SUBSPECIFIC VARIATION IN WINTER POPULATIONS OF SAVANNAH SPARROWS: A STUDY IN FIELD TAXONOMY

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In 1951 an extensive area in Aiken and Barnwell counties, South Carolina, was selected as the site for the Savannah River Plant, whose genesis and general management fall within the province of the United States Atomic Energy Commission and whose construction, maintenance, and operation are due, in the main, to the efforts of the Commission's prime contractor, E. I. du Pont de Nemours & Company. As is commonly known, the main work of the plant revolves about the production of materials used in the H–bomb and other atomic weapons; most of the critical operations, to be sure, go on behind guarded gates in restricted areas, and many details of the work are necessarily veiled in secrecy. With the establishment of the plant area, which includes some 250,000 acres, all human inhabitants sold their lands and moved out, leaving behind two or three "ghost towns," many house and farm sites, and thousands of fields on which crops had been grown. Biologists from the universities of Georgia and South Carolina were invited to conduct faunistic, floristic, and ecologic studies, under government contract (with support from the Atomic Energy Commission), in the less restricted, non-industrialized parts of the Savannah River Plant area. Among the more concerted studies undertaken have been those of old fields with stress on such matters as biomass, aspect dominance, and successional change. These were carried out principally by members of the Georgia group working under the direction of Dr. Eugene P. Odum. As was early recognized by Dr. Odum, the old fields, now permanently abandoned, offered spacious, relatively simple, rapidly changing communities ideally suited to studies in synecology.

Among the more important and influent animals inhabiting the old fields were wintering fringillids, and of these the Savannah Sparrow (*Passerculus sandwichensis*) was the most abundant species, at least in fields abandoned for three or more years. Because of its abundance and importance as a harvester of seeds, the Savannah Sparrow, among other old-field fringillids (notably the Vesper Sparrow, *Pooecetes gramineus*; Grasshopper Sparrow, *Ammodramus savannarum*; and Leconte Sparrow, *Passerherbulus caudacutus*), was subjected to rather close study in the winters of 1954–55 and 1955–56. In both winters large-scale banding operations, which were promoted and supervised by Dr. Odum, were carried out by the junior author, who supplied many Japanese mist nets and did the banding. He was assisted by a number of others who helped drive sparrows into nets as well as remove them to gathering cages. Those assisting in January-February, 1955, are acknowledged by Johnston (1956); those participating in January-February, 1956, besides Dr. Odum and the authors, are acknowledged in a subsequent paragraph. The results of the banding studies, including data on repeats and returns, are presented in another paper (Hight and Odum, 1956: in press).

As marked variation in plumage was noted in the Savannah Sparrows netted in 1955, a series of 21 birds was selectively retained. These were prepared by David Johnston, identified subspecifically by Dr. John W. Aldrich, and reported on by Johnston (1956). From this endeavor the presence of five geographic races of *Passerculus sandwichensis* (*P. s. savanna, mediogriseus, labradorius, oblitus,* and *nevadensis*), of which three were additions to the South Carolina list, was established for the Savannah River Plant area. This qualitative determination of the subspecific makeup of the Savannah Sparrow populations, while of obvious value intrinsically, was also a necessary preliminary to the present study in which an attempt was made, in the winter of 1955–56, to identify subspecifically all the Savannah Sparrows handled (whether banded or collected), the

total numbering 559 birds. Most of the sparrows in this sample came from a single, 150-acre field, no. 3–412, where they were banded, identified, and then promptly released. The senior author is responsible for the subspecific identifications and for the analysis and interpretation of them.

It is of incidental interest that a large proportion of the Savannah Sparrows obtained in the netting operations of the first winter, as recorded by Johnston (1956), was also obtained in field 3–412. This field was especially favorable for an intensive study, for aside from being relatively large it supported, in several of its sections, unusually high densities of Savannah Sparrows (locally, as many as 20 birds per acre). In 3–412, roughly 90 per cent of the standing crop of vegetation was comprised of forbs, with the composites *Haplopappus divaricatus* and *Heterotheca subaxillaris* as outstanding dominants; and roughly 10 per cent was made up of grasses (and low-growing sedges), including strips of *Sorghum halepense,* patches of *Digitaria* and *Cynodon,* and scattered clumps and patches of *Andropogon virginicus.*

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PROCEDURE

Since field taxonomy, which may be defined in part as the practice of making racial identifications of living birds handled under field conditions, has not been tried heretofore in this country on any sizable scale (except by Aldrich, 1952), some explanation of both the philosophical and procedural bases of the present study should perhaps be set forth.

