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DENSITY, RACIAL COMPOSITION, SOCIALITY, AND SELECTIVE PREDATION IN NONBREEDING POPULATIONS OF SAVANNAH SPARROWS

By ROBERT A. NORRIS*

The study of populations of plants and animals under laboratory conditions is generally predicated on the belief that such populations, although not always accurately illustrative of plant-animal groupings under natural circumstances, do tend to exhibit, even if in oversimplified, overaccentuated, or otherwise imperfect fashion, population characteristics which are not unlike those inherent in more complex states of nature. It follows that, at least with respect to larger organisms such as vascular plants or vertebrates, concerted studies of populations under *seminatural* conditions lead to better understanding of many aspects of the structure and dynamics of natural populations than do studies carried out under more artificial, experimental conditions. It would seem, further, that concurrent study of given organisms in a relatively simple, seminatural population, which might also be described as semi-experimental, together with the same organisms in a relatively complex natural population, affords a most promising means of gaining insight into the nature of the latter population. If field conditions are not carefully simulated in the laboratory, then the laboratory becomes a modified part of the field.

The seminatural population involved in the present study occupied a part of a field; it was small, being controllable as to size or density; it was confined by an enclosing barrier; it was susceptible to a measure of experimental manipulation. Ground surface, cover and food, and other environmental features were essentially the same for this limited population as they were for a natural population inhabiting the same general area. More specifically, a group of wing-clipped, color-banded Savannah Sparrows *(Passerculus sandwichensis)* was kept in a large enclosure; both the enclosed space and much larger, exclosed areas were characterized by open herbaceous vegetation. The area was populated by a rather dense assemblage of flying Savannah Sparrows, many of which visited the enclosure and mingled with the wing-clipped birds. Hence there was opportunity to investigate both the natural and seminatural populations and to learn something of their interactions as well as of their separate characteristics.

At present there tend to be gaps, whether these be at conceptual or at working, methodological levels, between "experimental populations"

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*Present address: 427 Eureka St., San Francisco 14, Calif.

and "natural populations." They are usually regarded as rather different entities (see, for example, Allee *et al.*, 1949: 333 ff.). It is my belief that the establishment and study of seminatural populations which are subjected to a measure of experimentation will tend eventually to bridge this gap and thus lay due stress on the already apparent fact that "experimental" and "natural" populations are, for the larger part, different not so much in kind as in degree. It is hoped that the present study will be of some help in building this bridge.

SETTING AND GENERAL PROCEDURE

The Savannah River Plant, operated jointly by the Atomic Energy Commission and E. I. Du Pont de Nemours & Company, occupies a fenced-in tract of more than 200,000 acres in Aiken, Barnwell, and Allendale counties on the Upper Coastal Plain of South Carolina. When the plant site was established in 1951, with the prime object being the production of materials used in the manufacture of the hydrogen bomb, all the residents of the area sold their properties to the government and moved out, leaving behind vast acreages on which field crops had been grown. These open farmlands were soon replaced by old fields, which have received special attention from biologists from the University of Georgia and the University of South Carolina. Working under AEC contract, these biologists are carrying on faunistic, floristic, and ecological studies in the Savannah River Plant area. Much of my own work has concerned wintering populations of sparrows, particularly the Savannah Sparrow, which is the most abundant bird inhabiting open, herbaceous vegetation of old fields in the nonbreeding season. Previous accounts of the Savannah Sparrow in the region in question have dealt with racial taxonomy (Johnston, 1956), field taxonomy and populations in abstract communities (Norris and Hight, 1957), and certain population characteristics as assessed by means of data from "repeat" and "return" records of banded sparrows (Odum and Hight, 1957).

The investigation reported in the present paper comprises two broadly overlapping phases: (1) the study, in the winters of 1955-56 and 1956-57, of natural populations of Savannah Sparrows in a large field area, no. 3-412, with additional, less intensive studies in many other fields; and (2) the study of a seminatural population of wing-clipped sparrows of the same species kept inside a one-acre, circular enclosure from January through May, 1957. Field 3-412 and vicinity, as well as the location of the enclosure, are illustrated in figure 1. (Ellenton Bay, a "Carolina bay," comprises a shallow marshy basin which, because of high water levels in both winters, was visited by very few of the sparrows.) The several parts of 3-412 in which most of the work was done (E, A, SW, and B) make up approximately 100 acres. The enclosure was built in B, an 11-acre section, for it was here that the sparrows and their natural food were most abundant. The barrier for the enclosure, which was constructed in December, 1956, was some 2½ to 3 feet high and was built of posts, poultry wire, and plastic storm-window material. All the way round there were two sheets of plastic, one on each side of the wire mesh; both sheets were secured by strips of tape and, along the bottom, by heavy shovelfuls

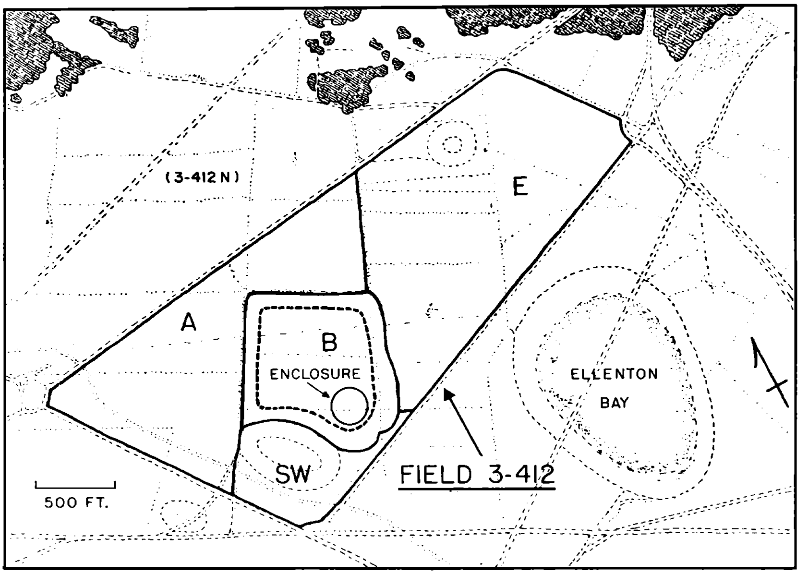

Fig. 1. Field 3-412 and vicinity, Savannah River Plant area, Aiken County, South Carolina. In winters of 1955-56 and 1956-57 studies of Savannah Sparrows were centered here; special attention was given B part and its one-acre enclosure, in which wing-clipped sparrows were kept.

of earth. Although the barrier needed minor repairs from time to time, it remained intact and essentially wind-resistant for five months. (When beset with the heat and heavy rains of early summer, however, the plastic material finally gave way.) To my knowledge none of the wing-clipped sparrows, which were introduced singly or in small groups in January, February and March, 1957, escaped from the enclosure. As the size of the enclosure exceeded that of the area occupied by any one of the confined birds, it is proposed that the term "*beta-confinement*" be used to distinguish between this situation and that pertaining to birds in very small enclosures or cages *("alpha-confinement")*.

Special procedures employed in the study are described (or appropriate references given) under various topics in subsequent sections of the paper.

Acknowledgments.—In the winters of 1954-55, 1955-56, and 1956-57, several hundred Savannah Sparrows were caught for purposes of banding and release. Many of these were from the 3-412 area. The services of persons who aided in driving sparrows into Japanese mist-nets in the first two winters have been acknowledged in previous papers (Johnston, 1956; Norris and Hight, 1957; Odum and Hight, 1957). Although in most respects the present study has been the responsibility of a single person, some of the data (especially those on racial composition) derive from the large samples of netted sparrows. Accordingly, I wish to express my appreciation to the following workers who helped with sparrow drives in 1956-57: John V. Barrows, B. R. Chamberlain, Clyde E. Connell (who was studying the weight and fat cycle in caged Savannah Sparrows), J. B. Gentry, Gordon L. Hight, Jr. (who banded many of the birds), Herbert W. Kale, and Eugene P. Odum. Dr. Odum, who supervises the University of Georgia ecological studies in the Savannah River Plant area, lent further help by arranging for the purchase of materials used in building the enclosure. The investigation was carried out under Contract No. AT (07-2)-10 with the Division of Biology and Medicine, U. S. Atomic Energy Commission. I am indebted to Drs. Keith L. Dixon and Francis C. Evans for their reading the manuscript and providing helpful criticism.

POPULATION DENSITY

Appraisal of population density: methods and results.—In the winter of 1955-56 I made use of two methods of estimating the density of populations of Savannah Sparrows and other open-field fringillids. These procedures were outlined previously (Norris and Hight, 1957: 49) as follows:

"One method, briefly put, involved a 1 1/3-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 percent—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 density 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 [*Pooecetes gramineus*], Grasshopper [*Ammodramus savannarum*], and Leconte [*Passerherbulus caudacutus*] were encountered in the old fields only infrequently."

From November, 1955, through March, 1956, in an abstract community involving about 70 different fields (these showing wide variation from forbiness to extreme grassiness), my census data obtained by means of circular quadrats and transects yielded average values ranging from about 3.5 to 6.1 Savannah Sparrows per acre, with a grand average of about 3.9 (Norris and Hight, 1957: 49). The first birds arrived in the last week in September. Their numbers built up gradually to peak densities in December and early January, remained large throughout March, and then declined rather abruptly in April. Only scattered individuals were to be found in late April and May *(ibid.)*

In 1956-57 the sparrows presented a similar picture. In this winter season, studies of population density were confined to about 100 acres which comprised a large part of field 3-412. For present purposes we shall consider this 100-acre tract, including parts E, A, SW, and B (fig. 1), as though it represents the whole field. In 1956-57 census methods were better standardized than they were in the previous year. Viewed as a whole, the density of sparrows in 3-412 in this season was

Table 1. Density of Savannah Sparrows in Field 3-412, Savannah River Plant Area, in 1956-57

Period	Number of Censuses in Period		Average Number of Savannah Sparrows per Acre					Percent of Total Population in B Part
	*B	A,E,SW	B	A	E	SW	All Parts (100 acres)	
(1) Oct. 8–25	4	4	2.2	1.1	0.7	0.5	1.2	20
(2) Oct. 29–Nov. 1	2	2	*8.8*	1.9	1.2	**3.6**	*2.6*	*40*
(3) Nov. 6–14	3	3	4.2	2.2	1.3	2.1	2.0	24
(4) Nov. 17–30	3	3	9.8	4.1	**2.6**	3.2	3.8	29
(5) Dec. 6–14	2	2	13.2	**4.9**	2.4	**4.0**	4.6	32
(6) Jan. 3–14	8	2	**29.0**	**5.0**	1.2	1.9	**5.5**	**60**
(7) Jan. 21–Feb. 22	6	4	**27.8**	3.4	**2.6**	0.5	**5.5**	**57**
(8) Mar. 2–25	7	3	6.7	1.2	1.9	0.0	2.6	39
(9) Mar. 29–Apr. 22	6	3	1.8	0.9	0.4	0.2	0.7	30
(10) Apr. 30–May 10	2	2	0.6	0.3	0.1	0.0	0.2	(65)

* Parts of field indicated by letter symbols are shown in figure 1.

very nearly the same as that found earlier in the abstract community. Thus, an aggregate average of average density values for the whole field in seasonal periods 3 through 8 (table 1) is 4.0 birds per acre. The B part of the field clearly supported the greatest concentration of sparrows: in the November-March period its density was about four times that of the "average" field, while in January and February it was more than five times that of the average field. The fact that between November and March the 100-acre tract supported, on the average, about four Savannah Sparrows per acre, indicates that some of its subdivisions, including most of the extensive E part, provided habitat of substandard quality. The extremely high averages of 28 to 29 birds per acre in 3-412B from early January to late February lead one to suspect that this period, rather than December and early January (as suggested by 1955-56 data), may be the usual one in which maximum populations are to be found.

