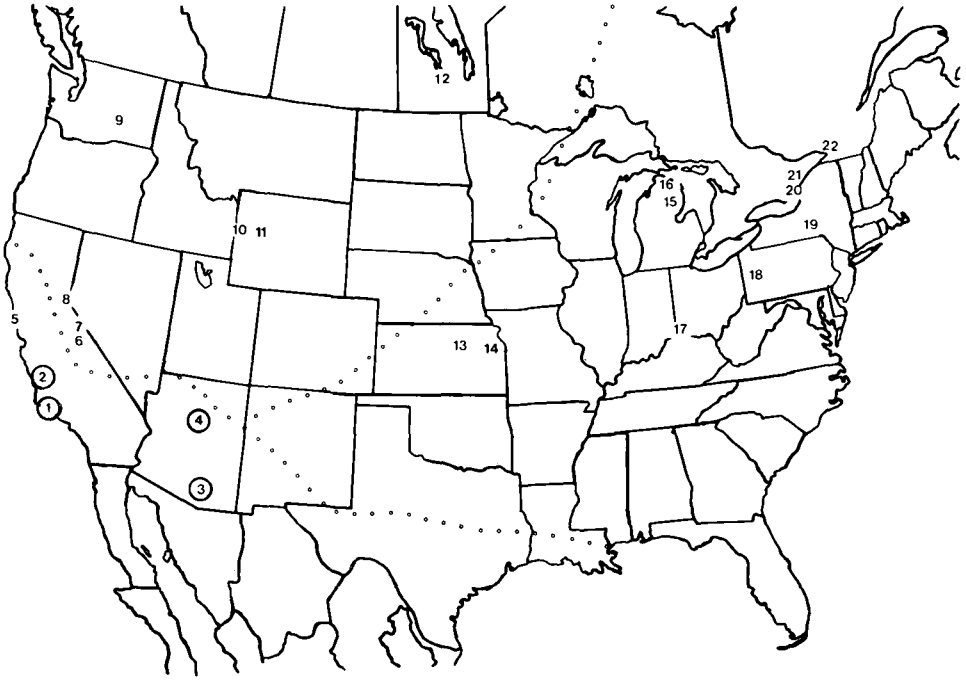

Fig. 1. Localities listed in Table 1. Nestling cowbirds at circled localities had yellow rictal flanges. Nestlings at other localities had white flanges, except for locality 5 where nestlings had pale yellow flanges and where some may also have white flanges (see text). The lines formed by the small circles delimit the ranges of the subspecies of the cowbird with *Molothrus ater obscurus* in the Southwest, *M. a. artemisiae* in the Northwest, and *M. a. ater* in the East. Ranges of subspecies are based on A.O.U. check-list (1957), Friedmann (1929: 146) and Grinnell and Miller (1944: 438).

The probability is $\leq .02$ if localities close to one another (numbers 1–2, 6–7–8, 10–11, 13–14, 15–16 and 20–21, Fig. 1) are counted as single localities.

DISCUSSION

The variation in rictal flange color appears to be stronger than geographical variation in other features of cowbirds. The races show differences in body size (Friedmann 1929: 145, Oberholser 1974: 842–843, Ridgway 1902: 207, 210) but they overlap in these measurements. Although Bendire (in Bent 1958: 454) believed the eggs of *obscurus* to be "somewhat less heavily spotted" than those of *ater*, he stated that eggs of both races are similar and no strong differences exist in egg coloration (pers. obs., see egg descriptions in Bent 1958: 438, 451, 454). The eggs of *obscurus* are smaller than those of the other races (Bent 1958, Friedmann 1929: 187) but as *obscurus* is a smaller bird, its small egg size may be a byproduct of selection for small adult size. However, the difference in rictal flange color is most likely caused by selection acting on the nestlings, as no reason exists to postulate that this difference is a byproduct of some adult trait. Adult cowbirds have been studied more intensely than nestlings and no racial differences in mouth, flange or tomium color have been reported (see Friedmann 1929, Oberholser 1974, Ridgway 1902).

I suggest that aspects of the hosts used by *obscurus*, or at least by cowbirds in localities 1 through 4 (and possibly 5), select for yellow flanges whereas aspects of the

hosts used by other cowbirds select for white flanges. Whatever features of the hosts select for a particular color, it seems almost certain that not all hosts within one region select for the same color. Rather, there may be an averaging process. The total range of hosts in some areas may select for yellow flanges while the assemblage of hosts in other areas selects for white flanges, even though particular host species in the same area select for different colors. Conceivably, the main source of such selection is one or a small number of hosts that select strongly for one color while the majority of hosts contribute little to selection for flange color.