Series for comparison.—How, one might ask, were the races identified? A series of seasonally comparable specimens of known racial identity, including ones borrowed from Johnston's series, was available in the field so that the living birds, when securely held by their tibiotarsi, could be compared directly with skins. Although many such direct comparisons were made, it was not necessary to do this in all instances, for continual practice in handling and appraising the variant individuals resulted, as we believed, in a certain steadily improving "feeling" for subtle differences and, as we proved, in a rather high degree of "internal consistency" in that given individuals twice or thrice caught were usually given approximately the same race designations on initial and subsequent occasions.

Consistency of identifications.—In what way, exactly, was this check on consistency made? First, a grid was set up with 17 categories of possible subspecific allocations (as *labradorius, labradorius* > *savanna, savanna* > *labradorius,* etc.) arranged both vertically and horizontally. All combinations of designations, or "combinants," were then given scores, for they were designed to represent all possible combinations of kinds of discrepancies that might result from the worker's failure to allocate an individual in the same manner on different occasions. All the identical combinants (as *savanna–savanna*) were scored 100; unlike combinants pertaining to very dissimilar races (as *labradorious–mediogriseus*) were scored 0; others ranging from very similar (as *savanna–savanna* > *mediogriseus*) to rather dissimilar (as *savanna–mediogriseus*) were marked according to the nature of the difference. The more striking or irreconcilable the difference, the lower the score. Because the scoring grid or some adaptation of it might be useful to others desirous of checking their own consistency, it is herewith reproduced in its entirety (fig. 1). In general there were lower scores, or more severe penalties,

where inconsistencies concerned dark-colored (*labradorius, oblitus*) versus light-colored race groups (*savanna, mediogriseus, nevadensis*), and higher scores where they concerned different populations within either the dark or light group. All possible combinations of discrepancies among variant classes broadly referable to a single race (as the race *savanna,* which would include *savanna* [the subdivision of "characteristic" individuals], *savanna* > *labradorius,* and *savanna* > *mediogriseus*), yielded a mean score of something less than 100. For this complex assignable to *savanna* the score was 82; for *oblitus* it was 76; for *labradorius,* 92; for *mediogriseus,* 78; and for *nevadansis,* 85. Considering all these races together, the best overall consistency score that one could possible make by twice assigning, on separate occasions, a given individual to the same

	NEV> OBL	NEV	NEV> MED	MED> NEV	MED> OBL	MED	MED> SAV	SAV> MED	SAV	SAV> LAB	LAB> SAV	LAB	LAB> OBL	OBL> LAB	OBL	OBL> MED	OBL> NEV
NEV>OBL	100																
NEV	90	100															
NEV>MED	30	90	100														
MED>NEV	20	50	90	100													
MED>OBL	30	10	20	40	100												
MED	20	20	50	90	90	100											
MED> SAV	10	10	20	40	30	90	100										
SAV >MED	0	0	0	20	10	40	90	100									
SAV	0	0	0	0	0	20	40	90	100								
SAV > LAB	0	0	0	0	0	0	0	10	90	100							
LAB > SAV	0	0	0	0	0	0	0	0	30	90	100						
LAB	0	0	0	0	0	0	0	0	10	30	90	100					
LAB>OBL	0	0	0	0	0	0	0	0	0	20	70	90	100				
OBL>LAB	0	0	0	0	10	0	0	0	0	10	20	40	90	100			
OBL	10	0	0	0	20	10	0	0	0	0	0	10	40	90	100		
OBL>MED	30	10	10	20	90	30	0	0	0	0	0	0	10	40	90	100	
OBL>NEV	90	20	20	10	30	10	0	0	0	0	0	0	0	20	70	50	100

Fig. 1. Grid for scoring degree of consistency between initial and subsequent racial identifications of individual Savannah Sparrows.

race *sensu lato* in every trial (assuming that exact "hits"—or identical combinants—plus each of the possible types of off-center hits were obtained with the same frequency) would amount to 87. Random hits and misses, involving all possible combinations, yield a mean score of 31, while all possible combinations involving misses, only, result in a mean score of 12. With some justification we may align this "all-miss score" of 12 with zero, and the "all-hit score" of 87 with 100 per cent. Thus we set up a new scale from which a final, overall consistency score may be derived. Now, among all the birds identified 36 individuals were identified at least twice (on separate occasions, usually some days or weeks apart; to the best of our knowledge, there were *no* instances of "remembered" individuals in this group). The various sorts of hits and misses were then scored by means of the grid. Averaging these figures, we obtained a mean raw score of 69 which, translated from the 12-to-87 scale to the 0-to-100 scale, gives a mean, overall consistency score of 76 per cent.

If an experienced museum taxonomist working with bird skins were to check on his own consistency in comparable fashion, taking into account the same categories of variants and scoring himself with a like grid, he would probably emerge with a higher rating of consistency than 76 per cent. But who can say that it would not be nearer 76 than 100 per cent? Should a museum taxonomist so test himself, he would of course have to guard against tricks of memory and association (thus: that open-billed skin with the pink label—*savanna*; that molting, greasy-bellied specimen—*labradorius*; and so on).