When the sparrows were most abundant in the B part (as well as in the whole field), an unusually high proportion of the total population (57 to 60 percent) was concentrated in the B part (table 1). This suggests that with increase in density the birds become less tolerant of the poorer parts of the field and are increasingly prone to frequent those parts with the richest seed supplies. (The sparrows appear to be tolerant of considerable crowding as long as food and cover are adequate.) As noted beyond, the B part had a particularly heavy crop of *Digitaria* seeds in 1956-57 (more than in previous years). Hence it was not altogether surprising to find that in mid- and late winter this part was supporting more than half the sparrow population in the 100-acre tract. Even so, it was of especial interest to learn that such a small section as B could support an average population of Savannah Sparrows which was in excess of 300 individuals.

There was a distinct, albeit minor, rise in the population on October 29 and November 1. This suggests that a migratory "wave" was passing through. Even if this be true, many of the individuals then present may well have been members of the wintering contingent. Although this late-fall peak was noticeable in the SW part as well as in the field as a whole, it was particularly obvious in the B part where, for a few days, there was an average of about 9 birds per acre (table 1). It was late November before this density was reached again. It is worth noting that during the late-fall peak about 40 percent of the total population was centered in B. In a small way this situation is analogous to that obtaining in the periods of high "centralized" density in January and February.

Savannah Sparrows began to leave 3-412 about the end of February. Their numbers declined sharply in March. In 1957 mass departures took place about a month earlier than in 1956. On March 23, 1956, there were no less than 4.5 sparrows per acre in 3-412 (about 10 per acre in the B part). By contrast, on March 25, 1957, the field had but 1.3 birds per acre (the B part about 2 per acre). From these samples it would seem that in late March, 1956, the population was more than three times as great as it was at the same time of the following year.

Relation between density of sparrows and frequency of Digitaria.—Like many other fringillids, the Savannah Sparrow has long been known as an eater of grass seeds (Judd, 1901). It was noted that one sort of grass, *Digitaria* spp., was far more abundant in 3-412B than in other parts of the field. An estimate of its relative frequency was obtained by dropping a metal hoop (which enclosed one square meter) onto the ground at regular paced intervals and by investigating each of the enclosed "temporary quadrats" for a period of one-half minute. In this brief, standardized period I would count the visible, whitish sparrow droppings and check for the presence of *Digitaria.* Among 75 quadrats examined in February in 3-412B, *Digitaria* was present in 58 (frequency, 77 percent); among 45 quadrats checked in A, E, and SW parts, only 4 contained *Digitaria* (frequency, 9 percent). This was the only grass that was really concentrated in B and that was infrequent or wanting in most other parts. The fact that the Savannah Sparrows were also concentrated in B is good circumstantial evidence as to what was their main food. It was found also that sparrow droppings were more numerous where *Digitaria* was present. Among 36 quadrats (all outside the enclosure) in which this grass was detected, a total of 45 droppings, or 1.25 per square meter, was counted, whereas among 52 quadrats in which *Digitaria* was not seen a total of 26 droppings, or 0.50 per square meter, was counted. The frequency and relative abundance of droppings tend to support evidence provided by the birds themselves that the seeds of *Digitaria* are in heavy demand. Preliminary analyses of stomach contents offer further evidence that in 3-412B in particular, and in certain other fields as well, this grass provides a staple item in the diet of Savannah Sparrows. (*Cf.* Quay, 1957, 1958.)

Density as estimated by the Petersen-Lincoln index.—As mentioned previously, from early January to May, 1957, special attention was given to the seminatural, enclosed population of sparrows. All the wing-clipped birds were color-banded and could be identified individually. In the enclosed area the supply of natural food seemed adequate even for an unusually large number of birds. (The frequency of *Digitaria* as sampled by numerous square-meter quadrats was almost 100 percent.) Neither supplementary food nor water was provided until mid-February, about six weeks after the first wing-clipped birds were introduced. From mid-February on, parakeet seeds or steel-cut oats were supplied intermittently for several weeks (until insects and other edible matter appeared with spring weather); water was supplied rather regularly, particularly after the weather grew warm. The extra food and water were placed only in a small central area of the enclosure. About two-thirds of the flightless birds and an indefinite number of fliers took advantage of these facilities. A number of the confined birds were caught and weighed at different times; there was no evidence of weight loss (or loss of interclavicular fat) among any of them. Thus in many ways the wing-clipped birds led a near-natural existence (far more so than caged birds) and proved well suited for certain kinds of ecological study.

Of the many flying sparrows that made use of the enclosed area, some were mere visitors whereas others were better classed as part-time, wintering "residents." Semiresident status was indicated by the fact that of the "regulars" a few could be identified individually. That some were only occasional visitors was indicated by the sharp fluctuations in the populations of fliers present on different days. (The topic of fluctuations is treated in a subsequent paragraph.) Within the enclosure the nonflying individuals were so well interspersed among the flying ones that it was possible, on any observation day, to use the known number of nonfliers as an estimator of the unknown number of flying birds. Specifically, by means of a slight modification of the Petersen-Lincoln index (the ratio, in this case, of the number of nonfliers to fliers as obtained by a series of observations made in random fashion), it was possible on each observation day to reckon the density of fliers (and, of course, total birds) and to compare results with those of other census methods, chiefly the transect method, employed in surrounding areas.

Several characteristics of the Savannah Sparrow population are brought into focus in table 2, *a*. First, it is apparent that for the winter period the density estimates based on the Petersen-Lincoln index correspond rather closely with those obtained by the transect method. In fact there was evidence, even before the enclosure was built, that the corner of 3-412B selected for the enclosure generally contained about as many sparrows per acre as was characteristic of the remaining parts of B. While average density in this corner exceeded that supported by some sections of B, it was somewhat less than that supported by some other sections—including the "one-acre segment" of the transect (see table 2, *a*). Hence, the fact that this segment shows an average of some 39 sparrows per acre, as against about 30 for the enclosed area (and about 29 for the total exclosed area of B), does not by any means point to a serious discrepancy due to use of different census procedures. In comparing methods one is indeed justified in emphasizing the census results from the enclosure (30.2 birds per acre) and from the total exclosed area of B (28.6 birds per acre). In so doing one gains confidence in the efficacy of both methods of appraising density. It is my feeling, nevertheless, that the data derived from the ratios of nonfliers (whose exact number was known on each observation day) to flying birds are on the whole the most reliable. This is especially true where populations are very dense. It is believed,

Table 2. Estimates of Density and Fluctuations of Populations of Savannah Sparrows (Fliers Only) in Enclosed and Exclosed Areas of 3-412B

(a)

Census Dates	Enclosed Area (Petersen-Lincoln Index Method)		Exclosed Area			
			Transect (4.1 Acres)		*1-acre Segment of Transect	
	No. Fliers Per Acre	** CV	No. Fliers Per Acre	CV	No. Fliers Per Acre	CV
Jan. 3,5,7	58, 13, 18	83	25, 16, 19	23	20, 24, 24	10
Jan. 8,9,11	31, 36, 66	43	33, 20, 32	26	54, 26, 36	37
Jan. 12,14,18–21	76, 32, 24	64	48, 39, 27	28	69, 46, 45	25
Jan. 30, Feb. 5,8	31, 18, 9	35	31, 26, 28	9	45, 34, 40	11
Averages	†[30.2, N=20]	56.2	[28.6, N=12]	21.5	[38.6, N=12]	20.8

(b)

Feb. 12,20, Mar. 2	15, 30, 2	—	23, 32, 17	—	14, 40, 10	—
Mar. 6,11,14–15	2, 1, 0	—	12, 5, 4	—	8, 8, 4	—
Mar. 17,25,27	1, 0, 0	—	6, 2, 1	—	4, 4, 0	—
Mar. 29,31, Apr. 2	0, 1, 0	—	2, 1.5, 0.5	—	2, 2, 0	—
Averages	[4.8, N=21]	—	[8.8, N=12]	—	[8.0, N=12]	—

* Location of transect was same throughout period of study, as was its one-acre segment (which was about 200–300 feet from the enclosure).

** The Pearson coefficient of variability, CV, reflects the degree of fluctuation among density values treated in sequential sets of three; averaged CV's reflect the general extent to which the populations fluctuate in the winter period.

† For each seasonal period the bracketed average (unweighted) for the enclosed area is based on the largest available sample of observation-sessions, *including* the 12 sessions as tabulated; for each period, averages for the exclosed areas are based on 12 sessions, as indicated by "N". For the different census areas, individual density values given in sets of three correspond positionally both to census dates and to one another (example: on January 9 there were 36 fliers in the enclosure, 20 in the transect, and 26 in the one-acre segment). For further explanation see text.

then, that this method serves as a useful check on the transect and, indirectly, on the rope-dragged-quadrat method. The point should perhaps be stressed that with very high densities, the efficiency of the transect and rope methods is lowered. But with high densities there is no reduction in the efficiency (there may be a gain) of the Petersen-Lincoln index method as applied to ratios of flightless to flying birds.

Tendency of flying birds to leave the enclosure.—The principal source of error in the ratio method lay in the fact that while walking about the enclosed area I would unavoidably cause some of the fliers to leave. A measure of compensation was offered in that birds would fly in from time to time in the course of a session of observations. By tallying the times birds were seen leaving and entering, I was able to estimate egress and ingress and to interpret these in terms of "estimated net egress." For each session, or census, the appropriate net-egress value (which, from January 3 to February 8, averaged between 3 and 4 birds per census) was added to the density value derived from the Petersen-Lincoln index ratio. (The values in table 2 have been cor-

Table 3. Relation between Population Size of Flying Birds in Enclosure (January 3 to February 8) and Proneness of Individuals to leave When Disturbed

Small Populations			Medium Populations			Large Populations		
No. Censuses	Av. No. Sparrows Per Acre	% Popul.* Leaving (Av.)	No. Censuses	Av. No. Sparrows Per Acre	% Popul. Leaving (Av.)	No. Censuses	Av. No. Sparrows Per Acre	% Popul. Leaving (Av.)
7	18.6	34	9	28.2	8	3	61.3	3

* Obtained by dividing mean estimate of number of individuals leaving (mean net-egress value) by mean estimate of total population of fliers (that is, the count as determined by Petersen-Lincoln index method plus appropriate net-egress value). For further explanation see text.

rected in this way.) It is of especial interest to note that on days when relatively few fliers were observed in the enclosure, these birds tended to be wilder and relatively more of them would be scared away (table 3). Conversely, with very dense populations, relatively few birds were inclined to quit the enclosure. On January 12, for example, with a record congregation of 76 fliers (not to mention 9 wing-clipped birds) in the area, not more than two individuals were seen to leave! Although increase in density was undoubtedly related to increase in tameness or tranquillity of the sparrows, this does not offer a complete picture of the situation.

