RELATIONSHIPS BETWEEN BLACK-EARED AND PLAIN-EARED FORMS OF BUSHTITS (*PSALTRIPARUS*)

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REVIEW of literature pertaining to relationships among bushtits (*Psaltriparus*) of the southwestern United States and northern Mexico reveals a long-standing divergence of opinion as to species limits. The point at issue is whether the populations characterized by black-faced males, occurring in Mexico north to approximately the international boundary, are specifically distinct from the northerly ones of the *plumbeus* type, which generally lack black.

Oberholser (1903), in a synoptic review of *Psaltriparus*, allocated black-eared populations to a distinct species, *P. melanotis*, and described briefly the basis of separating specimens of its northern race, *P. melanotis lloydi*, from the specimens of the partially sympatric plain-eared form, *P. plumbeus* (presently considered as a subspecies of *P. minimus*). Other than presence or absence of black coloration on the head, he mentioned only the greater contrast between the colors of head and back in young males of *lloydi*.

Ridgway (1904: 429–431) admitted difficulty in separating *P. m. lloydi* and *P. plumbeus* and found evidence of intergradation, but he retained the species separation between *P. melanotis* and *P. plumbeus*. Apparently he relied upon the opinion of Oberholser, "who has had excellent opportunities of studying both forms in life [and] assures me that they not only both breed in the same localities in southwestern Texas, but that they each have distinctive peculiarities of voice, etc."

Swarth (1913, 1914), although aware of indications of conspecificity, appears to have been influenced by Ridgway's and, more particularly, Oberholser's opinions and did not recommend nomenclatural merger.

The prevalence of this view of specific distinctiveness was terminated in the early 1930's. In the fourth edition of the A.O.U. Check-list (1931), all forms of bushtits were listed as geographical races of *P. minimus*. Shortly thereafter, Hellmayr (1934: 88–92) used a similar treatment but admitted unfamiliarity with *lloydi* and pointed out the need for a "thorough investigation" of the relationship between this form and the plain-eared *plumbeus* and *cecaumenorum*.

In the report of the first study of this problem which was actually conducted in the zone of contact between black-eared and plain-eared forms, Van Tyne and Sutton (1937: 64–67) adduced evidence of species divergence between *lloydi* and *plumbeus*. Their interpretation was based, among other things, on the occurrence in the Chisos Mountains and other ranges of west Texas of two distinct populations, partially separated by altitudinal preferences. Thus, they treated the populations as members

of two species, *P. melanotis* and *P. minimus*. However, they did call for additional study of relationships.

In the absence of such additional study, most subsequent treatments have followed Van Tyne and Sutton in retaining black-eared and plain-eared groups as separate species—notable examples are the fifth edition of the A.O.U. check-list (1957) and the check-list of the birds of Mexico (Miller *et al.*, 1957). Agreement has not been unanimous, however; van Rossem (1945: 178–180), Blake (1953: 388), Phillips (1958), and Phillips *et al.* (1964: 111–112) are among those who have held contrary views. A number of recent authors have emphasized the uncertainty as to relationships (e.g., Miller *et al.*, 1957; Davis, 1959; and Eisenmann, 1955).

In consideration of these conflicting views and expressions of uncertainty, it was obvious that only a thorough study, including additional field work and examination of pertinent specimens already available, could hope to solve the question of species limits and elucidate relationships within this group of populations. It also appeared probable that such a study would add to knowledge of the processes of speciation. Accordingly, I began an investigation of these problems in the spring of 1960.

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METHODS

Field work.—From the outset I assumed that field work should be concentrated in the critical "islands" of bushtit habitat in west Texas, especially the Chisos Mountains, the area that Van Tyne and Sutton had reported as a region of sympatry. Results of early work confirmed this assumption, and 12 trips were made there. Another critical region, embracing portions of Arizona, Chihuahua, New Mexico, and Sonora, was visited 11 times. Other field work was carried out both north and south of these areas of possible sympatry or intergradation so that information on "typical" *P. melanotis* and *P. minimus* could be obtained for comparative purposes.

Field work generally included collection of specimens and observations on ecological factors and on behavioral phenomena such as social groupings, nest construction, feeding of young, territoriality, and vocalizations.

The usual procedure was to locate a social group (such as a flock, mated pair, or family), to document the behavior of the birds, and then to attempt to collect the entire group.

Collecting efforts yielded 427 specimens, 357 from areas especially pertinent to this problem (see Figure 1).

Tape recordings of various types of vocalizations were made in nine different localities, with a Nagra III H B tape recorder at 15 i.p.s. Sound spectrograms were made on a Kay Electric Company Sonagraph.

Specimen study.—Over 1,000 specimens were examined, including those taken during the study and those in collections. Plumage coloration, especially of head, back, and flanks, was noted for each specimen. The bill and tarsus on all adult specimens were measured with dial calipers.

Tail length and wing chord (from bend of wing to tip of longest primary) were measured on all specimens collected in late autumn, winter, and early spring (by late April, rectrices and longer primaries are very badly worn).

SEX AND AGE DETERMINATION AND MOLTS

Sex and age groups vary in presence and amount of black facial coloration and in other morphological characters that also vary between populations of *Psaltriparus*. As pointed out by Miller (1955: 169), Phillips (1958), and Phillips *et al.* (1964: 111–112), failure to appreciate the nature of this normal intrapopulation variation has contributed significantly to the confusion in understanding of interpopulation relationships. For this reason, I paid particular attention to sexual dimorphism and to morphological changes with age.

Molts.—The molt cycle in *Psaltriparus* is simple. The postjuvenal (first prebasic) molt appears to be complete; there is no evidence of juvenal feathers retained beyond the first autumn. Subsequent to the postjuvenal molt, bushtits undergo only one molt annually, the postnuptial or prebasic molt, which is complete. Phillips *et al.* (1964: 112) gave similar descriptions of molts in *Psaltriparus*. In the populations of this study, postjuvenal and postnuptial molting extend from late summer through October.

Sex determination.—Gonads are difficult to find and distinguish in these very small birds, especially in individuals which have not bred for the first time. Uncertainty of sex is indicated on the labels of a number of specimens, and many indicate a sex but give no description of gonads. Specimens of this latter sort are particularly numerous in older collections made by professional collectors. (Labels on birds in such collections seldom contain indications of uncertainty on the part of the collector.) For specimens collected in areas where black faces predominate among males, the possibility suggests itself that sex determination was based only on this plumage characteristic.

In bushtits there is sexual dichromatism of the iris, which is usually straw-yellow in adult females and dark brown in adult males (van Rossem, 1935; Phillips, 1958). This dichromatism is not present at hatching but develops gradually, the dark iris of the female nestling becoming paler and more tinged with yellow during the juvenile period. The distinction between male and female irides becomes sufficiently obvious for sexing purposes at about the time of full growth of juvenal flight feathers. In my collection of over 400, only one specimen of a fully grown bushtit had an eye color which was at variance with the sex as determined by gonadal examination.

This character serves, then, when information on gonads is lacking or

incomplete. Unfortunately, many collectors failed to include the iris color on labels.