One possible source of selection is crypsis, with the nest placement of hosts in some areas making yellow-flanged cowbirds most cryptic, while white is most cryptic in other areas. It seems more likely though, that hosts in various areas respond differently to each flange color. While some facet of the hosts' responses to nestling cowbirds may be the ultimate factor responsible for the variation in rictal flange color, it is unlikely that many (if any) hosts reject certain nestlings, as is done with certain egg types (Rothstein 1975a, 1975b). I know of no reliable records of host rejection of cowbird nestlings. Cowbird nestlings appear to be fed whether or not their flange color matches that of the host nestlings. Table 1 shows the flange colors of cowbird and host nestlings at each locality for which both colors are known. Even in cases where the flange colors of cowbird and host nestlings contrast, the cowbirds were fed, as all such records are based on fledglings or on nestlings that reached an advanced age. Moreover, the same host species may care for white- and yellow-flanged cowbirds in different areas even though the flange colors of their own nestlings do not vary (Brewer's Blackbird—locality 2 versus 9, Common Yellowthroat (*Geothlypas trichas*)—locality 1 versus 22, Table 1). Lastly, the rictal flange data in Table 1 give only a partial indication of the differences between host and cowbird nestlings. For example, R. F. Norman's photograph from locality 20 shows that although the Wood Thrush (*Catharus mustelina*) and cowbird nestlings both had white flanges, the mouth lining of the thrush was yellow while that of the cowbird was red. Similarly, Ficken (1965) pointed out that some of the cowbird's most common hosts have yellow mouth linings that contrast with the red of the cowbird. Besides the gape, other major differences occur between cowbird and host nestlings, such as those in down coloration (see Nice 1937: 156).

Rather than complete rejection of certain nestlings, it is more probable that hosts in the various areas accept any type of nestling but provide better care for those with a particular color. Hosts may provide the best care for nestlings whose gape is most similar to that of their own young and possibly the most important hosts in the Southwest have nestlings with yellow flanges. Alternatively, hosts might provide the best care for a nestling that is distinct from their own. Within a brood, host nestlings usually outnumber cowbird nestlings. If birds try to equalize feedings among nestlings (see Pullen 1945), a distinctive nestling that is in the minority would receive a disproportionate amount of food if the hosts alternated the type of nestling fed on each visit to the nest. Also, if hosts develop recognition of the young in their nest, this recognition might be strongest for the first nestling to appear. Thus, a distinctly-colored cowbird might receive more attention than the host's own young because cowbird eggs usually hatch before those of the host. Lastly, a cowbird that is distinct from the host's nestlings and that is in the minority might provide a stronger stimulus than the host's own young because of habituation.

It may be adaptive for cowbird nestlings to be distinct from host nestlings for a reason unrelated to host care. Adult cowbirds, on at least rare occasions, remove host

young from nests containing cowbird nestlings (Tate 1967). If the adult cowbirds responsible for such removal are the parents of the cowbirds in these nests, then selection might favor features that facilitate discrimination between host and cowbird young to ensure that cowbirds do not mistakenly harm their own offspring.

I have suggested that the geographical variation in flange color is related to the cowbird's parasitism. This interpretation will be supported if it can be shown that nonparasitic birds generally lack comparable geographical variation. However, some hosts may have evolved geographical variation in nestling appearance in response to cowbird parasitism; just as brood parasitism may exert selective pressures on host eggs (Rothstein 1974), it may also influence the appearance of host nestlings. While several studies have reviewed the appearance of nestling passerines (Saunders 1956, Wetherbee 1957, Wetherbee and Wetherbee 1961, Ficken 1965), the data are too few to allow an intensive investigation of geographical variation. Available data show no variation in two nonparasitic icterids along transects over which the cowbird's flanges shift from yellow to white. Brewer's Blackbirds have white flanges at Shandon, California (pers. obs.), Othello, Washington (R. K. Furrer pers. comm.), and Logan, Utah (Balph 1975). Red-winged Blackbirds (*Agelaius phoeniceus*) have white flanges at Santa Barbara, California (pers. obs.), Manhattan, Kansas (P. F. Elliott pers. comm.) and Brooklyn, New York (pers. obs.).