An important complicating factor was that of weather. The heaviest concentrations of fliers in the enclosure tended to be associated with days that were relatively cold and calm. The smaller assemblages were often associated with milder and, not infrequently, more windy conditions—with velocities rated as 3 (moderate) or 4 (moderately strong). When wind velocities were really strong (rating of 5), censusing was not attempted. It is worth noting that on but three days was the number of individuals leaving (net egress) in excess of 40 percent of the total estimated population of fliers; these three days were characterized by moderately strong winds. These and other data tend to bear out my general impression that the birds were more nervous and more likely to leave the enclosure on a windy day. One is tempted to theorize that the movements of the wind-tossed vegetation (including a "tumbling" composite, *Heterotheca subaxillaris)* combined with continual rustling sounds might blunt somewhat the sparrows' visual and auditory responses, including responses to potential dangers, and might in consequence give rise to a compensatory mechanism which expresses itself in the "keyed-up" condition and readiness to take flight. In any event, the suggestion remains that both temperatures and wind conditions tended to affect the density of populations of fliers in the enclosure, and that both wind velocity and population density *per se* tended to modify the birds' responses to human disturbance.

Fluctuations of populations.—Aside from broad seasonal changes in density of populations, short-term fluctuations were evident in three sample areas. As shown in table 2, *a,* coefficients of variability (CV) based on triplets of density values provide indices as to degree of density fluctuations both for several-day periods and for the longer "midwinter period," January 3 to February 8. (See also figure 2.) As compared with exclosed parts of the field, the population of flying birds inhabiting the enclosure displayed sharp fluctuations, the mean CV for this spot being almost three times as great as that for either of the other two areas. It is true that one would expect a somewhat greater variability in the density of a population inhabiting a one-acre enclosure than in one inhabiting a four-acre (transect) area in the exclosed part of B. However, the one-acre segment of the transect, whose location was constant, is comparable in area with the enclosure, so that one might expect its fluctuations to compare closely with those of the enclosure. But this is not the case. Rather, the one-acre segment resembles the four-acre transect in that its CV is comparatively low. I am therefore led to believe that the population of fliers inhabiting the enclosure in midwinter showed significantly sharper fluctuations in numbers than did those of the exclosed areas of B (whether considered as a whole or in terms of one-acre units).

Possibly this marked rising and falling in numbers of fliers occupying the enclosure signified a "crowding effect." Whereas an average of approximately 30 fliers was here between January 3 and February 8, if we add the wing-clipped birds we find that in this period the *average* number of Savannah Sparrows in this one-acre space was 47.5 (extremes 21 and 92). This amounts to a 66 percent increase over the average for the exclosed area of 3-412B. Since B, taken as a whole, contained a remarkably high density of sparrows, there can be little doubt that on many days the enclosure population was in a saturated or supersaturated state. Hence it does not seem unreasonable to postulate that the rather drastic day-to-day changes in numbers of birds utilizing the enclosure may be due, at least in part, to a crowding effect.

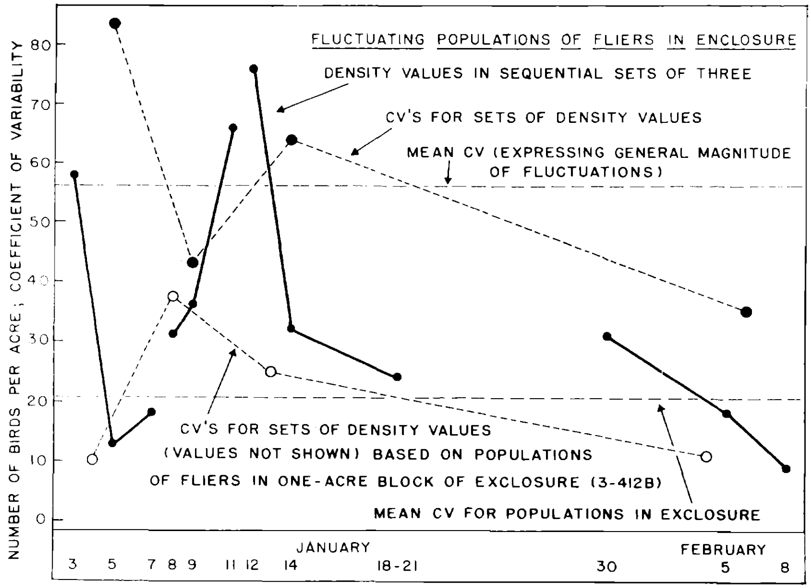

Fig. 2. Comparison of magnitude of fluctuations in numbers of Savannah Sparrows (fliers only) inside and outside the enclosed area; sharper fluctuations within enclosure suggest a "crowding effect."

If we compare once again the average density values for flying birds in the enclosure with those for the four-acre transect in the exclosure (table 2, *a*), we are led to conclude that the presence of the wing-clipped birds, whose numbers grew from 4 (on January 3) to 28 (on February 5) and averaged about 17, did not appear to depress the average population of fliers, even though it may have influenced fluctuations. In the late winter and early spring, however, it seemed that the numbers of fliers inhabiting the enclosure were depressed, for they tended consistently to be lower than those estimated for samples from nearby exclosed areas (table 2, *b*). This is illustrated by the average number of fliers per acre, which was about 80 percent higher in exclosed parts of B than in the enclosure. Birds in the saturated population may of course have so fully harvested the seeds in the enclosure that this place held, in late winter and spring, less food per unit area than did other parts of 3-412B. It is unlikely that the density of the enclosure-frequenting fliers in late winter and spring was depressed simply because of the presence of flightless birds. It seems more likely that two factors—relative paucity of food and relative crowding (the number of wing-clipped birds averaging about 15 in March)—tended to discourage the presence of flying birds in the enclosed area in late winter and spring.

Comparison of preceding methods of estimating density with a method involving "Marking-Recapture Ratios."—Odum and Hight (1957: 210) made an estimate of the population of Savannah Sparrows inhabiting a 100-acre tract in 3-412. They state that in each of the winters, 1955-56 and 1956-57, almost 300 individuals were captured and marked (number-banded) within an area of about 15 acres and that "recapture ratios indicated a population of about 1,000 in 'contact with nets.'" They say further: "If we take 100 acres as a reasonable 'order of magnitude' estimate of area sampled with lines of nets in 'A' and 'B' then there were about 1,000 birds in this area [over a several-week period in 1955-56]. During the same period Norris estimated on the basis of strip censuses that there were about 700 birds in the same area." (This value, based on some of my preliminary notes, is almost surely an *overestimate* with respect to the population present at any given time, for in 1955-56 I carried out relatively more strip censuses in A, B, and contiguous areas, and relatively fewer in E and other parts of 3-412 having sparse populations.) Odum and Hight go on to say that "confidence limits of marking-recapture estimates are rather wide so that the two estimates [700 and 1,000] are actually not so far apart."

In point of fact, the two figures, 700 and 1,000, should not be compared directly, not merely because the 700 is now recognized as an overestimate but also because my census methods, whether transect or otherwise, yield estimates of density as it exists at a given moment or in a very short interval, whereas the method used by Odum and Hight yields an estimate of the total number of individuals present in a 100-acre area over a period of several weeks. Because of movements of birds and groups of birds (which, as Odum and Hight point out, in "a period of 3 or 4 weeks . . . range over an area larger than 15 acres but perhaps not as large as 150 acres"), the number of individuals occupying 100 acres over a period of several weeks is greater than the number present in the same area at any one time. The smaller the area, the larger the ratio of the number of individuals per unit of area to the number of individuals per unit of area in the several-week interval.

If it be assumed that short-term home ranges, or "core ranges," of individuals in 3-412B and vicinity are about 8 acres in extent (see p. 203), and that the average density in the 11 acres of B is about 320 birds, one might reckon, in crude terms, that about half these birds (160) would occupy the enclosure at one time or another in the course of a week, and that a greater number (say, 200 individuals) would occupy it—some paying only one or two visits and others spending more time therein—over a period of several weeks. (We might note, incidentally, that this estimate is less than three times the maximum number of flying individuals [76] present in the enclosure at any one time.) Using 30 as a good estimate of the mean number of fliers per acre in the enclosure and 200 as a fair estimate of the total number of fliers using the enclosure in a several-week period, we find the ratio of these values to be 1 to 6.6. My best mid-winter estimate of 550 birds per 100 acres (table 1) together with Odum and Hight's estimate of 1000 birds per 100 acres for a several-week interval indicates that the ratio for this much larger area is about 1 to 1.8. These relationships lead one to suspect that for an area of intermediate size (say, 15 acres) the ratio would be larger than 1 to 1.8 but smaller than 1 to 6.6. For this reason a ratio was estimated for a 15-acre area, including most of B and a small part of A, by the following procedure:

The average mid-winter density of 10 acres of B and 5 acres of A was estimated to be about 22 birds per acre; 22 x 15 gives an average of some 330 individuals in the 15-acre tract at any one time. Tabular data provided by Odum and Hight (1957:211) enable one to estimate the number of banded individuals present in this area in December and early January, 1956-57 (this total refers only to those banded in previous years, including some of those banded here in the winter of 1954-55 and about 40 percent of those banded here in 1955-56). The estimated number of banded individuals is 203. Now, the population of flying birds in the enclosure, although fluctuating, was considered representative of the population in the 15-acre tract in question. On ten days, from January 3 to 21, 1957 (as well as on many subsequent days), I made random observations of wing-clipped and flying birds in the enclosure. Among the fliers, of which 224 observations were made in the 10-day period, 25 percent had been banded in the previous winters. Hence if 203 banded individuals comprised 25 percent of the total individuals inhabiting the 15 acres over a several-week period, then 203 x 4, or 812, would be a fair estimate of the total individuals in this 15 acres in the same period. So, for the 15-acre area 330 is an estimate of the mean number of fliers, whereas 812 is an estimate of the number of individuals frequenting the same area over a period of several weeks. The derived ratio, 1 to 2.4, is intermediate, as expected, although closer to that for the 100-acre area than that for the one-acre enclosure. In table 4 are given the ratio-values or factors by means of which one can relate "area density" to "time-area density," where time refers to a several-week period and area ranges from one to 100 acres.

Table 4. Effect of Increase of Census Area on Ratio of Sparrow Density per Areal Unit per Short Interval (DAI) to Density per Areal Unit per Several-Week Period (DAP).

Area (acres)	*1	6–10	*15–20	35–40	55–60	75–80	*95–100
Ratio (DAI:DAP)	1:6.6	1:3.3	1:2.4	1:2.2	1:2.0	1:1.9	1:1.8

* For these three acreages, methods of deriving ratios are explained in text; other ratios are estimated by interpolation.

Odum and Hight (1957:210) say that "it seems likely that strip censuses might underestimate and recapture ratios overestimate density." I agree in part. As mentioned earlier (p. 180), the efficiency of the strip census is reduced somewhat where density is very high; however, the Petersen-Lincoln index method, as applied to flightless and flying birds, serves as a useful check on the strip method and seems efficient regardless of population density. That recapture ratios tend to overestimate density, as Odum and Hight suggest, appears to be true only in the sense that these ratios refer to a larger number of individuals occupying a given area through a considerable period of time, rather than to a smaller number of individuals which characterize that area at some one particular time. Thus, it appears that there is no real discrepancy between results of my methods and those of the "marking-recapture ratio" used by Odum and Hight. We are really measuring populations of two different sorts, or two different dimensions, of which one—that which is present in an area through a considerable period of time—is necessarily larger than the other.