Sexual dimorphism in plumage coloration is found in all populations of *Psaltriparus* included in this study. The principal sex differences are to be found among adults; they include white throats in males versus pale buffy-gray ones in females, more vinaceous wash on flanks of males, and more and darker ventral buff coloration on females. However, these characteristics vary geographically. Also, many specimens are so worn and feathers so disarranged that these differences are obscured. In the juvenal plumage these differences appear to be unreliable—they are either absent or less striking, and wear of feathers obscures them rapidly. The presence and amount of black coloration on the head is also sexually dimorphic in some populations, but geographical and age variation renders this feature useless for sex determination except among known adults in southern populations which I studied.

In summary, the use of iris color and plumage characters may aid in sex determination of some individuals, but the lack of sufficient information for some specimens has resulted in persistent uncertainty as to their sex.

Age determination.—In *Psaltriparus,* ossification of the skull is completed relatively early in the first year, apparently soon after the completion of the postjuvenal molt. Thus, the character is useful for separating juveniles from adults but does not serve to segregate birds in their first winter plumage. Unfortunately, only a small proportion of summer and fall specimens bear labels indicating the degree of skull ossification.

Fully grown juveniles may be distinguished, until about mid-June, by the general laxity of plumage and by the fresh, unworn appearance of some feathers, notably the rectrices. By the end of June the plumage of most juveniles has become worn sufficiently to obscure this latter difference; hence, considerable difficulty may arise with specimens collected in late summer or early fall if the stage of skull ossification is unknown. There is plumage-color variation with age but it is unreliable because of wear and sexual and geographic variation.

The difficulties of age determination were in large part overcome in this study through the use of an age criterion discovered and described to me by J. T. Marshall, Jr. This is the difference in size and shape of the tenth (outermost) primary remex between juvenal and winter (basic) plumages. Marshall has described the difference (*in* Phillips *et al.*, 1964: 112), but some additional observations appear warranted here. In the juvenile this feather is longer, broader, and more nearly oblong than in the adult. Shape and length are variable, but among juveniles the length, from insertion to tip, is rarely less than 15 mm, while in the adult it rarely exceeds this length; and in juveniles the taper at the tip almost

never includes more than one-third of the length of the vane, while in adults the vane is nearly always tapered for more than one-half its length. The combination of these differences readily permitted age determination in all but a few cases. Checks on this method, based on aging of particular specimens independently by Marshall and myself and on comparison with determination by skull ossification, have upheld its validity in all instances.

SPECIES LIMITS

A synopsis of the relevent distributional descriptions given for the two species (A.O.U., 1957: 395–396; Miller *et al.*, 1957: 137–139) follows. *P. melanotis*: from the Davis Mountains, Texas, south through Coahuila and from the San Luis Mountains of New Mexico—Sonora—Chihuahua south throughout the main Sierra Madre Occidental; *P. minimus*: from the Chisos Mountains and Edwards Plateau of Texas north, and from central Sonora (west of the Sierra Madre) north through the San Luis Mountains and into New Mexico and Arizona. Areas of implied sympatry thus include the Chisos, Glass, and Davis mountains and intervening, restricted areas of bushtit habitat of west Texas, and the San Luis Mountains, which lie across both the international boundary and the Sonora-Chihuahua boundary. Possible points of contact are implied for the little-known western edge of the northern Sierra Madre in Sonora. Figure 1 shows the locations of these areas. The eastern and western zones of presumed sympatry are separated by a sizeable gap in the range of *Psaltriparus* on the northern plateau of Chihuahua.

It was in these areas of supposed sympatry that the main portion of this study was concentrated. The results bearing directly upon the question of species limits are presented for each locality separately.

Chisos Mountains.—The Chisos Mountains contain the largest portion of bushtit habitat in the region studied by Van Tyne and Sutton (1937). Van Tyne and Sutton examined 17 males, 11 females, and one juvenile of unknown sex from the Chisos Mountains. Their study of these, and of an additional 17 specimens (13 males, 4 females) from other parts of Brewster County, led them to state: "All of the . . . Brewster County specimens we have examined are without exception clearly *melanotis* or *minimus*." Their principal basis for this separation was that *melanotis*, as compared with *minimus*, has "black on the sides of the nape and on the auricular region, gray crown contrasting strongly with the more olivaceous back, throat usually much whiter than the rest of the underparts, strong vinaceous wash on sides and flanks. In addition the 'face' is not Drab or Light Drab as in *plumbeus*, but is Hair Brown (in males this brown is usually suffused or mottled with black in varying degree)."

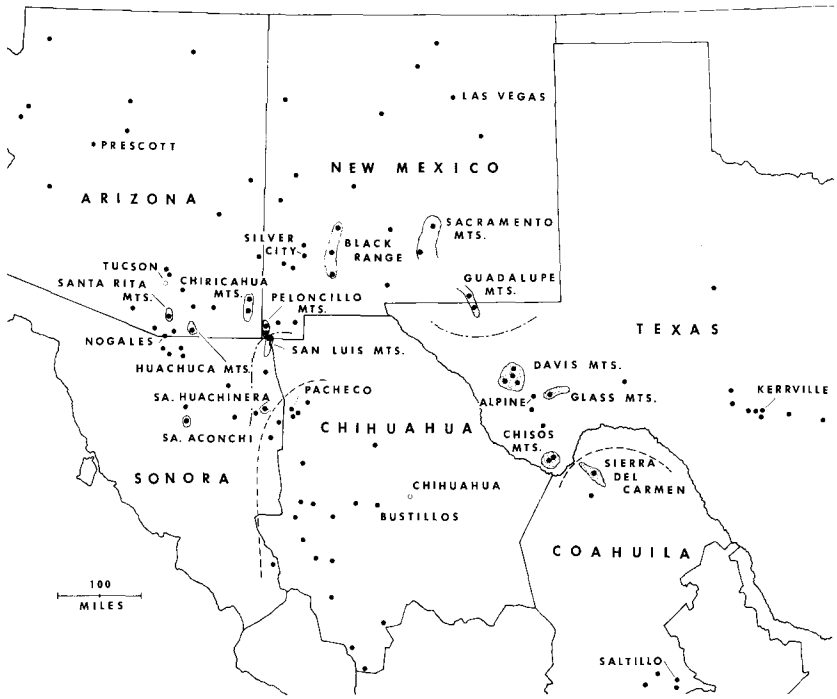

Figure 1. Map of the area within which *Psaltriparus* was studied. Solid dots indicate localities from which specimens were examined. A few specimen localities north and south of the main area are not shown. Stippled areas indicate some mountain ranges containing bushtit habitat. Open circles indicate two major cities included for orientation. Populations of *Psaltriparus* south of the regularly broken lines contain no plain-eared adult males. Those north of the long-short lines (and those west of the one in Sonora) contain no black-eared adult males. Populations between lines are polymorphic.

Considerable variation in facial coloration is described for *melanotis*. A habitat difference between the two species is imputed: "*melanotis* is confined to higher altitudes more definitely than is *minimus*, but the breeding ranges of the two forms overlap widely." One bit of evidence against species distinction is given: "an adult *melanotis* in company with a breeding female *minimus*," that "seemed to be traveling together" with no other bushtits around, were both collected on 5 May 1932.