A field taxonomist, on the other hand, can easily avoid linking individual features (excepting obvious abnormalities) or band numbers with particular race designations. This is especially true when large numbers of birds are being handled in a limited period of time.

Advantage of large sample.—Even though subspecific identification under field conditions may be appreciably less accurate and hence less satisfactory than that in the museum (where the worker often has more uniform light conditions, larger series for comparison, and more time for observation, measurement, and statistical evaluation of specimens), such field identification as we undertook offered certain singular advantages, namely, that we dealt with a remarkably large sample of Savannah Sparrows in comparable plumage, in a restricted seasonal period (mostly between January 18 and February 12, 1956), from a limited wintering area (mostly from a single field, 3–412). Surely few collectors could, or would, endeavor to secure and prepare a series of comparable nature. It is therefore our view that any disadvantages inherent in the practice of field taxonomy, which admittedly may result in somewhat greater, or more frequent, errors in the ascription of *individuals,* are more than offset by the advantages inherent in the handling of a large *mass* of individuals.

Recognition of intermediates.—One further advantage in our field approach is that we were cognizant, at the outset, of the presence of racially atypical or intergradient birds. Whereas ornithologists making extensive studies of racial variation usually take into account specimens showing intermediacy (as, for example, Peters and Griscom, 1938), there is a tendency even in some monographic studies to regard geographic races —not only isolated races but also nonisolated ones which intergrade with neighboring races—as though they were more or less satisfactory entities or units, and to attach names accordingly. A number of others (for example, Rand, 1948:428) have levied similar criticism, but it nevertheless bears repeating in different words and contexts. It is all too usual for a single trinomial, designating simply one geographic race or another but giving no indication of intermediacy or other variant condition, to be applied to a specimen or series of specimens. This seems especially true of routine identifications. For instance, among 22 Savannah Sparrows taken in southern Georgia in recent years, all were ascribed by well-known taxonomists to one subspecies or another, with no suggestion of intermediacy written on any of the labels. The same was true of 15 Song Sparrows (*Melospiza melodia*). A like tendency is amply reflected in numerous state bird books in which species accounts *as such* are nonexistent; each species, haplessly, is fragmented as so many geographic race-units. There is nothing original in this criticism; it has been expressed by reviewers (as Johnston, 1955) in the past and will probably need repeating in the future. This accentuation, if not exaltation, of the geographic race at the expense of the more nearly objective species category may be found not only in state works but in many annotated lists and other writings (even the Bent life-history series); such a convention, seemingly inexorable, may well encourage the taxonomist's practice of applying neat trinomials referring to one race *or* another to the vast majority of specimens handled. And the converse may be true—causal relationships are not always clear. Thus, on specimen labels as well as in manifold writings, undue stress has been placed on populations conceived, at least by implication, to be essentially characteristic of given geographic races, and too little stress has been placed on those populations whose characters are intergradient or atypical in one way or another. Consequently, we believe that the actual situation is best presented by an emphasis, if not overemphasis, on the relative numbers of atypical or intermediate individuals.

Desirability of naming variants.—In designating the different sorts of variants in Savannah Sparrows, we have felt it better to use Latinized subspecies names instead of

breeding-range designations, which would offer no advantage with respect to wintering populations, or number designations, which might be less cumbersome in labeling various intergrades but which are, to our minds and others' as well, not nearly so peculiar, euphonious, or interesting as are names. As Ernst Mayr has written (*in* Sibley, 1954: 108): "With subspecies names we can designate phenotypically similar populations regardless of geography. Since it is the object of the classifier to designate such phenotypically similar populations, I don't see how, particularly in insular regions, he can do without subspecies, but he must realize at all times that the subspecies is a strictly arbitrary concept." Although we may wonder a little about the word "strictly" as used by Mayr, we are in essential agreement with the thoughts in this quotation. Despite the fact that the subspecies is anything but a neat, objective category, we recognize the value of making, as best we can, subspecific identifications of both living, banded birds and collected specimens, "regardless of geography." In so doing we learn among other things something of relative abundance, of habitat preference and other aspects of niche, of general region of birth or breeding of individuals (which might be verified by recoveries), and of approximate distances traveled as well as general directions taken by the different geographic variants.

Previous work in field taxonomy.—We should like to emphasize that some precedent for studies in field taxonomy may be found both in this country (Aldrich, 1952) and in at least one bird observatory in Britain (Williamson, 1949, 1950). It seems likely that more studies of this nature, including ones embodying such refinements as temporary anaesthetization of captive birds and extensive collection of millimetric, gravimetric, and colorimetric data, will appear in the not-distant future. In fact, Williamson and his associates (*ibid.*) have already made a significant start in this direction.