RACIAL COMPOSITION OF POPULATIONS

Field taxonomy: a brief description of method.—A full account of the 1955-56 studies in field taxonomy, which has been defined in part as the practice of making racial, or subspecific, identifications of living birds handled under field conditions (usually banded and released), has recently been published (cf. Norris and Hight, 1957). Similar studies were conducted in the nonbreeding period, 1956-57. It suffices here to say that all birds netted for purposes of banding or other study, as well as all birds collected as museum specimens, were identified as to geographic race or subspecies. Specimens of known racial identity were available in the field for use as standards against which the living birds could be compared. With continued practice, however, the color characters distinguishing the races became familiar and fixed in mind so that it became unnecessary, except on rare occasion, to make direct comparisons. More than half the birds were racially atypical or noncharacteristic; although treated as intermediates, these were invariably placed nearer one race or another. A few examples of races and recognized types of intermediate categories are: *oblitus, oblitus>mediogriseus, mediogriseus>oblitus,* and *mediogriseus.* Individual sparrows netted on two or more occasions (days or weeks apart) were identified each time they were handled; this made it possible to check one's "internal consistency" in assigning the race designations. As tested rigorously by a method previously outlined (*ibid.*: 41-43), consistency was found to be relatively high. It was in fact deemed comparable to that which one would expect from a museum taxonomist (should he work with series of Savannah Sparrows, recognize the same categories of variants that we recognize, and test himself by means of the aforementioned method). In both nonbreeding periods, 1955-56 and 1956-57, the field-taxonomic identifications were made by the same person, so that this, too, contributes to overall consistency in method. Further evidence indicative of the validity of field-taxonomic studies conducted in the Savannah River Plant area will be offered subsequently.

A simplified characterization of the races.—The subspecies may be divided into two broad groups, the "light races" and the "dark races." Only essential information concerning their breeding ranges and types of coloration will be presented here. More detailed characterizations can be found elsewhere (Peters and Griscom, 1938; Aldrich, 1940; Norris and Hight, 1957).

LIGHT RACES

P. s. savanna.—Colors relatively light, with browns predominating. (Nova Scotia, Prince Edward Island, Magdalen Islands, and part of Newfoundland.)

P. s. mediogriseus.—Compared with *savanna,* colors somewhat darker and more grayish brown. As brought out previously (Norris and Hight, 1957:44), we believe that the population described by Aldrich (1940) as *mediogriseus* is quite distinctive and merits nomenclatural recognition. Hence we cannot follow the opposite conclusion reached by the American Ornithologists' Union Committee on Classification and Nomenclature (with the result that *mediogriseus* is not included in the Fifth Edition of the American Ornithologists' Union Check-list, 1957).

P. s. nevadensis.—Colors light, even pale, and decidedly grayish. Bill relatively narrow. (British Columbia and Alberta south to northern California, Utah, and Nevada, east to Minnesota and southern Wisconsin.)

DARK RACES

P. s. labradorius.—Colors dark to very dark, with black and brown predominating. Essentially a heavily melanized *savanna.* (Northern Ungava south and east to Labrador and Newfoundland.)

P. s. oblitus.—Colors dark to very dark, predominantly black and gray. Essentially a heavily melanized *nevadensis* or *mediogriseus.* (West side of Hudson Bay south to northern Minnesota, east to central Quebec.)

Relative abundance of races.—For present purposes of analysis, the various racial types and intermediates are lumped under five principal racial categories, as listed above. Although the relative abundance of the races in the nonbreeding period of 1955-56, based on some 559 identification-records, was published elsewhere (Norris and Hight, 1957:45 ff.), it seems desirable to incorporate that information in table 5, which summarizes all the data for 1955-56 and 1956-57. The size of the final aggregate sample (N = 1758) for both these periods is approximately three times as great as that for the 1955-56 period alone. If data for the two years are compared, the relative abundance of the five races is found to be similar. We shall use a simple, semi-statistical means of comparing ratios. For two ratios being compared, the differences between the percentage values for each race are obtained

Table 5. Relative Abundance of Races of the Savannah Sparrow in the Savannah River Plant Area*

Sample and Seasonal Period	Light Races				Dark Races			
	medio-griseus	*savanna*	*nevad-ensis*	Totals; percent-ages	*labra-dorius*	*oblitus*	Totals; percent-ages	All Races (Totals)
(1) Oct.	15 (35.7)	10 (23.8)	0 (0.0)	25 (59.5)	11 (26.2)	6 (14.3)	17 (40.5)	42
(2A) Nov.–Dec., 1955	19	4	2	25	1	2	3	28
(2B) Nov.–Dec., 1956	70	62	9	141	48	17	65	206
(2S) **Nov.–Dec. (total)**	**89** (38.0)	**66** (28.2)	**11** (4.7)	**166** (70.9)	**49** (20.9)	**19** (8.2)	**68** (29.1)	**234**
(3A) Jan.–Feb., 1956	132 (28.2)	139 (29.9)	30 (6.4)	301 (64.5)	86 (18.4)	80 (17.1)	166 (35.5)	467
(3B) Jan.–Feb., 1957	91 (24.6)	110 (29.7)	5 (1.3)	206 (55.6)	102 (27.6)	62 (16.8)	164 (44.4)	370
(3C) Jan.–Feb., 1957**	188 (34.0)	158 (28.6)	21 (3.8)	367 (66.4)	98 (17.7)	88 (15.9)	186 (33.6)	553
(3S) **Jan.–Feb. (total)**	**411 (29.6)**	**407 (29.3)**	**56 (4.0)**	**874 (62.9)**	**286 (20.6)**	**230 (16.5)**	**516 (37.1)**	**1390**
(4A) Mar.–Apr., 1956	10	10	2	22	10	12	22	44
(4B) Mar.–Apr., 1957	18	13	2	33	8	7	15	48
(4S) **Mar.–Apr. (total)**	**28** (30.4)	**23** (25.0)	**4** (4.4)	**55** (59.8)	**18** (19.6)	**19** (20.6)	**37** (40.2)	**92**
Totals	**543**	**506**	**71**	**1120** ——	**364**	**274**	**638** ——	**1758**
Percentages for Races and Groups	(30.9)	(28.9)	(4.0)	—— (63.7)	(20.7)	(15.6)	—— (36.3)	——

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* Included are 22 specimens from southern Georgia (non-selective collections) and 26 from northern Florida (a late-October series killed in migratory flight at a TV tower and contributed by Herbert L. Stoddard, Sr.).

**This sample pertains to *field observations* of different racial types (for explanation, see text); all other samples pertain to *handled* birds (mostly captured for banding, some collected for specimens).

Table 6. Comparison of Relative Abundance of Races of the Savannah Sparrow in Three Midwinter Samples, Including a Sample Based on Sight Observations (3C)

Compared Samples	Absolute Differences Between Percentage Values by Race*					Sum of Differences Between Percentage Values by Race (= *p.d.*)	Ratio-Difference (= *r.d.*, = p.d./2)
	mediogriseus	*savanna*	*nevadensis*	*labradorius*	*oblitus*		
3A—3C	5.8	1.3	2.6	0.7	1.2	11.6	5.8
3B—3C	9.4	1.1	2.5	9.9	0.9	23.8	11.9
3A—3B	3.6	0.2	5.1	9.2	0.3	18.4	9.2

* Based on data in Table 5.

separately, then summed, and the sum is divided by two; the result may be termed the percent difference between ratios (*r.d.*). (See table 6.) Comparison of ratios for samples 3A and 3B (tables 5, 6), both of which were taken principally from one large field (3-412), reveals a rather low *r.d.* value, 9.2 percent. A measure of "shift" in ratio with addition of the second year's data was obtained by comparing the 1955-56 ratio with that for both years (table 5). That this shift was very slight is indicated by a very low *r.d.* value, 4.0 percent. These findings point to little change in the relative abundance of the races from one year to the next.

The five geographic races differ not only in overall relative abundance (see totals, table 5) but also in seasonal pattern of relative abundance (fig. 3). *Mediogriseus,* whose numbers are only slightly greater than those of *savanna,* is the only one which seems clearly to reach peak relative abundance in November and December. Even though its absolute numbers may have increased by January, its relative numbers among the five races have then declined to about 30 percent, where they tend to remain. The relative numbers of *savanna* were fairly constant although the percentage value was lowest for October, highest for January and February. Clearly, the race *nevadensis* was the least common of the five subspecies. It was not recorded before mid-November, after which it made up about 4 percent of the population. Taken together, these "light races" comprised about 64 percent of the aggregate sample; the "dark races," 36 percent. This holds not only for the total sample shown in table 5 but also for the total based solely on the 1955-56 season (*ibid.*). Consequently, there was no change in the relative abundance of the two race groups from one nonbreeding season to the next. This would, of course, be expected in view of the low *r.d.* value obtained through comparison of the 1955-56 ratio with that for 1956-57.

Judging from the small October sample, of which only a part was taken in the Savannah River Plant area, the race *labradorius* made up over 25 percent of the sample in October and about 20 percent of samples in months that followed (during which its relative numbers were remarkably constant). The fact that *oblitus* appeared to be relatively less common in November and December than in October (or in the January-to-March period) may mean that numbers of this far-northern race passed through the region in a primary migratory wave in late fall (at which time there was a small density peak, as indicated in fig. 3), and that it was only considerably later, in late December and early January, that subsequent influx resulted in populations with relatively larger numbers of *oblitus*. As suggested by the October sample, *labradorius* may likewise tend to pass through the region in October and early November en route to more southerly latitudes. The percentage values of *oblitus*, unlike those of the other races, show substantial increase from November-December to March-April. Extrapolating, one might well predict that *oblitus* would be one of the last of the races to depart in spring. Limited data support this hypothesis; the only specimens taken in May were of the dark races—two *oblitus* and two *labradorius*. Taken together, the two dark races as compared to the light ones were slightly more prevalent in October and, as noted previously (Norris and Hight, 1957:50), in March and April. They were least prevalent in November and December, in which period they contributed less than 30 percent to the total sample.

A case for field identification of geographic races.—By late December, 1956, my familiarity with Savannah Sparrows and their various types of plumage had led me to wonder whether it would be rewarding to attempt to identify subspecifically these sparrows as they were observed in the field. I realized, to be sure, that such an attempt would be subject to criticism. Indeed, I was respectfully aware that in Peters

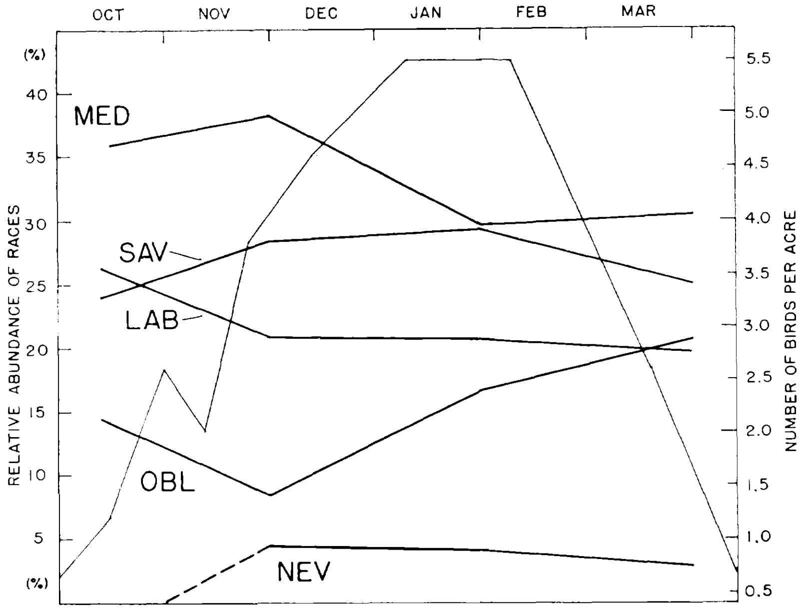


Fig. 3. Seasonal shifts in relative abundance of five geographic races of Savannah Sparrow in the Savannah River Plant area (based on 1758 identifications made in course of two winters); superimposed curve indicates seasonal changes in average density of the species in 100 acres of field 3-412, as recorded in 1956-57.

and Griscom's monograph (1938: 454) there were, in the discussion of the race *labradorius*, admonitions such as these:

"About one third of the 60 breeding specimens from [Newfoundland] examined are intermediate between *labradorius* and *savanna.* It follows that sight records of this race are out of the question, in adding anything definite to our knowledge. While it is quite possible to observe slightly darker and paler Savannah Sparrows among our migrants in the east in life, only critical comparison of such birds in the hand can settle whether a darker bird was really a *labradorius* or a dark extreme or more worn specimen of *savanna.* It is characteristic of modern 'opera glass ornithology' that the only sight record of *labradorius* published to date comes from an inland region without an authentic record, and that it was made in all sincerity by an observer blissfully unaware of nearly everything written above, who never laid eyes upon an authentic specimen or compared it with a *savanna!* Let us hope there will never be another such observation!"