Their allocation of Chisos Mountains specimens to the two species was as follows: *melanotis*, 16 males and 3 females; *minimus*, 1 male, 8 females, 1 juvenile of unknown sex. The fact that the sex ratios in both groups are unbalanced and in opposite directions is worthy of note.

I have examined 169 specimens from the Chisos Mountains, including

TABLE 1
DISTRIBUTION OF BLACK FACIAL COLORATION: EASTERN AREA[1]

Group	*Face color*				*Total*	*Ratio: black/plain*
	No black	*Restricted black*	*Partially black*	*Entirely black*		
Guadalupe Mountains, New Mexico-Texas						
Male						
adult	14	0	0	0	14	0/14
juvenile	0	1	0	0	1	1/0
Female						
adult	10	0	0	0	10	0/10
juvenile	2	0	0	0	2	0/2
Davis Mountains, Texas						
Male						
adult	29	1	1	0	31	2/29
juvenile	2	2	2	2	8	6/2
Female						
adult	27	0	0	0	27	0/27
juvenile	1	0	0	0	1	0/1
Glass Mountains and Alpine area, Texas						
Male						
adult	16	3	2	0	21	5/16
juvenile	1	1	0	2	4	3/1
Female						
adult	4	0	0	0	4	0/4
juvenile	1	0	1	1	3	2/1
Chisos Mountains, Texas						
Male						
adult	28	12	13	10	63	35/28
juvenile	0	4	12	16	32	32/0
Female						
adult	48	0	0	0	48	0/48
juvenile	12	7	4	4	27	15/12
North Coahuila (Sa. del Carmen, Sa. de la Encantada)						
Male						
adult	0	0	0	13	13	13/0
juvenile	–	–	–	–	–	—
Female						
adult	8	0	0	0	8	0/8
juvenile	–	–	–	–	–	—
Edwards Plateau, Texas						
Male						
adult	5	4	1	0	10	5/5
juvenile	7	1	3	0	11	4/7
Female						
adult	9	0	0	0	9	0/9
juvenile	1	0	0	0	1	0/1

[1] First five localities arranged in north-south order. Edwards Plateau is at latitude similar to Alpine but lies east of other areas.

101 collected during this study. Among the 68 from other collections were all but one of those listed by Van Tyne and Sutton.

Of the variable morphological characters within this series, the occurrence of black feathers on the head is the most significant, for it is this character that has been the principal diagnostic feature whenever species separation has been maintained. The black may be restricted to a small patch above and behind the auriculars or to a narrow supraocular line, or it may include the entire face and extend in a line completely across the nape. All intermediate conditions are represented; commonly, black occurs as patches of a few feathers, or on portions of feathers, on a face otherwise brown; reciprocally, brown can appear as patches on a generally black face. The distribution and extent of those patches show little regularity and the outcome is often a mottled appearance.

For convenience of analysis four somewhat arbitrary categories of extent of black coloration have been used (Figure 2): (A) absence of black, (B) black restricted to a superciliary line or small post-auricular patch, or both, (C) black and brown approximately equal or face at least obviously mottled, (D) face entirely black. The distribution of individuals of these four categories in the four sex and age groups is given in Table 1; the proportions of black to non-black individuals are also shown in Figure 3.

Among adult males and juvenile females, the numbers of individuals with and without black are about equal, and support may be found for postulating two species. However, among adult females and juvenile males there is but a single exceptional individual in each, and both of these probably have been wrongly sexed. The sole adult "female" exhibiting black was collected 5 June 1901, by L. A. Fuertes. The label provides no information on gonads or iris color. In view of this and of the bird's exceptional possession of black, as well as the fact that it is of the male type in *all* plumage characters in which adult males and females of this area differ, I think this specimen should be regarded as a male. A plain-eared juvenile specimen, labeled as a male, was collected on 19 May 1933, by Albert Lloyd and bears his number 1028. Kenneth C. Parkes has pointed out to me that Lloyd collected another bushtit at the same locality on the same date. The label on this specimen bears Lloyd's number 1029, and it is an unsexed adult that has female plumage characteristics. It seems very likely that the labels of these specimens were switched and that one is an adult male and the other a juvenile female.

In summary, the complete lack of breeding females with black and juvenile males without black argues strongly against the occurrence of separate "plain-eared" and "black-eared" species.

The other characters said to differentiate *P. minimus* and *P. melanotis* also fail to support a thesis of species status if larger samples are examined

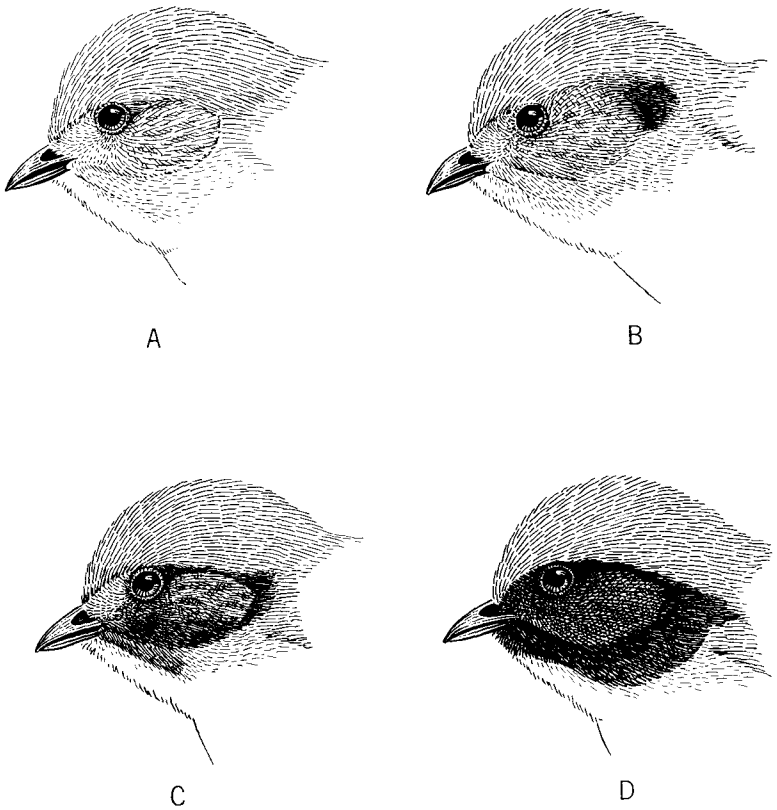

Figure 2. Drawings of heads of adult males of *Psaltriparus* from the Chisos Mountains, Texas. The letters correspond to the four categories based on the degree of black coloration (see text).

and due account taken of sex, age, and geographic variation. Among adult males and juvenile females, which are variable as to presence of black on the head, there is no correlation between the presence of black and the color of throat or dorsum. Black-eared individuals tend to have a greater amount and intensity of vinaceous coloration on the flanks, but this latter character is variable in both sex-age classes among both black and non-black groups, and the correlation that does exist is insufficient for allocation of all specimens to either a black, more-vinaceous group or a plain, less-vinaceous group. In my series of breeding females, there are 13 for which information is available as to the character of probable mates. There are no apparent differences in coloration of face, throat, dorsum, or flanks between those associated with plain males and those with black males.