BRIEF CHARACTERIZATION OF THE RACES

Some of the more salient aspects of plumage coloration and markings, as well as of breeding distribution, are presented below. These descriptive notes are based, in the main, on Peters and Griscom (1938), Wetmore (1939, 1940), and Aldrich (1940). These workers, among others, have recognized that color characters are far more useful than linear dimensions or proportions in the identification of races of the Savannah Sparrow occurring near or along the eastern coast. For convenience in discussions beyond, we subdivide this assemblage into two groups, the light and the dark races.

Light Races

P. s. savanna.—Nova Scotia, Prince Edward Island, Magdalene islands, and part of Newfoundland. Dorsal surface: generally medium brown; feathers with dark centers and light brown edgings. Sides of head: relatively light colored, often with buffy suffusion; loral region usually yellow or yellowish. Ventral streaks: somewhat reduced (as compared with dark races), medium to dark brown. Greater secondary coverts: medium brown.

P. s. mediogriseus.—Gaspé Peninsula south (excluding Nova Scotia) to New England and New Jersey west to Minnesota and Iowa. Dorsal surface: generally grayish brown (grayer and darker than *savanna*); feathers with dark or blackish centers, with light grayish brown or brownish gray edgings. Sides of head: colors usually of medium depth, more or less grayish brown, sometimes with ochraceous suffusion; loral region yellow, olive-yellow, or whitish. Ventral streaks: somewhat reduced, medium to dark brown or grayish brown. Greater secondary coverts: medium grayish brown.

The population described as *mediogriseus* by Aldrich (1940) is in our opinion a valid race readily separable from *savanna,* although it might on occasion be confused with intermediates between *oblitus* and *nevadensis,* or even with *nevadensis* whose characters, as shown by specimens from the breeding ground, are not particularly constant (Peters and Griscom, 1938:469, 470).

P. s. nevadensis.—British Columbia and Alberta south to northern California, Utah, and Nevada, east to Minnesota and southern Wisconsin. Dorsal surface: pale gray; feathers with dark centers

reduced and with broad, pallid edgings. Sides of head: relatively grayish; loral region with limited area of creamy or pale yellow. Ventral streaks: reduced, brownish or grayish brown. Greater secondary coverts: relatively pale brownish gray. (The bill of this race is relatively narrow.)

Dark Races

P. s. labradorius.—Northern Ungava south and east to Labrador and Newfoundland. Dorsal surface: very dark, black and brown; feathers with extensive black markings and rich brown edgings. Sides of head: relatively dark, especially in auricular region, with brown and buff elements noticeable; loral region usually bright yellow. Ventral streaks: heavy, usually deep brown or black. Greater secondary coverts: dark, warm brown.

P. s. oblitus.—West side of Hudson Bay south to northern Minnesota, east to central Quebec. Dorsal surface: dark to very dark, black and gray; feathers with extensive black markings and light gray edgings. Sides of head: relatively dark, especially in auricular region, with brown and buff elements lacking; loral region usually bright yellow. Ventral streaks: heavy, usually deep brownish black or black. Greater secondary coverts: medium or relatively light brown or grayish brown.

Table 1

Relative Abundance of Races of the Savannah Sparrow in the Savannah River Plant Area*

Time of year (1955–56)	Light races				Dark races			All races (Totals)
	mediogriseus	*savanna*	*nevadensis*	Totals; percentages	*labradorius*	*oblitus*	Totals; percentages	
Oct.	7	3	0	10 (62.5)	4	2	6 (37.5)	16
Nov.-Dec.	19	4	2	25 (89.3)	1	2	3 (10.7)	28
Jan.-Feb.	132	139	30	301 (64.5)	86	80	166 (35.5)	467
Mar.-Apr.	10	10	2	22 (50.0)	10	12	22 (50.0)	44
May 4–10	0	0	0	0 (0.0)	2	2	4 (100.0)	4
Totals	168	156	34	358	103	98	201	559
Percentages for races and groups	(30.1)	(27.9)	(6.1)	..... (64.1)	(18.4)	(17.5)	..... (35.9)	.....

* Included are 22 specimens from southern Georgia (non-selective collections).

RESULTS

Relative abundance of races.—As shown in table 1, the five subspecies reported by Johnston (1956) were again found in the winter of 1955–56. In the grand total of 559 records, 447, or 80 per cent, pertain to the January-February sample of banded birds. The remaining records refer in part to banded individuals, in part to collected specimens. Included among the specimens are 22 birds collected in southern Georgia (previously mentioned); the rest are from the Savannah River Plant area.