For workers having no taxonomic experience with this group of sparrows, the Griscomian thoughts expressed in this passage are most applicable and should be borne in mind. They do not necessarily apply, however, to a worker who has grown familiar with plumages of the races of Savannah Sparrows known to occur in a particular region. In fact I am now convinced that for such a worker it is not only "possible to observe slightly darker and paler Savannah Sparrows . . . in life," but also it is possible to name them subspecifically with a degree of accuracy which approaches that achieved with birds in the hand. Nor am I alone in this belief. In reporting on some observations on migrants from South Bass Island, western Lake Erie, in April, 1951, Trautman (1956: 275) states: "At the time I was particularly interested in obtaining information upon the relative abundance of the various subspecies of Savannah Sparrows occurring in the island region, so was examining with field glasses all individuals which I encountered."

In addition to having a close familiarity with the taxonomic group or subgroup of birds on which one intends to make field observations of different subspecies, one needs to make the observations under as favorable circumstances as possible. In and about the enclosure in 3-412B circumstances were generally favorable. Only those individuals that were seen clearly and relatively close at hand (with 7 x 35 binoculars) were identified in terms of infraspecific categories. It was found that a moderately bright day sufficed for these field observations. For a practiced eye it made little difference whether the sky was cloudy, hazy, or clear, so long as a heavy overcast or stormy conditions did not make it a really dark, gloomy day. As a rule observations were made when the sun was well up (seldom before 9 a.m. or after 3 p.m.).

One particular advantage, which might be considered among the "favorable circumstances," was that in the enclosure were a number of racially identified, wing-clipped, color-banded birds (each bird having a "key band" which referred to its racial type). These confined birds enabled the observer frequently to *review* plumage characters in the field and, occasionally, to compare directly "unknowns" among the fliers with "knowns" among the nonflying sparrows. Because the various individuals among the wing-clipped birds were so frequently observed, they provided standards that were in some respects more useful than the study skins used in early phases of the regular field-taxonomic work. Although the race *nevadensis* was not represented among the flightless birds, I did keep one individual in an outdoor pen for some days and compare it with birds of other races at distances of 15 or 20 feet. As indicated by this individual as well as several others, the comparatively pallid, decidedly grayish plumage of *nevadensis* can easily be appreciated under suitable field conditions.

All the infraspecific categories *(savanna, savanna > mediogriseus, mediogriseus > savanna, mediogriseus,* etc.) employed in the regular studies in field taxonomy were also used in tabulating the field observations of the different races. It was my belief that even though this endeavor could be regarded as "splitting it too fine," it was characterized by certain advantages. With 17 potential categories or pigeonholes it was possible to "place" individuals more speedily. For example, instead of vacillating for a minute or more as to whether a given bird displaying a fairly dark, decidedly brownish type of coloration should be called *savanna* or *labradorius,* I would judge as best I could whether it seemed nearer the former or the latter race, calling it, with little hesitation, either *"sav>lab" or "lab>sav."* By having two categories of intermediates, it was possible to analyze data in terms of relative numbers of the five races *sensu lato* (in the broad sense the term *savanna* encompasses not only characteristic *savanna* but also *"sav>lab"* and *"sav>med").* Second, if one thinks in statistical terms —not of data gathered in one observation-session but rather of those amassed over a longer period such as January and February—one can see that such mass results in no wise suffer from the use of a technique which some might consider to be rife with "false accuracy." One could in theory have this situation: "Flying individual A" (which if examined in the hand would, let us assume, be called *labradorius>savanna)* would happen to be observed closely on five different occasions (say, January 3, 5, 14, 16, and 25). The observer would not recognize it as an individual and would tally it each item. He might call it *lab* once, *lab>sav* thrice, and *sav>lab* once. If he were to use broad racial categories only, he might call it *lab* four times and *sav* once. But unlike the procedure of lumping under broad categories, the procedure involving finer placements (among which four out of five reflected the observer's judgment that this particular type of coloration was intermediate between *lab* and *sav,* and among which three out of four reflected his judgment that it was nearer *lab)* has advantages in that it enables the observer to obtain with greater rapidity, with less uncertainty, and with fewer misgivings, useful information on the relative abundance of the five races *sensu lato.*

The question now arises, what evidence is there that field observations of the races were sufficiently accurate to yield useful data, including data on abundance ratios of the different races? One method of testing the validity of the procedure was that of having another worker (Herbert W. Kale) arrange color bands in different combinations (taken at random from a long list of combinations) on large series of birds which, in addition to being number-banded by Gordon

L. Hight, Jr. and weighed by Clyde E. Connell, were identified subspecifically by me. This was done in late February, 1957. After being processed, the birds were released where caught, in 3-412B. Since the data on subspecific allocations and on color-band arrangements were kept separately and could be linked to individuals only by reference to band numbers, I was completely unaware as to the way in which any member of any particular race had been color-banded. Hence I was in good position to test the consistency with which I identified individuals first in the hand and second under field conditions. Unfortunately I was unable to do this for more than about three individuals (consistency gave promise of being satisfactory but was inconclusive with so small a sample), for shortly after this late-February banding operation a majority of the birds migrated. (This was unexpected as it took place a month earlier than it had the previous year.) At present it is necessary that I rely on other evidence which bears on the validity of the procedure.

The best evidence, which may be as satisfactory as any I could have got from the above-described plan, is incorporated in table 5. If the abundance ratio of sample 3C, which is based wholly on sight observations of birds in and near the enclosure, is compared with others of the same seasonal period (3A, 3B, and 3S) it is seen to be essentially similar to them. If the samples 3A, 3B, and 3C are compared with one another, it is clear from ratio-difference values (*r.d.'s*, table 6) that C tends to differ from A and B in about the same degree as does A from B and C, or B from A and C. If the mean *r.d.* between 3A-3C and 3B-3C be computed ($\frac{5.8 + 11.9}{2} = 8.8$), it is seen to be slightly less than that pertaining to the comparison of 3A with 3B (*r.d.* = 9.2). This indicates that 3C, the ratio based on field observations, comes as close to matching the other two ratios 3A and 3B, considered together, as do 3A and 3B come to matching one another. A comparison of 3C with the final percentage values for the races (table 5) results in an *r.d.* of only 3.4, a notably high degree of correspondence which seems worth pointing out even though the compared ratios are in this case not strictly comparable seasonally. Among the ratios, then, 3C, the one whose basis might be regarded as questionable by some, is manifestly no "outlier."

It is my belief that under suitable conditions and with due caution an experienced observer can, with the aid of binoculars, make relatively accurate subspecific identifications of living birds. Such an observer should, of course, study intensively the taxonomic group or groups with which he proposes to work. It seems likely that endeavor along this line will supplement, although not supplant, more detailed studies in field taxonomy involving examination of birds in the hand. Field observational procedures are perhaps best thought of as a restricted aspect of field taxonomy. Of course not all subspecies will lend themselves to this kind of study. In general, those exhibiting rather strong color differences will be more usable than those showing only slight differences in color or in size. Study of differentiates of the latter type will involve either (1) careful identification of birds in the hand, including comparisons with reference series of skins and perhaps other refinements of technique, or (2) such bird-in-hand identifications as these followed by studies of the same birds color-marked according to race and kept under alpha- or beta-confinement. In the present study it was fortunate that the most abundant species of sparrow wintering in old fields in the Savannah River Plant area was also one whose several races showed relatively well-defined types of coloration (even though intermediates were common). In this study, the peculiar nature of the selected organism (small-sized, winter-resident, abundant, polytypic, field-inhabiting, readily caught, easily marked, and amenable to study under beta-confinement) was most important and served to indicate the types of problems to be attacked.

ASPECTS OF SOCIALITY

Spatial distribution of sparrows.—In the nonbreeding season Savannah Sparrows were distributed over the old fields in locally varying patterns. Patches of food and cover naturally affected their spatial relations. In 3-412B, there was, as brought out previously, a high concentration of birds—about 30 per acre in midwinter—owing to suitable forb and grass cover and to an ample supply of edible seeds. *Digitaria,* whose seeds provided the staple food, grew rather more thickly in some parts of B than in others, and correspondingly the sparrows tended to aggregate where this grass was most abundant. However, the general picture was such that neither the best food areas nor the aggregations of birds were distributed in patchy, clumped, or highly "contagious" fashion. A net impression gained in the course of two winters of work in old fields was that groupings of birds *tended* more to be contagious where overall density was relatively low. Even where overall density was low, however, it was apparent that the term "flock" was scarcely appropriate. Better terms would seem to be "gathering," "aggregation," or "concentration," since each connotes a grouping or assemblage involving appreciable numbers of birds but not involving discrete or observable flock limits or bounds. One is tempted to liken populations of these sparrows, such as those inhabiting 3-412 at large, to a tract of country of high relief, with valleys representing low densities, slopes moderate densities, and summits high to very high densities. Thus, Savannah Sparrows exhibited a tendency toward being scattered over the fields, and although they were concentrated in some places they were nowhere bound, as it were, into closely knit, easily defined flocks.

Certain distributional patterns of sparrows within the enclosure, as recorded on February 5, 7, 8, and 11, were subjected to statistical analysis. Both wing-clipped and flying birds were included in the samples. Location-records of all individuals closely observed in daily observation periods (each of the four periods lasting from 2 to 2½ hours) were placed on maps. A separate map was used for each period. Although it was not possible to determine at any one moment the spot-locations of all individuals within the enclosure, it was believed that such locations as could be pinpointed for various individuals (these including, usually, about half the total individuals present) in that period of time necessary to accumulate a sufficient number of observations, would give a rough indication as to how the enclosed population might be distributed at any given moment. For each period the number of observations deemed sufficient was, on the average, roughly equivalent to the total number of birds (wing-clipped and flying) estimated to be present in the enclosure at that time. The distribution of spot-locations was analyzed by the method developed by Dice (1952) for the study of spacing between individuals among plants.

For each map the use of the Dice method entailed (1) the selection of a number of points of origin (six in the present case); (2) the superimposition, on a random basis, of a radially symmetrical, six-limbed figure delimiting sextants (the figure being inked on tracing cloth and mounted on a cardboard frame) on the map so that the center of the figure corresponded to the selected point of origin; (3) the measurement of the distances from the origin to the nearest spot-location in each sextant, with similar measurements being made from the other points of origin; and (4) the statistical analysis of the distribution of the square roots of the distance values (of which there was an array of 36 for each map). In general, the greater the variability within and among the sets of six measurements, the greater the degree of positive skewness of the distribution. Results of the analysis are presented in table 7. The g_1 statistic, which may be derived from the third moment (see, for example, Mode, 1941, whose "a_3" is equivalent to g_1; or Snedecor, 1956: 200), reflects, in approximate fashion (as Dice, *ibid.*, points out), the degree to which the distribution is skewed, whether positively or negatively, while the degree of skewness reflects whether the population is clumped to some degree (positive values for g_1), randomly distributed (g_1=equalling 0), or spaced more evenly than random (negative values for g_1). As shown by *t*- and P-values in table 7, *a*, none of the four sample distributions differs from the random to a really significant degree. One is led to the tentative conclusion that the assemblage of wing-clipped and flying birds (whose combined numbers averaged 46 per acre in these four study periods) was distributed within the one-acre enclosure in an approximately random fashion.