As with black on the head, these other color characters show considerable sex and age variation. In adult males the throat is white and contrasts with the breast and the flanks, and flanks exhibit more vinaceous coloration, whereas in adult females the throat is gray and tends to blend in color with the breast and vinaceous is absent from the flanks. Juveniles of both sexes may have vinaceous on the flanks, but nearly all males have some and only a few females have a faint tinge. Throat coloration of juveniles resembles that of adult males but is perhaps slightly more gray. Wear rather quickly alters their dorsal appearance but juveniles appear to have backs that are less rich in olive with correspondingly less contrast between back and crown. No sex differences in this character are discernible.

These same characters of coloration of flanks and dorsum vary clinally in this region along axes parallel to clinal variation in black on the head. The geographic variation will be described in more detail later, but it is pertinent here to point out that populations of northern Brewster County (e.g., Glass Mts.) have less black, less vinaceous, and less dorsal contrast. Thus, within Brewster County as a whole, "black-earedness" is associated with white throat, vinaceous flanks, and olive back, while "plain-earedness" is associated with different combinations, in part because of sex differences, in part because of age variation, and in part because of parallel clines.

Differences in standard mensural characters also do not correlate with presence or absence of black. Mean lengths of bill, tarsus, wing, and tail of black-eared adult males in fresh plumage from the Chisos Mountains are not significantly different from those of a comparable series of plain-eared birds.

The morphological evidence from a large sample of bushtits from the Chisos Mountains, then, gives strong indication of a single, variable population rather than of two sympatric species.

On the basis of the information just presented, production of black-eared juvenile males, and perhaps females, by plain-eared parents must be the rule in the Chisos Mountains. In May, 1963, Robert D. Ohmart and I found three nests containing nestlings and were able to collect what appeared to be all of the adults attending the nests; in two cases these were pairs and in the third, two males. The failure to collect the female parent in this latter case seems irrelevant because all adult females lack black. A fourth group of young collected included four young fledglings being actively fed by a single adult male. Before they were collected we followed them closely for nearly an hour, and no other adults were observed. Results of these collections are summarized in Table 2. They provide strong confirmation of the conspecificity of black-eared and plain-eared forms.

TABLE 2
FAMILY GROUPS, CHISOS MOUNTAINS, MAY, 1963

Location	Date	Adults		Young			Remarks
		Sex	Head color category[1]	Stage	Sex	Head color category[1]	
Basin	9 May	1 ♂ 1 ♀	C A	nestlings ready to fledge	3 ♂ ♂	D	
½ mi N of Boot Spring	10 May	1 ♂ 1 ♀	A A	nestlings	1 (?) 1 ♂ (?) 1 ♂ (?)	D B[2] B[2]	Young maintained in captivity for several days
½ mi SW of Basin	13 May	2 ♂ ♂	A	nestlings	3 ♀ ♀	1,D; 2,C	Young maintained in captivity
Panther Pass	12 May	1 ♂	A	early fledglings	3 ♂ ♂ 1 ♀	2,D; 1,C A	Fledglings capable of only weak flight; fed frequently by adult

[1] See page 511 and Figure 2 for descriptions of categories.

[2] Some black present, but bird died before full extent of black could be determined; at least category B, may have been C or D.

Ecological and behavioral information gathered in the Chisos Mountains and bearing on species limits (discussed later) does not contradict the conclusions based on color variation.

Other west Texas areas.—The other principal bushtit habitats in west Texas lie in the Glass Mountains (Brewster County) and in the Davis Mountains (Jeff Davis County) (Figure 3). Smaller areas of habitat are in the Santiago Mountains, which lie between the Chisos and the Glass mountains, and on Mount Ord and in other localities immediately south of Alpine. These areas also lie in the implied area of sympatry.

Distribution of black head coloration in the samples from the Davis Mountains and the combined Glass Mountains—Alpine area is indicated in Table 1 and Figure 3. As in the Chisos, all adult females lack black. The proportions of black-bearing adult males and juveniles decrease in a clinal manner from the Chisos through the Glass and Davis mountains.

Although in these more northerly areas three of the sex-age groups show a mixture of black and non-black individuals, as contrasted with two in the Chisos Mountains, there is no evidence which would contradict the conclusion of conspecificity arrived at on the basis of larger samples and more intensive studies in the Chisos area. The general situation in *Psaltriparus* in west Texas is polymorphism in black coloration, varying between sex and age groups and with a clinal decrease in black from south to north, at least in adult males.

Northeastern Sonora and adjacent localities.—Geographical relationships between black-eared and plain-eared bushtits in the area centered in north-

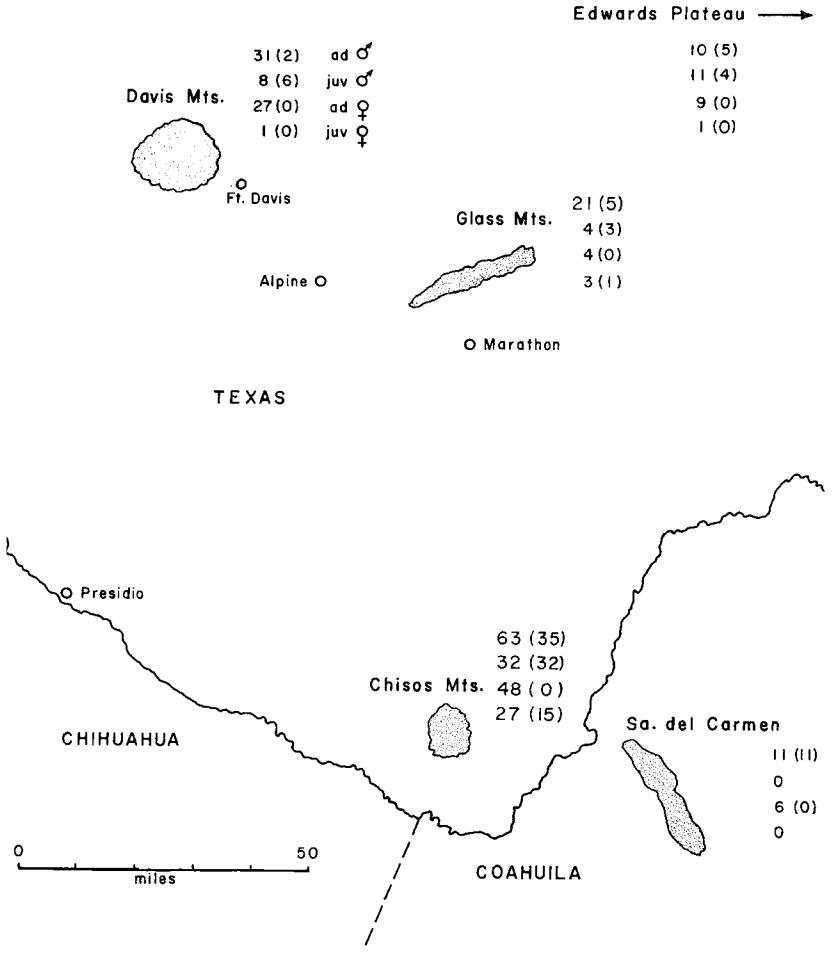

Figure 3. Map of the west Texas—northern Coahuila cline in polymorphism in occurrence of black head coloration in *Psaltriparus*. Numbers give the total size of samples for each sex-age group. Numbers in parentheses are the numbers of black-eared individuals in the group. Order of listing of the four sex-age groups, as given for the Davis Mountains, is the same for all localities.