As is evident in table 1, the more southern, light-colored races *mediogriseus* and *savanna* were most often encountered in the old fields. Their relative prevalence is very similar, and together they comprise about 58 per cent of the total sample. The more northern, dark-colored races *labradorius* and *oblitus*, of which one was about as common as the other, together make up close to 36 per cent of the total. The westernmost race *nevadensis* contributes about 6 per cent and, as one might expect on geographic grounds, is clearly the least abundant among the five races. In aggregate the lighter colored races account for about 64 per cent of the whole sample and thus outnumber the darker races almost two to one. It is possible that the poor representation of *labradorius* and *oblitus* in the November-December subsample is misleading, for in this period among twenty-odd Savannah Sparrows closely observed with binoculars at least a third was comprised of decidedly dark individuals which, had they been collected, would probably have been referable to the *labradorius-oblitus* group.

In the early 1940's the race *nevadensis* had been reported as far east as Ohio (Aldrich, 1940) and Mississippi (McAtee *et al.*, 1944:156). Its presence, as well as that of *oblitus,* in the samples from South Carolina provides additional evidence of considerable eastward as well as southward migration. Of these more western races, there is some evidence that *oblitus,* at least, is relatively more common on the coast of Mississippi than in the southern Atlantic coastal region. Thus, in the former area Burleigh (1944:146, 147) collected 53 specimens of the Savannah Sparrow, of which 24, or almost half, were referable to *oblitus.* Among the remaining races the breakdown was: *savanna,* 18; *mediogriseus,* 7; *labradorius,* 3; and *nevadensis,* 1. Despite the fact that west-to-east movements are characteristic of some of the migrants of this species, it is

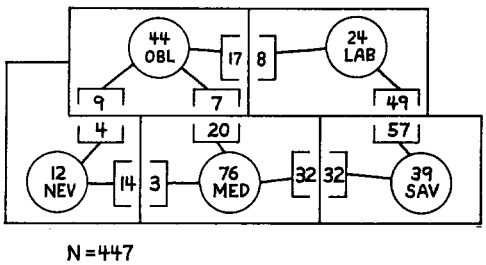

Fig. 2. Numbers of characteristic individuals (encircled figures) and intermediates (figures in brackets) among the races of the Savannah Sparrow in the sample of banded birds of January-February, 1956. Intermediates are subdivided to show nearest racial affinities.

clear that many of the birds travel chiefly in southward and, considering the profile of eastern North America, in south-southwestward directions.

Intermediates.—As we have noted, a number of the birds could not be placed exactly as to race and so were classed as intermediates. All intermediates were judged in terms of whether they seemed nearer one race or another (fig. 2). It is possible that some individuals were intergradient between three races, but no attempt was made to set up categories with three trinomials. The intergrades or "non-characteristic" individuals accounted for about 56 per cent of the large January-February sample. (Essentially the same percentage applies to the total array.) Among birds assigned to three of the races —*savanna, labradorius,* and *nevadensis*—"characteristic" individuals indeed seemed in the minority, whereas those assigned to *oblitus* and to *mediogriseus* seemed relatively more frequent.

Partial confirmation of the results from our study of intermediates, which was done almost entirely on the basis of coloration, was obtained when we averaged wing-length in each of two intermediate groups (*labradorius* x *oblitus* and *labradorius* x *savanna*) and found the average for each intermediate category to be less than that of the relatively long-winged *labradorius,* but greater than that of the shorter-winged races *oblitus* and *savanna* (whose own mean wing lengths are subequal). Further information on wing measurements is discussed beyond.

If the proportion of intermediates between two races be taken as indicating the magnitude of the zone of intergradation between or, better, the degree of overlap between or "inseparability" of those two races, and if we consider only the four races that are better represented (omitting *nevadensis*), we may say that subspecific overlap appears greatest between *savanna* and *labradorius,* less between *savanna* and *mediogriseus* and

between *oblitus* and *labradorius*, and least between *oblitus* and *mediogriseus*. We did not attempt seriously to subject our data on intermediacy or overlap to statistical treatment. Whereas it would be possible to set up linear arrangements of number sequences for races and intergrades, calculate standard deviations and other statistics, obtain *t* values or "joint nonoverlap" figures, etc., this would be of little consequence if only because the exact nature and relative degree of difference between mean values for the races would be so poorly known.

The fact that so many birds fell in the category *savanna* x *labradorius* may merely reflect our having too narrow an idea of the scope of variation in "characteristic" birds of either group. Any line or zone between the two would be more or less arbitrary, even in museum taxonomy, and probably no two workers would show it in quite the same way. Nevertheless, the apparent preponderance of these intermediates might reflect, first, what may be in point of fact an extensive zone of intergradation—in Newfoundland and perhaps elsewhere—between *savanna* and *labradorius* and, second, a stronger tendency for the northernmost and westernmost segments of the breeding population of *labradorius*, wherein dark coloration seems to reach its highest expression (cf. Wetmore, 1940:568), to travel farther south—to the gulf coast and into Florida—than do many of the more southern, less well characterized populations of this race.