One could argue that the method by which the spot-records were accumulated does not provide a picture closely comparable to what one would get if one could, at a given moment, stop the sparrows in their tracks, find all of them *in situ*, and thus ascertain their relative locations. Such an argument is not invalid. By way of answer we can say only this: the method employed appeared to be the best available under the circumstances, and until a more efficient one can be developed it seems desirable to accept, if only as rough indications or first approximations, the data yielded by this method.

Actually there was evidence that Savannah Sparrows, whether wing-clipped or not, occurred at times in small, rather closely knit groups of two, three, or occasionally more. So far as individuals are concerned, these seemed often to be chance associations. Wing-clipped birds, fliers, or both might be involved. Usually the groups could be dispersed easily and would often remain so. When, for instance, a loosely associated threesome of wing-clipped birds was approached closely enough, the group would usually disband, its members moving off separately through

Table 7. Analysis of Manner of Spacing of Savannah Sparrows in Enclosed Area, with Significant Departure from Random Being Indicated Only for Composite Sample (b)

(a)

Dates (1957)	No. Mapped Spot-Locations	No. Sextant Meas-urements	Total Birds Present	Mean* $\sqrt{DV}$	Stand-ard Devi-ation	g_1 (or α_3)	t	P (ap-prox.)
Feb. 7	45	36	57	2.74 ± 0.18	1.09	0.635	1.56	0.13
Feb. 11	45	36	45	2.72 ± 0.15	0.89	0.032	0.77	0.43
Feb. 8	40	36	37	2.71 ± 0.22	1.29	—0.001	—0.003	0.50+
Feb. 5	40	36	46	3.17 ± 0.15	0.91	—0.542	—1.33	0.18
				(b)				
Feb. 5, 7, 8, 11	170	36	46 (av.)	2.46 ± 0.15	0.92	—1.89	—4.64	0.01

* Mean square root of distance values as determined by use of sextant-overlay device; see text for explanation of this and other column headings.

the vegetation or along the open path just inside the barrier. These birds might then remain separated for the remainder of the observation period. The fact that small, loose groups did exist, however, indicates a certain degree of sociality and of contagious spacing of birds in the population. Consequently the extremely low degree of clumping, where indeed there seemed to be any clumping at all, as suggested in table 7, *a*, may well *minimize* the real situation, in which the degrees of clumping probably average significantly different from what one would expect on a random basis.

Among the drawbacks in the method here used, that connected with the rather long time interval of two hours or more is perhaps of greatest importance. The fact that a distribution of spot-records was recorded over so long a period meant that there were duplications and even replications of spot-records for certain relatively conspicuous individuals. This doubtless results in certain distortions due to repetitive superimposition of spot-records pertaining to this individual or that. And the fact that some individuals were not tallied does not necessarily offset or compensate for this difficulty. Moreover, the movements of individuals (except for some few which, in a two-hour period, would merely "oscillate" in a very small area) tend to contribute to error. It is likely that I have erred in the foregoing analysis (table 7, *a*) by overemphasizing the element of randomness and by underemphasizing the element of contagion or clumpedness. Suggestive evidence for this kind of error is provided by the distribution of spot-record data for *all four periods* superimposed on a single map (170 spot-records). As shown in table 7, *b*, this distribution proves to be more evenly spaced than random. Because of the excessive crowding of spot-records on the composite map, the suggested tendency toward clumped distributions, as indicated for February 7 and 11, is not only completely masked in the superimposed spot-pictures but tends in fact to be reversed—and to a significant degree. It would seem then, that the repetition of records tends to introduce errors such that the population is made to seem more uniformly distributed than it would be at any particular moment or short interval of time. Thus, a certain measure of repetition and superimposition in-

Table 8. Incidence of Groups (Twos and Threes) and of Associations among Racial Types in Savannah Sparrows in the Enclosed Area

			Incidence of Associated Birds			Index of Association Between Races	
Seasonal Period (1957)	No. Observation Sessions	Total No. Observations	% Among Total Observations	Intra-Racial	Inter-Racial	MWDr* / MWDo	Difference Between MWDr and MWDo Significant?
Jan. 3–Mar. 6	27	967	4.9	18	29	0.92	No (P = .50+)
Mar. 14–Apr. 22	19	660	7.0	22	24	1.23	No (P = .40)

* MWDr = mean of weighted differences between various racial types as would be expected on basis of random association; MWDo = mean of weighted differences between various racial types actually observed in close association. Further explanation is given in text.

herent in a map of spot-records gathered over a two-hour period (which may be a somewhat analogous situation) may well contribute a picture of essential randomness even if the distribution, as it exists at any one time, tends in actuality to depart from the random and to show a really significant degree of clumping. Nevertheless, both the spot-records and general observations furnish abundant evidence that almost nowhere are the wintering Savannah Sparrows distributed in a "highly contagious" manner.

Incidence of associations of individuals and of racial types.—That the birds were distributed in a manner not greatly different from random was supported by the relatively infrequent observations of twosomes, threesomes or, rarely, larger groups of birds (table 8). Actually, observed associations were somewhat more frequent than is indicated in the table, since the tabulated frequencies pertain only to those records for which both, or all, group members were closely observed and identified as to band combination and/or racial type. In some instances only one group member could be seen clearly, so that some records of singles ought in fact to have been set down as twosomes or threesomes. It is my belief that the values showing percent incidence of associations (table 8) should be increased, perhaps doubled. Even if doubled, they would suggest that only about 10 or 15 percent of the individuals in the enclosed population are likely to be closely grouped in twos or threes at any given time.

Role of flying and flightless birds.—In the course of the period January 3-March 6, wing-clipped birds made up, on the average, about 39 percent of the population inhabiting the enclosure. They averaged about 43 percent of the sample of birds that was closely observed. In the course of an observation session there was usually a net egress of part of the population of fliers (see p. 180); while unavailable for close observation, the outgoing birds were tallied and were taken into account in estimating the total number of fliers for any given session. Because of these evasive birds, the wing-clipped individuals are, on the average, somewhat more prevalent in relation to the closely observed sample than to the total estimated sample of birds.

Although nonflying sparrows were decidedly fewer than flying ones in January (in which period I wing-clipped and introduced 17 individuals), from February on they outnumbered the fliers. The wing-clipped birds numbered almost 30 by mid-February, at which time the flying population had begun to decline. Thus the proportion of flightless to flying birds increased from early January to early March. In the period from March 11 to April 22 very few fliers were seen in the enclosure, and the wing-clipped birds, although reduced in numbers because of predation, made up, on the average, more than 98 percent of the population.

Among the twosomes and threesomes recorded, flying sparrows were involved just about as often as one would expect on the assumption that their sociality was essentially like that of the confined birds. In the January-March period, fliers yielded 25 out of 47, or 53 percent, of the records of birds (which included repeats of certain individuals) observed to occur in twos or threes. This compares closely with 57 percent, the mean relative number of fliers in the closely observed sample in the same period. In the March-April period there was but one flying individual involved among 46 records of associated birds (incidence about 2 percent), which checks with the approximate 2 percent incidence of fliers in the enclosure in the same period. Practically all the regular observations, including those referred to in table 8, pertain to birds seen foraging on natural food in various parts of the enclosure. A mere handful pertains to the central area where, after mid-February, food and water were provided intermittently. The quantitative evidence lends support, then, to my general impressions that the flying birds mingled and associated with the flightless ones in a normal manner, not only at the favored site with food and water but also in other places throughout the enclosure.

Interracial mingling.—As noted earlier (Johnston, 1956; Norris and Hight, 1957: 49), there is no gross evidence of ecological segregation among the races of Savannah Sparrow in the fields of the Savannah River Plant area. Nor is there evidence of segregation in the social sense. Studies in the enclosure indicate that the different races intermingle freely on the wintering ground. As is shown in table 8, some of the instances of associated individuals involved members of the same racial type, others members of different racial types. In this table the relative numbers of birds involved in the intraracial and interracial associations are of no more than suggestive value, for these numbers are not evaluated in the light of the relative abundance of the different races. Too, in this breakdown of numbers the racial types are considered only in the broad sense (five categories: *oblitus, nevadensis, mediogriseus, labradorius, and savanna*). In order to demonstrate whether or not the same or similar racial types tend to "stick together" a more rigorous method of analysis is needed. Accordingly, a set of difference ratings based on kind and degree of difference in coloration was established in a semi-arbitrary way for a complex of 153 potential comparisons or combinations of racial types and subtypes. Two illustrative combinations are: *savanna—savanna>mediogriseus*, difference = 10; *savanna—oblitus*, difference = 70. Briefly, the more drastic the color difference, the larger the difference score. In general, the degree of difference stands in direct proportion to the degree to which the racial variants are separated geographically in the breeding season. The color differences likewise provide at least a crude index as to genetic differences between the populations in question. One can readily see that a marked tendency for a series of birds to associate with identical or closely similar color types would result in a lower average-difference score than one would get from a series of birds associating on a chance basis. For each seasonal period it was necessary, however, to weight the difference values in accordance with the average relative numbers of the different races in the enclosure. (For the earlier period this involves the proper weighting and incorporation of abundance ratios from both flying and nonflying contingents; for the later period the average ratio of types among nonfliers enables one to estimate suitable weight factors.) In short, the weighting of difference values for a given series of combinations or associations corrected for potential, differential availability of individuals of different racial type or affinity. The sum of the weights divided into the sum of the weighted differences gave a mean weighted difference (MWD). For each seasonal period the difference that one might expect on a random or chance basis (MWDr) was divided by that derived from direct observations (MWDo). Quotients are given in table 8. The probabilities resulting from standard *t*-tests indicate that for either seasonal period there is no significant difference between random and observed MWD's.

If there is a slight tendency for members of identical or similar racial types to associate, this tendency would seem to characterize the spring rather than the winter season. From the data summarized in table 8, however, it seems best generally to conclude that there is no racial segregation of any significance among the Savannah Sparrows in the nonbreeding season. As we have expressed before in connection with observations of gross spatial overlap of the races (Norris and Hight, 1957: 49), interracial association appears to constitute an aspect of sociality which has selective value for the various populations concerned. After migration is under way at least some of the different racial types of necessity become segregated, if only in the later stages of their journeys to higher latitudes, but so far is is known to me there is no segregation (unless it be partial due to some races leaving earlier) and no differential habitat selection prior to the birds' leaving their southern wintering ground.

Social behavior.—From mid-February on, the Savannah Sparrows were supplied intermittently with extra food and water placed at the center of the enclosure. As mentioned earlier, the food consisted of oats and other types of small grain. A pool of water suitable for both drinking and bathing was maintained in the shallow concavity of an old, battered-in car door, which was partly sunk in the ground. About 30 feet away a blind, which was fashioned from an old sleeping bag, was set up and left permanently in position. This facilitated close observation of the sparrows visiting the central area. More than half the wing-clipped birds came in to feed, drink, and bathe. Some appeared only infrequently, whereas others were regular "customers." In addition a number of flying birds paid visits, particularly in the period from February 15 to 25, during which fliers were still present in force in the 3-412 area. From the first day's observations, it was apparent that some of the sparrows were rather hostile and tended to drive others away from favored spots. By accumulating observations on color-banded individuals in late February and March, I was able to determine which of the birds were disposed to dominate others and which tended to be lower in the social hierarchy. A summary and partial analysis of observations is offered in table 9.