eastern Sonora are more complex than in western Texas. Figures 1 and 4 illustrate the ranges approximately as they are understood. The main Sierra Madre Occidental, which bears effectively unbroken bushtit habitat, extends north to approximately the latitude of Casas Grandes, Chihuahua (30° 15′ N), and westward into extreme eastern Sonora. To the north and west of this large upland are at least partially isolated bushtit habitats of varying size, on ridges extending from the main Sierra (e.g., Sierra

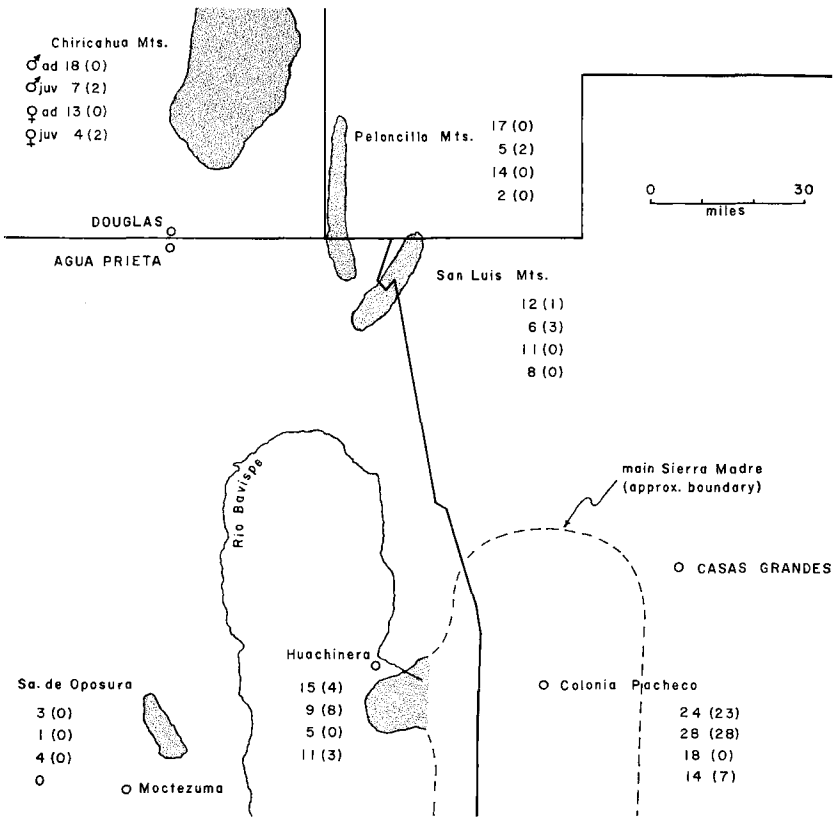

Figure 4. Map of the western clines in polymorphism in occurrence of black head coloration in *Psaltriparus*. Numbers give the total size of samples for the particular sex-age group. Numbers in parentheses are the numbers of black-eared individuals in the group. Order of listing of the four sex-age groups, as given for the Chiricahua Mountains, is the same for all localities. The western spur of the Sierra Madre Occidental south of the town of Huachinera, Sonora, is referred to in the text as the Sierra Huachinera.

Huachinera) or on separate mountain ranges (e.g., San Luis, Peloncillo, and Chiricahua mountains, and Sierra de Oposura). Maps and descriptions provided by Marshall (1957) indicate the geographical distribution of bushtit habitat in this region; continuous bushtit habitat occurs in areas enclosed on his maps by the lower boundaries of the oak woodland (encinal) community type.

Published information includes the San Luis Mountains as the only area of sympatry in this region; populations of the main Sierra Madre are implied to be strictly typical black-eared ones and those of outlying

ranges other than the San Luis to be of the plain-eared type. The results of the present study are summarized in Table 3 and Figures 1 and 4. A larger sample than heretofore available from the San Luis Mountains shows that black head coloration occurs only in a very small proportion of adult males and in about half of juvenile males. This pattern of occurrence is approximately that found in the Davis Mountains of Texas and offers little support for a view of separate species. Among bushtits inhabiting mountains north of the San Luis (e.g., Peloncillos, Chiricahuas), the occurrence of black is limited to a small number of juveniles.

Before the present study there were no published records of black-eared forms (other than the occasional juvenile males) in Sonora west of the Sierra Madre. However, the nature of bushtits occupying the habitats on the Sierra Huachinera and other adjacent uplands, which lie between the Sierra Madre and the main canyon of the Rio Bavispe, was unknown. The few specimens available from this area included both black- and plain-eared adult males. This indication of either polymorphism or sympatry in an area intermediate in geographical position prompted additional collecting. Variation in black in the 40 specimens of the combined sample from the Sierra Huachinera and the vicinity of Aribabi (Table 3) falls into a pattern similar to that of the Chisos Mountains. As with other localities of mixed occurrence of black-eared and plain-eared phenotypes, the situation in this area seems best interpreted as one of polymorphism, variable with sex and age, rather than as the overlap of two species.

Ecological and behavioral comparison.—The two principal indications of ecological and behavioral differences between the two forms were the statement by Oberholser reported by Ridgway (1904: 431) and repeated by Swarth (1914: 523) that they show "distinctive peculiarities of voice, etc." and the report of Van Tyne and Sutton that the two "species" are partially separated altitudinally in Brewster County, Texas.

I found no difference in altitudinal occurrence of black-eared and plain-eared forms in the Chisos Mountains. The lowest extensions of suitable bushtit habitat in these mountains are at about 5,000 feet and the highest point in the mountains, still within the altitudinal range of *Psaltriparus,* is Emory Peak at 7,835 feet. Within this comparatively narrow range in elevation (2,800 feet) an altitudinal separation would require an unusual narrowness of tolerance or fidelity on the part of the forms. Phillips *et al.* (1964: 112) report a similar conclusion. Observations and collections at all seasons revealed an effectively random occurrence of the two morphs with respect not only to altitude but also to other environmental variables, such as floristic composition, density of woodland canopy, and availability of water.