Weights, measurements, and ratios.—The weights of specimens averaged about 17 grams in fall and winter, showing increases, which were apparent in all races, in late winter and spring (table 2). *Oblitus* averaged heaviest; *labradorius*, oddly enough, and *mediogriseus* were lightest; the small samples of *savanna* and *nevadensis* seemed intermediate. Actually, interracial variation in weight in the races of Savannah Sparrows under consideration is relatively low, the smallest race weighing about 92 per cent as

Table 2

Mean Weights, in Grams, of Races of the Savannah Sparrow Based on Collected Specimens

	labradorius	*oblitus*	*mediogriseus*	*savanna*	*nevadensis*
October	16.3 (3)*	17.0 (2)	16.8 (4)	17.8 (4)	.....
December-January	16.7 (2)	18.2 (1)	17.1 (6)	16.5 (2)	17.7 (1)
February-March-April	17.5 (3)	19.7 (8)	18.0 (6)	19.4 (5)	18.6 (1)
May	21.3 (1)	17.9 (1)	.....	.....	.....
Means by race	17.3 (9)	19.0 (12)	17.4 (16)	18.3 (11)	18.1 (2)

* Number of individuals.

much as the largest. By contrast, in Fox Sparrows (*Passerella iliaca*) the smallest race weighs only 71 per cent as much as the largest (calculation based on Amadon, 1943:173, table). The total of 50 weights for the five races of Savannah Sparrow obtained at different times in the nonbreeding season indicates an overall average of 18.0 grams (table 2).

Measurements of wing length (chord) were recorded to the nearest millimeter, mostly by the junior author, from nearly all the 447 sparrows banded in January-February, 1956. Means based on this sample are as follows: *labradorius*, 69.4; *oblitus*, 68.1; *savanna*, 67.8; *nevadensis*, 67.4; and *mediogriseus*, 67.3. In all races the range was considerable, extending from about 61–63 to 72–74 millimeters. In this sample the range, like the mean, necessarily pertains to both sexes. Compared with *oblitus*, *labradarius* seems to have a slightly longer wing, not only absolutely but also relative to body weight. Although *mediogriseus* resembles *labradorius* in its light weight, it differs from the darker race in having an appreciably smaller wing (in both length and area). Table 3 gives a more precise comparison of wing size relative to body weight. Thus, in *labradorius* the wing is large in relation to body weight, in *mediogriseus* it is small, and in

the other races intermediacy is shown. Taken as a group, the dark races, coming from high latitudes, feebly illustrate "Bergmann's rule," in which more northern races tend to be larger or heavier than more southern ones. If, however, the more northern and hence presumably more strongly migratory races have larger or longer wings relative to body weight (cf. Mayr, 1942:92), this is clearly suggested only in the comparison of *labradorius* with *mediogriseus*.

Table 3

Relative Wing Length and Wing Area in Races of the Savannah Sparrow

Ratios*	*labradorius*	*oblitus*	*mediogriseus*	*savanna*	*nevadensis*
WL/Wt	100.0 (18)**	95.0 (12)	97.0 (16)	96.3 (11)	96.6 (2)
WA/Wt	97.5 (4)	98.6 (7)	96.0 (5)	100.0 (5)	98.2 (2)
WS/Wt	100.0	98.0	97.7	99.4	98.5

* The ratio WL/Wt was derived by taking wing length, in millimeters, × 3.73 over cube root of weight; for a discussion of this procedure see Amadon, 1943. The ratio WA/Wt was derived by taking square root of wing area (wing fully outstretched, traced, and measured with planimeter), in square centimeters, × 3.68 over cube root of weight. In each instance the factor given in the numerator is the one required to increase the largest of the included ratios to 100 (cf. Amadon). The ratio WS/Wt is an average (unweighted) of the other two ratios, again multiplied by an appropriate numerical factor so that the largest ratio is increased to 100.

** Number of individuals.

Fall arrival and spring departure (1955–56).—In field 3–412 the first Savannah Sparrow was glimpsed in the early afternoon of September 27. An hour or so later call-notes of this species were heard. (On the 26th, when considerable time was being spent in this field, there were no signs of sparrows.) According to the senior author's notes: "Next day [the 28th] I saw 3 together in another part of this field, and I shot at one but missed. On the 29th I noted several individuals—all singles—in different parts of 3–412 . . . . Probably 4 were seen and/or heard. Stalked and followed two of these in vain, again failing to get a specimen." On October 3 and 4 three collections were made—two *oblitus* and one *labradorius*. By the 10th "Savannah Sparrows had increased somewhat . . . ," and in the latter part of the month there were observations, on different days, to the effect that "although the birds have increased since the first week in October, the increase has not been very great." On November 3 the following entry was made: "Savannah Sparrows seem to be commoner and more widely distributed over the fields hereabouts than at any time before. I didn't flush many, but I was impressed with the number of *tzeet*s heard over the fields and the many different spots from which they emanated. Too, as the birds have been getting more common, so they have been getting tamer—flushing close at hand and flying no great distance. They are proving to be visible on the ground now and again, contrary to the way things were earlier in the season, when the vegetation was denser and the birds more wary." (By November 7 censusing of sparrows was under way.)