It was not possible to include many flying birds in table 9 because most were not individually identifiable. Although in late February some of them were caught and color-banded, a majority of the fliers migrated shortly afterward; hence efforts to color-band birds in this category did not augment appreciably the study of social dominance. However, flying individuals were frequently involved among the birds dominated by, say, a spirited bird like A1Y-OR, whose 30 "successful" contacts were with fliers in about two-thirds of the instances. In contrast, some fliers, notably the distinctive individuals "*obl>med* I" and "yellowtail C," were relatively high on the dominance-aggressiveness scale. Considerable evidence pointed up the fact that ability to fly had little or nothing to do with a bird's position on the dominance scale. Between the two

Table 9. Relative Positions in Dominance Hierarchy of Individual Savannah Sparrows As Observed Near Supplementary Food and Water in Central Part of Enclosure

Individual	Apparent Sex	(A) Times Dominating Others	(B) Times Dominated by Others	(C) Relative "Success"	(D) No. Individuals Dominated	(E) Dominance-Aggressiveness Rating (CxD)
A1Y-OR*	Male	30	0	1.00	22	22.0
"obl > med 1"	?	11	0	1.00	10	10.0
A1B-BB	Male	8	1	0.89	7	6.2
"Y-tail C"	Male	12	4	0.75	8	6.0
YA1-Y	Male	6	4	0.60	7	4.2
A1Y-OY	Male	4	0	1.00	4	4.0
BA1-BY	Male	3	0	1.00	2	2.0
A1-RB	Female	5	5	0.50	3	1.5
A1-R	Male	2	1	0.67	2	1.3
A1Y-OO	Male	3	8	0.37	3	1.1
A1-RY	Male	1	0	1.00	1	1.0
A1-OBR	Male	1	0	1.00	1	1.0
A1-BBR	Female	1	0	1.00	1	1.0
YA1-YB	Female	1	1	0.50	1	0.5
A1-YBY	Male	1	2	0.33	1	0.3
A1-RR	Female	1	3	0.25	1	0.2
GA1-RG	Female	1	4	0.20	1	0.2
RA1-RY	Male	0	1	0.0	0	0.0
YA1-YR	Female	0	1	0.0	0	0.0
A1R-B	Male	0	3	0.0	0	0.0
A1Y-B	?	0	4	0.0	0	0.0
A1O-OG	Female	0	5	0.0	0	0.0
A1O-OB	Female	0	5	0.0	0	0.0

* Symbols or letters designating types or colors of bands used on wing-clipped birds are as follows: A1 (aluminum, numbered), R (red), B (blue), Y (yellow), O (orange), and G (green); those to left of hyphen refer to right tarsus; those following hyphen refer to left tarsus. The first-listed (or only) color band on left tarsus identifies geographic race according to this scheme: *savanna*, red; *oblitus*, blue; *mediogriseus*, yellow; and *labradorius*, orange. The two designations in quotations refer to flying individuals.

top-ranking birds, A1Y-OR and "*obl>med* I," only one close contact was seen; in this A1Y-OR gave an incipient sign of aggression (an intention movement) but was rebuffed by a warning from the flying bird.

Hostile display of a warning nature may characterize either a bird intent upon aggression or one on the defensive. Sometimes it seemed best interpreted as an intimidatory challenge (which was not always successful). At other times it was not clearly associated with either offense or defense. It was shown, for example, by one member of a twosome engaged in bathing, with the result that a "showdown" was forestalled. The most prominent features of this display consist of the bird's facing its opponent, lowering and apparently "pulling in" its head, opening its bill, and raising its wings. The intensity is variable. Sometimes the bill is opened but little, the wings raised slightly. At other times the mouth gapes rather widely and the wings are raised over the back. A warning display would normally last but two or three seconds, although it might be repeated.

Whereas the sparrows occasionally had short-lived fights, usually accompanied with rather buzzy or harsh call notes (*schwürt-t*), it was far more usual for one simply to dash toward another and drive it off some distance. Again, the intensity varied: a retreating bird might go several feet or it might go only a few inches. Although "warning encounters" were not counted in tabulating results in table 9, "driving encounters" of all intensities were counted.

As indicated by wing measurements, males (with longer wings) were especially prevalent among those individuals having high social rank. Although adults may tend to rank higher than immatures, the data are far from conclusive. Among 20 individuals which were aged satisfactorily (some were skull-aged in December, while others were aged by the shape of their rectrices), 10 adults had a mean dominance-aggressiveness rating of 2.0 against 0.9 for 10 immatures. Considering only those birds judged to be males, 7 adults had a mean rating of 2.2 against 1.4 for 4 immatures.

As to the four principal racial categories represented among birds using the central area of the enclosure, *labradorius* (*sensu lato*) scored highest on the dominance scale (four males and two females averaging 4.7), *oblitus* next (four males, one female, and one bird of uncertain sex averaging 3.2), *mediogriseus* third (three males and two females averaging 2.2), and *savanna* last (three males and three females averaging 0.7). Among records of flying birds not included in table 9 was one of the racial subtype *nevadensis>mediogriseus;* this bird was not seen to dominate any other but was dominated by others on two occasions and thus scored a 0 on the dominance scale. Because of the small series involved, these indications of hierarchical standings for the different racial groups should be regarded as only rough approximations which may change considerably with increase in size of samples. It is of some interest, however, to note that in table 9 the dark races *labradorius* and *oblitus* are represented among the first three birds (including the most aggressive individual, A1Y-OR). They contribute 8 out of the first 14 birds, whose dominance ratings are 1.0 or more. This suggests that in the near vicinity of food and water the dark races from far-northern regions more than hold their own in the social hierarchy.

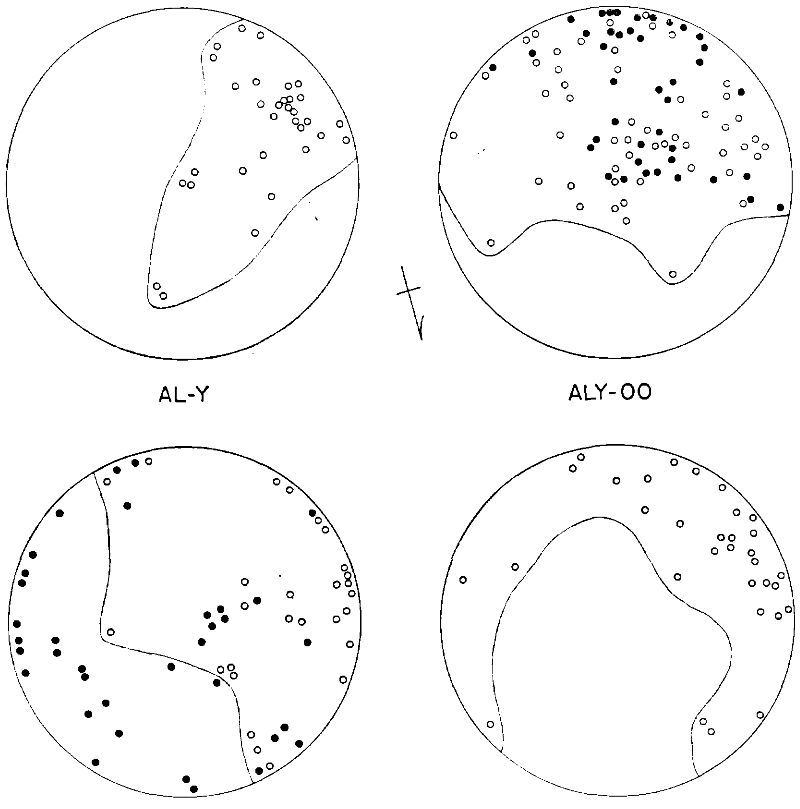
It should be added that in the central part of the enclosure many of the sparrows tended to feed and associate peacefully, and it was not uncommon for two or more to feed only inches apart, or for two to bathe at the same time. Most of the associations of individuals recorded in other parts of the enclosure were also of harmonious nature. For example, only 3 out of 47 records of associations of individuals between January 3 and March 6 (table 8) referred to birds that were having altercations. Even so, hostile encounters, usually betrayed by *schwürt-t* notes, were in evidence from time to time in various parts of the enclosure. Although in many observation-sessions none of these notes was recorded, they might be recorded three, four, or more times in other sessions (suggesting a minimum of two or three fights or driving encounters—not to mention silent warnings—in the course of an hour). None of the vocal evidences of encounters was recorded in April and May, when there were 13 or fewer birds inhabiting the enclosure. Ordinary contact notes (single high-pitched *tzeets*), although heard throughout the period of study, seemed relatively more frequent in late winter and early spring—about the time the greater part of the flying population was departing for the north.

OTHER CHARACTERISTICS OF THE POPULATION

Summary statement of build-up, maintenance, and decline of wing-clipped population.—On January 3 the first four wing-clipped birds were placed in the enclosure. This population was gradually built up, as follows: January 7, 7 birds; January 9, 11; January 11, 14; January 12, 16; January 18, 17; February 3, 23; February 4, 27; February 5, 28; February 19, 29; February 26, 30. By March 6 one of the 30 sparrows had been removed by a predator, and thereafter the population declined as a result of further predation. The nature and effects of this predation are discussed beyond. Reduced to nine birds by March 20, the population was augmented by my adding five individuals on the 21st. In four days these 14 birds were reduced to seven, so six additional birds were added on the 25th and four more on March 28. The population of 14 birds present on March 28 then gradually dwindled; it was cut in half by mid-April, and the last two individuals disappeared between May 18 and 20. For a graphic description of the decline of the wing-clipped population and its subspecific components, as well as the decline of the population of flying birds in exclosed parts of 3-412B, see figures 5 and 6.

Size of home range of beta-confined individuals.—As noted previously, the area of ground or home range occupied by an individual, wing-clipped Savannah Sparrow was less than the total available area within the one-acre enclosure. Four representative home ranges are illustrated in figure 4. Of these, that of A1-Y is relatively small, that of A1Y-OO rather large, and that of A1B-BO medium-sized and occupying relatively peripheral parts of the enclosed area. The home range of A1O-O is of especial interest in that it, unlike that of A1Y-OO (both A1O-O and A1Y-OO were comparatively long-lived birds), tended to shift from its earlier, January-March position to a new, more northeasterly position in April and May. In estimating average home-range size for individuals and groups, only the initial, stable, or nonshifting ranges were considered. These ranges were, however, mapped over periods of weeks or (for some individuals) even months, so that they represent fairly accurately the general space requirements of the different individuals. As indicated in table 10, the average home range of a wing-clipped sparrow occupied about 57 percent of the enclosure. Although there were great differences between extreme sizes, there were only slight and surely nonsignificant differences between averages for the separate race-groups (table 10).