TABLE 3

DISTRIBUTION OF BLACK FACIAL COLORATION BY SEX AND AGE: WESTERN AREA[1]

Group	*Face color*				*Total*	*Ratio: black/plain*
	No black	*Restricted black*	*Partially black*	*Entirely black*		
	Peloncillo Mountains, New Mexico					
Male						
adult	17	0	0	0	17	0/17
juvenile	3	1	1	0	5	2/3
Female						
adult	14	0	0	0	14	0/14
juvenile	2	0	0	0	2	0/2
	San Luis Mountains, New Mexico-Sonora-Chihuahua					
Male						
adult	11	1	0	0	12	1/11
juvenile	3	2	1	0	6	3/3
Female						
adult	11	0	0	0	11	0/11
juvenile	8	0	0	0	8	0/8
	Sierra Huachinera, Sonora					
Male						
adult	11	3	1	0	15	4/11
juvenile	1	4	3	1	9	8/1
Female						
adult	5	0	0	0	5	0/5
juvenile	8	2	1	0	11	3/8
	Col. Pacheco area, Chihuahua					
Male						
adult	1	8	10	5	24	23/1
juvenile	0	2	10	16	28	28/0
Female						
adult	18	0	0	0	18	0/18
juvenile	7	4	3	0	14	7/7
	Central and southern Chihuahua					
Male						
adult	0	0	1	30	31	31/0
juvenile	0	0	1	35	36	36/0
Female						
adult	19	0	0	0	19	0/19
juvenile	0	0	8	0	8	8/0

[1] Localities arranged in general north-south sequence; Sierra Huachinera is west of main axis.

An explanation for an apparent altitudinal separation reported by Van Tyne and Sutton is that they apparently considered all of their Brewster County specimens together. Since the proportion of black individuals declines to the north (Figure 3, Table 1), 19 of 24 of the specimens they allocated to *P. melanotis lloydi* were from the Chisos Mountains and 12 of 22 of the *P. minimus plumbeus* were from the Glass Mountains and other more northerly localities. From this geographic difference in proportions would derive an apparent altitudinal difference because of the fact that

the Chisos Mountains are much higher than the more northerly bushtit habitats.

General comparison of habitat types of typical black-eared populations in Mexico with those of plain-eared ones in Arizona and New Mexico revealed no outstanding difference. In all of the area of the southwestern United States and Mexico in which field work has been carried out, the habitat preferences of the two morphs are essentially similar. The nature of vegetation inhabited is almost always woodland, dominated by one or more species of the genera *Pinus, Juniperus,* or *Quercus.* In various portions of the study region the species and life forms of the dominant trees vary considerably, and the nature of understory vegetation is quite variable, but bushtit populations are almost invariably found in woodland of the same general character. Variation in floristic and structural features of occupied habitat within a single mountain range, usually correlated with elevation, is often as great as or greater than variation between habitats favored by plain-eared populations as opposed to black-eared ones.

Incidental but numerous observations were made on a variety of aspects of behavior of populations of both "pure" types and of polymorphic ones. In respect to foraging behavior, flock size, annual cycle in social behavior, and vocalizations—aspects of behavior on which a significant amount of observation was made—no reliable interpopulation differences were noted.

Because of the possible importance of vocalizations, special attention was paid to the physical characteristics of vocalizations, to the patterns of utterances, and to the social contexts in which they were given, with a view toward determining differences between black- and plain-eared forms. Grinnell (1903) has described the vocalizations of *Psaltriparus* in California, and his descriptions are applicable to all populations that I encountered, whatever the color of the birds.

Most vocalizations of bushtits are comprised of various combinations of two basic elements: a short unmusical note described as *tsit* by Grinnell and a rapid high-pitched trill. Sound spectrograms were made of recordings of these calls from within the area of overlap of the morphs and from a number of areas in the range of each of the "pure" types. No correlation between call characteristics and head coloration can be detected; nor, in fact, is any coherent pattern of geographic variation apparent.

Results of a limited experiment indicate that individuals of *P. m. plumbeus* do not discriminate between their own calls and those of black-eared individuals from Durango, Mexico. In April, 1963, nesting behavior of two pairs of bushtits was studied in the Sacramento Mountains, Otero County, New Mexico. The reactions of members of both pairs

to play-back of both recordings of their own voices and of those of birds from Durango were aggressive and identical. Alternate placement of stuffed models of black-eared and plain-eared bushtits near the sound source produced no difference in the reactions. The temporal pattern of attack on the model was highly correlated with the pattern of cessation and resumption of broadcast, indicating that auditory cues from the broadcast were probably more important in evoking the reactions then were visual cues from the models.

The similarities in habitat selection, habitat utilization, and social behavior, including vocalizations, complement the morphological evidence in pointing to close, conspecific relationship between black-eared and plain-eared forms. Areas formerly thought to be inhabited by separate sympatric populations contain instead single, polymorphic ones.

GEOGRAPHIC VARIATION

In the foregoing analysis some of the main outlines of geographic variations were described, but thorough examination of geographic variation is desirable in order to determine more precisely the nature of relationships.

Black head coloration.—Variation by sex and age in the presence and amount of black head coloration within certain populations is indicated in Figures 1, 3, and 4, and in Tables 1 and 3. The geographical pattern is one of two principal separate, parallel clines, one in the eastern portion of the study region and one in the western. The general nature of these clines is a south-to-north decrease in percentage of individuals with black and in extent of black on the individuals that exhibit it. Intrapopulation variation in this character has already been shown to be striking (Figure 2). Adult females can be characterized readily, however, for virtually none, in the entire region encompassed by this study (i.e., south through Coahuila and through Chihuahua into Durango), of them has any black. Among adult males, those from Coahuila and central and southern Chihuahua (and all populations to the south) have black, which usually includes the entire face. The amount of black in this group declines progressively so that in the San Luis and Davis mountains only a small proportion of adult males exhibit a small amount of black, and in populations to the north black is absent (see Figure 1). Among juvenile males, the occurrence of black is also uniform and universal in southern populations, but, in comparison with adult males, a greater proportion of black individuals occurs in all of the intermediate populations; furthermore, black occurs in juvenile males in populations well to the north of the area under consideration. Swarth (1913) reports such juvenile males in Nevada. Heimerdinger (1955) reports black adult males from Colorado,

but Phillips (1958) thinks they were juveniles and my examination of these specimens supports his opinion. Cursory examination of specimens in the collection of the University of Utah revealed several Utah specimens of juvenile males with small patches of black feathers. In localities in Arizona and New Mexico, from which adult males with black are unknown, juvenile males with black are not uncommon (e.g., two of seven from the Chiricahua Mountains, Arizona; one of two from the Silver City area, New Mexico). Samples of juvenile females from populations in which adult males are polymorphic, show similar variation in the two groups. However, at both north and south ends of the clines, juvenile females are more variable. They are the only group that is polymorphic as far south as the Colonia Pacheco–Rio Gavilán area of Chihuahua (one exceptional plain-eared adult male collected south of Colonia Juarez, Chihuahua, 19 December 1964, hardly invalidates this generalization). Yet, an occasional black-eared juvenile female occurs as far north as the Chiricahua Mountains of Arizona and the Silver City area of New Mexico. John C. Hubbard collected a juvenile female with an entirely black face on 4 July 1963, 6 miles north of Silver City.

Thus, each of the two major clines may also be thought of as three parallel but somewhat independent clines, one each in adult males, juvenile males, and juvenile females. The two main clines are quite similar and would probably appear even more similar if more collecting were done in Coahuila and northern Sonora.

Discussion of variation in black in populations of the Edwards Plateau of Texas has been deferred and inserted here somewhat parenthetically because these populations are in a sense a side issue. They occur in a rather narrow extension of the range of bushtits into central Texas eastward to the edge of the Edwards Plateau west of Austin. Information given in Table 1 and Figure 3 indicates that in amount and distribution of black, bushtits of this area are similar to those of the Glass Mountains—Alpine area farther west at about the same latitude. Thus, in terms of the clines in black, this area should perhaps be regarded as an eastward extension of the Glass Mountains—Alpine stage or step.