Although exact quantitative data on abundance are lacking for both October and April, the decline in the sparrow population in early April seemed more abrupt than the build-up in late October. Yet some birds remained into May, and the last, a lone individual in field 9–111, was seen on May 16. As indicated in table 1, specimens obtained in May belonged to the dark races *labradorius* and *oblitus*.

Habitat and population density.—As Johnston (1956) and Hight and Odum (1956: in press) have brought out, Savannah Sparrows may occur both in old fields and in moist, marshy, shallow basins called "Carolina bays." For the general region the habitat afforded by the bays, in contrast to that in the fields, is areally restricted and is, in a sense, less satisfactory for study purposes, for the sparrows can make only limited use of these grassy expanses except at times of low water, when both the substratum and

myriads of fallen seeds become exposed. The bays were mostly filled with water in the winter of 1955–56, so in this season almost all attempts to appraise the composition and density of populations were carried out in old fields. As reported by Johnston (1956), for one Carolina bay and two rather dissimilar fields (one supporting grasses predominantly and the other composites and other forbs), there was no indication of habitat (or other) segregation of the races of Savannah Sparrow. So far as could be shown by the nettings operations in January-February, 1956, as well as by other observations, captures, and collections made in the same winter, a similar lack of segregation among the races of Savannah Sparrow again seemed to be the rule. This seemingly complete spatial overlap of the races on their wintering ground may be presumed to be selectively advantageous to the species as a whole.

In the course of the winter of 1955–56 the senior author, using two census methods found to yield closely comparable results, endeavored to work out an approximation of the overall density of Savannah Sparrows in old-field areas. One method, briefly put, involved a 1⅓-acre circular quadrat over which a rope, with one end looped over a stake, was dragged half or full circle; by whirling or whipping the rope one could cause every sparrow—with rare exception—to leave the ground (and often leave the quadrat, also, on the first flight). The other method involved a transect approximately 100 feet wide and of variable length; within this strip a certain proportion—averaging close to 50 per cent—of all sparrows on the ground would flush (the farther from the center line, along which the observer walked, the fewer the birds that would show themselves). Hence the total number of birds flushed times a correction factor (approximately two) enabled the calculation of density per acre. Tests revealed that this estimate of density was very close to that obtained from rope-dragged quadrats. Whenever there was doubt as to the identity of sparrows that flushed, the birds were pursued and flushed again; after a second or third flushing, one could usually be certain of the species. Compared with the Savannah, other sparrows including the Vesper, Grasshopper, and Leconte, were encountered in the old fields only infrequently. Savannah Sparrows in fact comprised about 75 to 80 per cent of the individuals among all birds wintering in the fields.

Table 4 contains a summary of the density of Savannah Sparrows as it was recorded in about 70 different fields. The numbers as shown for the December-early January period may be a little too high, for in this period a good deal of the censusing was done

Table 4

Density of Wintering Savannah Sparrows in Old Fields in the Savannah River Plant Area, South Carolina

Period (1955–56)	Number acres censused	Number fields sampled	Number sample areas*	Average number Savannah Sparrows per acre
November	23.4	20	49	3.6
December-early January	71.0	35	39	6.1
Late January-February	49.5	12	38	3.6
March	53.1	26	51	3.5
May 4	27.1	1	5	0.1
Totals and grand average	224.1	(about 70)	182	3.94

* Circular quadrats and/or transects. For methods of censusing, see text.

in comparatively favorable parts of one field, 3–412, in which counts of 8 to 15 or more sparrows per acre were not uncommon. In fields of crabgrass (*Digitaria*) near Raleigh, North Carolina, similar high counts of Savannah Sparrows were made by Quay (1947: 386), who reported "an average of 67 individuals per census on plots that averaged eight acres in size [or about 8.4 birds per acre]." Quay's findings (*ibid.*: 385) not only

in areas of crabgrass but also in other types of open habitat (ranging from "Bare Field" to "Tall Weeds-Broomsedge" and "Broomsedge-Pine") suggest, however, a considerably lower overall density of Savannah Sparrows, possibly only two or three birds per acre, in what might be called an abstract, heterogeneous community of old fields in different stages of succession. It is probable that comparable heterogeneity obtained in the fields dealt with in the present study: some in 1955–56 were in their fourth year of abandonment, while some had lain fallow even longer; some were decidedly more