RICTAL FLANGE AND MOUTH COLOR IN OTHER COWBIRDS

The reports in this paper of yellow flanges are the first such published records for the entire cowbird assemblage of six species, except for Crandall's report (in Friedmann 1929: 358) of yellow flanges in two *Scaphidura oryzivora* nestlings. Friedmann (1929) reported that the following have white flanges: *Molothrus badius* (p. 28), *M. rufo-axillaris* (p. 51), *M. bonariensis* (p. 122) and *M. aeneus* (p. 334). However, all these records are based on single nestlings and Rosendo M. Fraga (pers. comm.) has recently found that *M. bonariensis* has a complex pattern of variation in its rictal flange color. Nestling *bonariensis* at Estancia La Candelaria, Lobos, Province of Buenos Aires, Argentina, show continuous variation in flange color, ranging from pure white to yellow. Such variation at one locality is quite different from the data available for *M. ater*; but perhaps *M. ater* shows comparable variation in areas transitional between yellow and white flanges. Fraga also reports that nestling *bonariensis* vary in the color of the skin and of the inside of the mouth. This variation correlates with that in flange color. Fraga has found that *M. rufo-axillaris* and *M. badius* have white flanges and red mouths, thus agreeing with Friedmann's data for these two species.

Except for *S. oryzivora* and *M. bonariensis*, Friedmann (1929) described the mouth color of all the cowbirds as red, thus agreeing with my data on *M. ater*. The mouth color of *S. oryzivora* was not described, but Friedmann reported that the nestling mouth color of *M. bonariensis* is orange-yellow, not red. Fraga reports that *M. bonariensis* nestlings at his study site have mouths ranging from orange-red to pink. Friedmann's and Fraga's reports of orange-yellow and orange-red mouth color in *M. bonariensis* are unusual. The great majority of nine-primaried oscines have red or pink mouths and Ficken's (1965) review listed red as the only color that occurs in the Icteridae.

Molothrus ater obscurus is the only race of *M. ater* that has yellow flanges. It is also the only race sympatric with any other cowbird, *M. aeneus*—a species that

apparently has white flanges. This situation raises the possibility of character displacement between *M. ater obscurus* and *M. aeneus*. Character displacement involving host usage by brood parasites has been termed alloxenia (Friedmann 1967). Such displacement could arise from selective pressures generated by interspecific competition for hosts. Although *M. ater obscurus* and *M. aeneus* overlap in host species and sometimes even parasitize the same nest (Friedmann 1963: 132, 1971), they have strong differences in overall host usage (Friedmann 1963: 173, Friedmann et al. 1977). Furthermore, there is partial temporal separation in breeding times, with *M. ater obscurus* commencing egg-laying a month earlier than *M. aeneus* (Friedmann 1929: 328). Character displacement also is suggested by the eggs of *M. aeneus*, which are immaculate (Friedmann 1929: 327). All other cowbirds have mottled eggs, the only exceptions being some populations of *M. bonariensis* that have both mottled and immaculate eggs (Friedmann 1929: 83) and *S. oryzivora* in which immaculate eggs may occur at low frequencies (see Friedmann 1929: 357).

A Request for Additional Data

Data from many additional localities within the range of the Brown-headed Cowbird must be gathered before a complete picture of the variation in rictal flange color emerges. Especially needed are data from the eastern portion of *obscurus*' range and from all areas where *obscurus* intergrades with *ater* and *artemisiae*. Additional data for the Bronzed Cowbird are also sorely needed. Unfortunately, such data cannot be derived from museum specimens as the rictal flange color fades. Considering the large numbers of cowbird nestlings seen in the field each year, the needed data might be compiled rather quickly through a cooperative program. I am continuing to compile data on this character and would greatly appreciate it if readers with colored photographs or written descriptions of cowbird nestlings or those who are likely to find nestlings in the course of their work contacted me. The types of information needed are: coloration of tomia, rictal flanges, mouth lining and eyelids of host and cowbird nestlings, host species, locality, and date.

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Note added in proof: New data collected during 1977 by Ernest Stevens and myself alter some of the generalizations stated in this paper. First, intralocality variation occurs in *M. ater* in the Owens Valley where the races *obscurus* and *artemisiae* intergrade; yellow- and white-flanged cowbirds have even been found together in the same host nest. Intralocality variation also exists near the Owens Valley at locality 6, although all previous observations at locality 6 were of white-flanged cowbirds (Table 1). Furthermore, a single white-flanged cowbird has been found at locality 1 where previously only yellow-flanged ones were found and three specimens collected in the Okanagan Valley, British Columbia and currently in the Museum of Vertebrate Zoology, University of California, had "whitish yellow gapes" although data in Fig. 1 would have led to the expectation of white flanges. However, most of the large amount of new data conform to the generalizations presented here. It seems that only white-flanged cowbirds occur in the eastern half to two-thirds of North America while both white- and yellow-flanged ones occur in the west with a distribution similar to, although somewhat more complex, than that suggested by Fig. 1. This new information increases the importance of gathering additional data, even from areas for which large samples are already available.