Variation in other color characters.—Color of back, breast, belly, and flanks also varies geographically. Variation in these characters within populations has already been described. Because of the great effects of plumage wear, juveniles and adults taken between April and the completion of the postnuptial molt are of little value in study of geographic variation in these characters. Adequate series of suitable adult specimens are available for only a minority of localities; therefore, only an incomplete outline of the variation can be provided. Variation in all of these characters is, in large part, clinal in a north-south axis; the different

characters are thus partially correlated with each other and with the occurrence and extent of black head coloration.

Dorsal coloration exhibits the most obvious geographic variation of any of these characters. The sexes appear not to differ as they do in ventral coloration, so populations are represented by larger usable samples. The crown is plain gray in all of the populations under consideration and the feathers on the back contrast with the gray crown to varying degrees. Least contrast is present in localities to the north and west. Individuals from the Pajaritos and Patagonia mountains, which are near Nogales, Santa Cruz County, Arizona, are nearly concolor dorsally, with only a faint tinge of olive on the back. In central and northern New Mexico and northern Arizona the backs also have only a slight olive cast, but the predominate gray is darker than in southern Arizona. Populations of southeastern Arizona (Santa Rita, Huachuca, and Chiricahua mountains), central Sonora (Sierra Aconchi and various localities south of Nogales), the San Luis Mountains, southwestern New Mexico (Peloncillo Mountains), and the Guadalupe Mountains of New Mexico—Texas are fairly uniform in that all exhibit definite dorsal olive mixed approximately equally with gray. The group of localities (Davis Mountains, Glass Mountains, Chisos Mountains, and Sierra del Carmen) shows increased dominance of olive over gray, and within the series this dominance increases slightly from north to south. A slight admixture of brown, producing a yellowish effect when mixed with the olive, begins to appear in some of these populations. Populations of Aribabi—Sierra Huachinera (Sonora), northern Chihuahua, and the Edwards Plateau, Texas, are similar to the Chisos Mountains individuals in dorsal coloration. To the south, in Coahuila, Chihuahua, and Durango, increasing green and brown and decreasing gray provide increasing contrast between back and crown.

In ventral coloration of females there is but slight variation. A southerly increase in the amount and richness of buff on the belly is evident, as is an irregular cline from east to west in increasing paleness of breast color. Populations of northern New Mexico and Arizona are darker gray on the breast than more southerly ones, but a trend toward increasing paleness appears not to continue into Mexico.

Among males, those in the north of the area studied have less buff coloration on the belly and are darker gray on the breast, and the buff increases in extent and richness toward the south. In Arizona there is an east-west trend toward less buff. From north to south (and east to west in Sonora) there is a definite but irregular increase in the extent and richness of the vinaceous coloration on the flanks. Within most of the populations of central Sonora, Arizona, and New Mexico and west Texas north of the Chisos Mountains, this character is variable; some have

vinaceous and some do not. In populations farther south, there is also variability but all adult males have at least a slight wash of vinaceous and many have considerable.

Geographic variation in other color characteristics is either too weak or too uncertain to merit description.

Mensural characters.—Measurements of length of bill, tarsus, tail, and wing all indicate a degree of geographic variation. Many of the differences between means are statistically significant according to *t*-tests, but the geographic pattern of variation in all of these characters (and in ratios between them) is largely irregular. Black-eared populations are not consistently different from plain-eared ones in any of the measurements. Inspection reveals but a single notable trend, a cline of increasing tarsus length from the Sierra del Carmen, Coahuila, northward through west Texas into New Mexico. This trend is apparent in samples of both sexes and is paralleled by similar but rougher trends of increasing length of tail and wing and, of course, by trends in coloration. Little in the way of additional interpretation can be based on this cline because there is not a counterpart to the west as there is in color; furthermore the trend is reversed even within the limits of Coahuila, samples from the vicinity of Saltillo resembling those of Texas and even New Mexico more closely than those of the Sierra del Carmen.

EVOLUTIONARY STATUS AND HISTORY

It is pertinent to consider the evolutionary status of these populations of *Psaltriparus*, beyond the mere question of species limits. The patterns of variation just described provide a basis for answering the question: What is the course of evolutionary history most compatible with variations of this nature?

A more specific, corollary question is whether the geographic variation in this portion of the range of *Psaltriparus*, which consists principally of parallel, north-south clines, is primary or secondary. A hypothesis of primary intergradation would appear to require that the variation be accountable in large part to the effects of local selective forces producing adaptations within local populations, and these forces would have to vary geographically concomitantly with phenotypic variation. Secondary intergradation, due to gene exchange between previously differentiated and geographically isolated gene pools, may assume patterns similar to those of primary intergradation (Miller, 1949). On the other hand, secondary intergradation may also be expected, at times at least, to exhibit other characteristics by which it may be distinguished; these include steepness of clines in the absence of radical environmental change, parallel and

concordant clines in a number of characteristics, and high intrapopulation variability within the zone of intergradation.

Interpopulation variation in occurrence of black on the face certainly appears to accord with a history of secondary intergradation and introgression. In a cline no more than 150 miles in length, black-eared populations are replaced by plain-eared ones. For approximately 800 miles to the north and 1,500 miles to the south of this zone, interpopulation variation in this character is slight. No suggestion for the adaptive significance of this character can be offered; it is perhaps a pleiotropic expression of an adaptive genotype. Whatever its adaptive and genotypic basis, no obvious steep environmental gradient presents itself, especially when one considers the wide and angular "front" along which intergradation occurs.

Likewise the peculiar polymorphic intrapopulation variation of this character, differing both within and between sex and age groups, appears to reflect differing degrees of recombination and expressivity that might be expected in a situation of secondary hybridization and introgression. The occurrence of black-eared juveniles well to the north of the main zone of intergradation can be explained as due to introgression of genes from Mexican populations through intermediate ones.

Variation in other characters is less helpful to such a hypothesis. As was pointed out, the general differences between black-eared and plain-eared groups as a whole are not great. Ecology and behavior appear nearly identical, and size characters do not appear to vary in any clear-cut pattern. Geographic variation is slight in most of the other color characters, but that which can be detected is in large part parallel to variation in black. Such parallelism is compatible with either secondary or primary variation unless breaks or steps in clines are geographically concordant or intrapopulation variation is greater in intermediate populations. Limitation of intensive study to areas within and slightly beyond the zone of intergradation prevents definite conclusions as to whether such characters as back color, belly color, and vinaceous wash on flanks satisfy the latter conditions. Evidence at hand indicates that all three do, at least in part. Color of the back varies clinally south through Mexico but predominance of olive over gray extends north about to the limit of penetration of black in adult males; in populations to the north gray consistently predominates. This character also appears to be more variable in intergrading populations but the degree of variation in this character is very difficult to evaluate. The extent of and intensiveness of buff around the vent also increases to the south and is apparently much reduced in all populations north of the polymorphic populations. No variation in intrapopulation variation is detectable. In the main study area, vinaceous on the flanks is, as stated earlier, correlated on an individual and a population basis

with black head coloration. This coloration decreases in extent and intensiveness south of the range of the race *lloydi* in Mexico and north of the zone of intergradation in the southwestern United States. It does appear to be more variable in the populations that exhibit polymorphism in black.