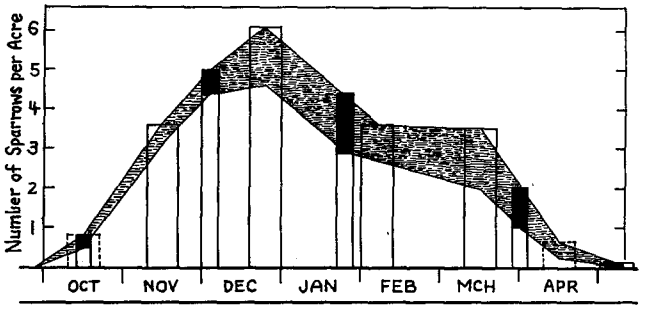

Fig. 3. Population of Savannah Sparrows in old fields in Savannah River Plant area. Height of broad bars represents density per acre, and narrow bars, with heights adjusted to curve suggested by the broad bars, show relative abundance of dark and light races (black and white areas, respectively). Hatched zone suggests relative abundance of two race groups in course of the sparrows' winter sojourn. Broad bars for October and April based only on rough estimates.

"grassy," while others were more "forby" (as determined by a semi-quantitative rating system). Details as to density of Savannah and other sparrows in relation to grassiness or forbiness of fields will be provided in a subsequent report. Even though the December-early January estimate of 6.1 birds per acre (table 4) may be somewhat high for the abstract community of fields in early winter, the grand average of approximately 3.9 Savannah Sparrows per acre is rather little affected by the high count and is deemed a close estimate of general density of the wintering population in more or less favorable habitat.

Some idea of the build-up, apparent peak, and decline of the population is conveyed in figure 3. Here we may note that shortly before the drop-off in numbers in early April, a relatively high proportion (50 per cent) of dark races was recorded; after the April drop-off there were only four specimens plus two or three close observations. These specimens, it will be recalled, pertained to examples of the dark races; the observations, also, *seemed* to refer to dark birds. There remains a strongly suggestive pattern in which the light races, as compared with the dark, are more abundant in the first part of the nonbreeding season and gradually become less abundant with the passage of the second part and the approach of the breeding season. Because the advent of the breeding season is relatively late for the more nearly boreal populations of *oblitus* and *labradorius,* it is not surprising that these races seem well represented among those individuals lingering until May on the southern wintering ground.

SUMMARY

In the Savannah River Plant area, Aiken and Barnwell counties, South Carolina, the Savannah Sparrow (*Passerculus sandwichensis*) was the most abundant bird inhab-

iting old fields that had been abandoned for three or more years. In January-February, 1956, some 447 individuals were caught, banded, and released (mostly in a single, large field); other birds, collected or banded at other times, brought the total sample to 559.

Aided by a series of sparrows identified as to subspecies or geographic race, we endeavored to assign race designations to all individuals that were handled. Birds considered racially atypical or non-characteristic were designated as intermediates but were always placed nearer one race or another. We found, as had Johnston (1956), who had assembled a series of specimens from the same area in the previous winter, that the population of Savannah Sparrows included birds referable to five races. Our figures on the relative abundance of these races were as follows: *P. s. mediogriseus,* 30.1 per cent; *savanna,* 27.9; *labradorius,* 18.4; *oblitus,* 17.5; and *nevadensis,* 6.1. Thus *labradorius* and *oblitus,* both dark-races with more northern breeding grounds, comprised about 36 per cent of the entire sample. Many of the birds wintering in the Savannah River Plant area had necessarily migrated eastward as well as southward; this "migratory drift" is best illustrated by the western race *nevadensis,* relatively uncommon in our sample. More than half the total birds examined were considered racial intergrades or non-characteristic individuals. Weights of specimens, averaging about 17 grams in fall and winter, increased to about 19 grams in spring. Specimens of the smallest-sized race *mediogriseus* weighed about 92 per cent as much as those of the heaviest race *oblitus.* In *labradorius* the wing was large relative to body weight, in *mediogriseus* it was small, and in other races intermediacy was shown in this proportion.

In 1955–56, the first autumnal migrant was noted on September 27. Common by early November, the species was abundant throughout the winter. Its numbers declined abruptly in early April, and the last bird was seen on May 16. For the nonbreeding season as a whole, in an abstract community involving about 70 different fields, there was an average of approximately 3.9 Savannah Sparrows per acre (as determined by two census methods). The dark races *labradorius* and *oblitus,* while represented among the earliest arrivals in fall, became relatively more prevalent in early spring, and were the only races recorded as late as May. There was no evidence of differential habitat selection or other segregation among the different races. This seemingly complete spatial overlap of the racially different populations, which had "funneled down" from far-flung breeding areas in the northern United States and Canadian regions, is presumed to be selectively advantageous to the species on its wintering ground.

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