Thus, the nature of variation in coloration, especially in black on the face, leads to a conclusion of secondary intergradation; that is, of a history of geographic isolation of black-eared populations from those of the *plumbeus* type, followed by secondary contact and introgressive hybridization. Over-all similarities in behavior, ecology, and morphology indicate relatively little divergence during isolation, and these similarities and the extent of intergradation point to a virtual lack of intrinsic reproductive isolation. The relatively lesser degree of variation in coloration of back, belly, and flanks, the possible extension of clines in these characters beyond the zone of intergradation in black, and the irregularity of variation in size may indicate the operation of selection subsequent to the onset of introgression. In characters of high adaptive value such smoothing out of variation is to be expected (Mayr, 1963: 377–378).

If a history of geographical isolation is postulated, then it might be expected that evidence for a past discontinuity would be found in other genera of birds that presently inhabit similar habitats. Such evidence is found in the distribution of *Aphelocoma* jays, in which the northern range of the Mexican Jay (*A. ultramarina*) nearly coincides with that of black-eared *Psaltriparus*, although its close relative the Scrub Jay (*A. coerulescens*) extends well south into Mexico; in titmice, the Plain Titmouse (*Parus inornatus*) and the Black-crested Titmouse (*P. atricristatus*) inhabit complementary ranges on either side of a boundary north of the Davis Mountains and *P. inornatus* and the Bridled Titmouse (*P. wollweberi*) are sympatric in a fairly narrow zone in southwestern New Mexico and central and southeastern Arizona; in the warbler genus *Vermivora* the southern limit of Virginia's Warbler (*V. virginiae*) approximates that of *P. m. plumbeus* and the closely related Colima Warbler (*V. crissalis*) extends north into the Chisos Mountains; and in White-breasted Nuthatches (*Sitta carolinesis*) apparent discontinuities between *S. c. nelsoni* to the north and *S. c. umbrosa* and *S. c. oberholseri* to the south lie within the zone of intergradation of *Psaltriparus*. Others among ecologically associated species which reach northern limits of their ranges in the zone of intergradation are the Painted Redstart (*Setophaga picta*) and Hutton's Vireo (*Vireo huttoni*, eastern forms); conversely, the Black-throated Gray Warbler (*Dendroica nigrescens*) reaches its southern limits in these areas.

It is apparent that occurrence of range boundaries of this latter group in the area of intergradation in *Psaltriparus* could well be considered as evidence of environmental changes which might be a controlling feature

for primary intergradation in *Psaltriparus*. However, such distributional patterns could also reflect previous shrinkage and geographical segregation of habitat ranges, with elimination of populations in northern or southern divisions. Evidence in the first group of species pairs and allopatric, well developed races lends weight to the latter interpretation and to the hypothesis of secondary intergradation in *Psaltriparus*.

NOMENCLATURAL PROBLEMS

Conspecificity of populations of *Psaltriparus* heretofore included in separate species requires changes in nomenclature. The oldest available name for the combined species is *Psaltriparus minimus* (Townsend), coined in 1837.

Nomenclature of subspecies presents a more difficult problem. Populations of northern Mexico are presently included in *P. melanotis lloydi* Sennett. However, the type locality of this subspecies is Limpia Canyon in the Davis Mountains, which lie almost at the northern edge of the zone of intergradation. Since black-eared individuals do occur among adult males and in a large proportion of juvenile males in the Davis Mountains and sharp breaks in clines do not occur between this locality and more southerly ones of the *lloydi* type, this subspecies should be retained under its present epithet. For the same reasons, the population of the Sierra Huachinera, and probably that of the San Luis Mountains, should be allocated to this race.

Presently, plain-eared populations of central and western Sonora and western Arizona are included in a separate subspecies *P. minimus cecaumenorum* (A.O.U., 1957). The race was named by Thayer and Bangs (1906) from a series of eight specimens collected at La Chumata Mine in the Sierra de San Antonio, Sonora, in May, 1905. I have examined six of these as well as nine fresh specimens from the Sierra Aconchi, a mountain ridge adjacent to the Sierra de San Antonio, and a number of specimens from various localities within the recognized range in Arizona, including recently collected unworn specimens from the Pajaritos Mountains. Of the six original specimens, five are juveniles and all are badly worn, as is usual in bushtits collected in May. Such specimens are unsuitable for use in determining geographic variation in such characters as paleness of general color and color of back, the bases for the original description. Fresh specimens from Sierra Aconchi are not noticeably paler or grayer on the back than comparable ones from some western localities within the range of *plumbeus* (Patagonia Mountains, Santa Rita Mountains, Arizona). Thus, I agree with the treatment of Phillips *et al.* (1964: 111–112), who apparently regarded *cecaumenorum* as invalid, since their map indicates no racial boundary in southern Arizona.

In summary, my recommendation is that populations presently included in *P. melanotis lloydi* be included in *P. minimus lloydi* and that *P. m. cecaumenorum* be regarded as a synonym of *P. m. plumbeus*, or of *P. m. santaritae* Ridgway if the racial separation of northern *P. m. plumbeus*, as proposed by Phillips *et al.*, is desirable.

SUMMARY

The status of populations of *Psaltriparus* of the southwestern United States and northern Mexico has been uncertain and controversial for a number of years. The question has concerned species limits between plain-eared and black-eared forms. This problem was pursued through field work in various habitat areas, and through examination of over 1,000 specimens, more than 300 of them collected during the study.

Results of work in the Chisos Mountains of west Texas appear to settle the question of species limits. Of 32 juvenile males from that area, none fail to bear black facial feathers, and of 48 adult females, none have any black (two exceptional specimens—one in each group—are almost certainly mis-sexed). Adult males and juvenile females are polymorphic. Additional evidence of conspecificity is the occurrence of black-eared nestlings and fledglings attended by plain-eared adults.

Other populations of west Texas and of Sonora are also polymorphic, and the geographic variation in this polymorphism is clinal, proportions of black individuals and extent of black decreasing toward the north and west.

In vocalizations, general behavior, ecology, and other color characters, black-eared populations fail to exhibit differences from plain-eared (*plumbeus*) ones sufficient to differentiate them at the species level.

Coloration of back, flanks, breast, and belly varies geographically in clines generally parallel to each other and to clines in black facial coloration. Size varies geographically but largely in an irregular fashion.

The steep slope and short lengths of clines, especially in black; the parallelism in these clines; and the variability of intermediate populations point to previous geographic isolation of black-eared populations followed by secondary contact and introgressive hybridization. Patterns of variation in some other bird groups with similar habitats in the same area tend to confirm a past discontinuity in bushtit habitat in this region.

All bushtits should be considered as a single species, *Psaltriparus minimus* (Townsend). Populations of northern Mexico and those of the southwestern United States that contain black-eared adult males should be included in *P. minimus lloydi* Sennett. The race *P. m. caecaumenorum* Thayer and Bangs is invalid.

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