A rough estimate of the home range of a flying sparrow.—In December 1956 I caught within a three-acre section of 3-412B, in the general vicinity of the enclosure (whose construction, at the time, had just begun), some 38 Savannah Sparrows, all of which were marked in semipermanent fashion with yellow plastic tape. This was accomplished by folding the tape round two or three individual tail feathers, including the central pair ("deck feathers") and usually an adjacent



AL-Y ALY-OO

ALO-O ALB-BO

Fig. 4. Representative "home ranges" of four individual, wing-clipped Savannah Sparrows confined to enclosure. Circles refer to location-records for the period January through March; dots, to records for April and May.

one. Birds so marked were called "Yellowtails." A few others were tail-clipped, becoming "Bobtails," and were also marked with yellow tape on the tertials. Numerous observations of fliers (totaling 190) in the enclosure from January 3 to 12 revealed that, on the average, yellow-marked individuals comprised 20 percent of the population of flying birds. (In the same area, from February 3 to 7, 96 observations indicated that they made up 19 percent of this population and, consequently, that relatively few of the yellow marks had been lost.) Repeated observations, both routine and special (including those made along strips radiating in eight different directions from 3-412B), indicated that the yellow-marked birds ranged over a total area of about 15 acres. They tended to remain concentrated near the area of capture. If we think of this aggregate of marked birds (which is an abstract, if more or less definable, population within a larger population) as occupying a tract of 15 acres, we may well suspect that an individual bird would, in a limited period (say, one week), range over an area smaller than this. If we now use the wing-clipped population (which is also a definable, yet theoretically abstract, population within a larger, enclosure-frequenting and surrounding population) as an analogy and again note that individual home ranges of wing-clipped birds cover from 13 to 95 percent, and average 57 percent, of the available area, we may with some justification estimate that home ranges of flying birds, as exemplified by yellow-marked birds in and near 3-412B, may for short periods fall between 2 and 14 acres and average about 8½ acres. There might of course be shifts from time to time (comparable to "seasonal shifts" of A10-0 and one or two other wing-clipped birds) so that for a considerable period (a week or more) the average individual might well range over 10 acres or more. Just as a given area will be occupied by a greater number of individuals in a period of a week or more (p. 183 ff.), so a given individual will occupy a larger area in a longer period of time than in a shorter one.

Peripheral tendency in confined birds.—That some of the flightless sparrows tended to live in more peripheral parts of the enclosure has been suggested already (fig. 4). A simple measure of peripheral tendency was obtained by subdividing with a compass the home-range map of each individual into five concentric zones of which the four outer ones were equal in width. The innermost zone was a solid, circular area, its radius equalling the width of each of the other zones. The central zone was numbered 1; the subcentral, 2; the middle, 3; the subperipheral, 4; and the peripheral, 5. For each individual the measure of peripheral tendency was a zonal average weighted according to the number of spot-records in different zones. To illustrate with three of the examples in figure 4: the peripheral-tendency value of AlY-OO was 3.6; of Al-Y, 4.0; and of A1B-BO, 4.7. A general summary of peripheral tendency is included in table 10. The tendency appears to be somewhat higher than "average" (3.82) in *oblitus* and *mediogriseus*, lower in *savanna* and (especially) *labradorius*. Since flying individuals of *nevadensis* tended rather strongly to frequent the earth bank just inside the plastic barrier, it is tempting to speculate that the peripheral tendency of confined individuals of this race would equal or exceed that of *oblitus* or *mediogriseus*. Several population characteristics in-

Table 10. Home Range and Peripheral Tendency in Races of the Savannah Sparrow (Wing-clipped Birds Only)

Geographic Race	Size of Home Range (% of 1-acre Enclosure) No. of Individuals Recorded	Mean	Extremes	Measure of Peripheral Tendency No. of Individuals Recorded	Mean	Extremes
Labradorius	12	59	26—86	13	3.65	2.8—5.0
Oblitus	8	57	41—85	8	4.10	2.9—5.0
Mediogriseus	8	56	13—95	11	4.10	3.5—5.0
Savanna	8	55	16—75	8	3.75	2.9—4.9
Total Sample	36	57.0	13—95	40	3.82	2.8—5.0

* Mean home-range size for each race is unweighted; mean peripheral-tendency value for each race is weighted in accordance with number of spot-records for different individuals.

cluding peripheral tendency will be examined subsequently with a view to revealing possible correlations.

Conspicuousness of individual, wing-clipped sparrows.—On any given day, the greater the frequency with which an individual is observed in the course of N observations carried out on a random basis, the more conspicuous that individual may be considered to be from the viewpoint of the observer. For the human observer working under the conditions prevailing in the enclosure, "conspicuousness" was almost synonymous with "tameness." In general, the tamer individuals were seen clearly and hence recorded with greater frequency than were the wilder ones. Consequently, differences in this aspect of temperament, far more than differences in coloration or general level of activity, were tied in closely with differences in degree of conspicuousness. One important variable, however, which cannot be overlooked is the total number of birds (wing-clipped and flying) present in the enclosure on any particular day. This number was usually large in January and February, declining from March to May. When it was large, the chances of one's seeing a given individual in an observation-session tended to be reduced; when small, the chances were increased. Accordingly, a suitable measure of the conspicuousness of an individual, which measure can be taken on any day under any circumstance of population density, was obtained through use of the formula

$$IC = \frac{(noi)\ (nWC+F)}{(nos)} \qquad (1)$$

where, for an observation-session on a given day, *noi* is the number of observations of a particular individual; *nWC* + *F* is the number of sparrows (wing-clipped and flying) continually present in the enclosure during the session; *nos* is the total number of observations of sparrows (wing-clipped and flying) made in the course of the session; and IC is the index of conspicuousness. In brief, the formula weights the frequency of observation *(noi/nos)* by multiplying by population density. This compensates for the fact that the individual's potential conspicuousness may be "swamped" when overall density *(nWC+F)* relative to extent of sampling *(nos)* is very high. Moreover, when density is very low (as it was in late April and May, when no fliers and only a few wing-clipped birds remained) and when extent of sampling is relatively very high (in order to be sure that all individuals are found), the number of observations of an individual, which is high, is reduced by the low value of $nWC+F/nos$.

As indicated in table 11, there is no significant difference between IC's for samples A and B, which are characterized by individuals which are associated, respectively, with dense and sparse populations. In spite of the fact that for individuals in the dense populations, *noi* and hence IC-values were on some days zero, and that zero values were taken into account in computing mean IC's for the different individuals or group-members, the aggregate average IC for the group connected with dense populations is still slightly larger than that for the group connected with small populations. It is of further interest that the most conspicuous individuals (notably A1-R with 2.65 and A1B-BO with 2.36) were associated with the denser populations (as were the least conspicuous birds). Even though the IC's of individuals in very sparse populations, more than those in denser populations, may tend to approach the norm for the wing-clipped birds (sample C), they still exhibit marked individual variability in that the lowest IC, as shown in table 11, is only about one-third as high as the highest.

Relations between conspicuousness, peripheral tendency, and aggressiveness.—With some of the sparrows it was noted that the more conspicuous birds were not often observed at or near the edge of the enclosure, whereas some of the less conspicuous ones were commonly present along or close to the edge. This relationship was due in considerable part to the proclivity of certain individuals to run along the relatively open path of disturbed earth just inside the barrier. This was their usual means of "getting away" from me. Although the openness of this peripheral situation did facilitate one's observations of relatively calm, foraging individuals or groups, it helped little or not at all with respect to birds that were running rapidly. Thus in a series of initial observations, or sightings, of various individuals, the sightings of "edge runners" were not as often accompanied or followed by identification of band arrangements as were those of birds which spent relatively more time in interior parts of the enclosure. Still, in spite of the fact that some of the birds exhibiting a high degree of

Table 11. Conspicuousness of Flightless Birds in Relation to Density of Surrounding Populations in Enclosure

Designation of Sample	Description of Sample	Mean Index of Conspicuousness (IC)	
		Group Mean*	Extremes
(A)	21 individuals associated with dense populations only (Jan. 3 — Mar. 20)	1.05	0.15—2.65
(B)	9 individuals associated with sparse populations only (Mar. 25 — May 20)	0.97	0.47—1.39
(C)	38 individuals (total for which IC data are available)	0.96	0.15—2.65

*A mean of means for the different group-members. For explanation see text.

peripheral tendency were among the more wary and less conspicuous individuals, a rank correlation between conspicuousness and peripheral-tendency values for a mixed-race sample of 38 individuals proved so low (—0.34) as to have no statistical significance. There was essentially no correlation (rank method again used, with a mixed-race sample of 21 individuals) between dominance or aggressiveness and peripheral tendency (+0.08). Hence there is absolutely no evidence that the more timorous individuals were, so to speak, crowded toward the periphery (or away from the intermittent supplies of food and water) by their "social superiors." This question was of particular interest in view of Calhoun's (1950) study in which brown rats *(Rattus norvegicus)* kept in a large pen, where food was continuously available at the center, developed a social gradient with the larger, more aggressive females selecting nesting sites close to the center, the others being crowded peripherally.

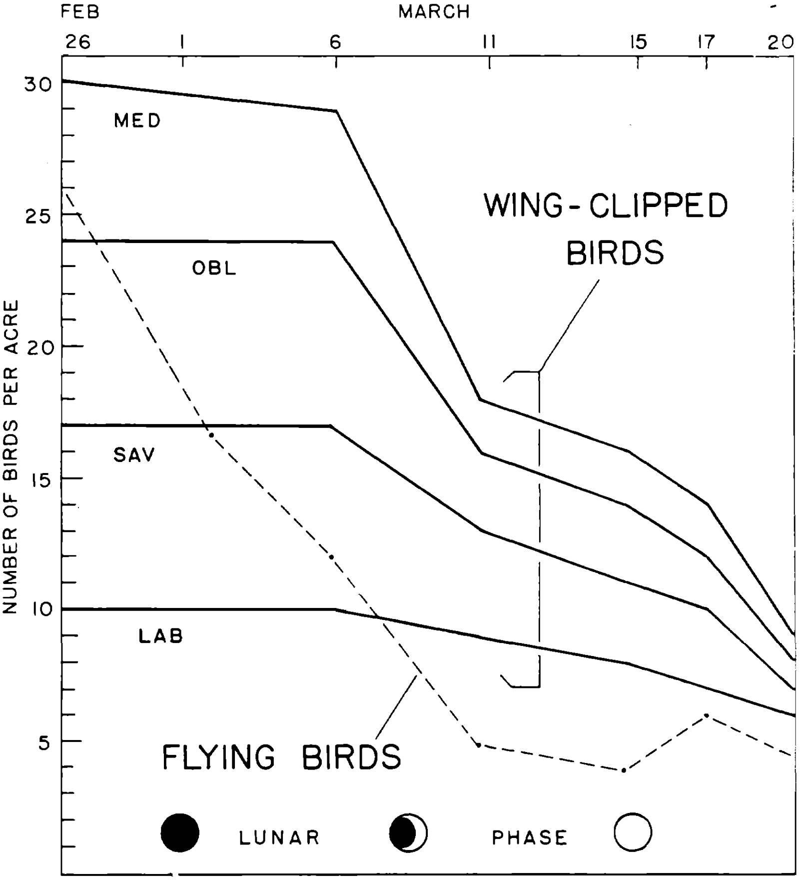


Fig. 5. Initial decline of the flightless sparrow population and its racial components due to owl predation, with concurrent decrease in population of fliers, as sampled in 3-412B, due to northward migration. Note relation of population density to phase of moon.

In a mixed-race sample of 21 individuals there was a very low rank correlation (+0.20) between aggressiveness and conspicuousness. Although the most dominant individual (A1Y-OR) was more conspicuous than average (1.21), the other wing-clipped birds with dominance ratings of 4 or more were decidedly less than average in conspicuousness.

DECLINE OF BETA-CONFINED POPULATION DUE TO PREDATION

Advent, nature, and intensity of predation.—As stated previously, there were no losses of birds from January 3 to February 26, in which period the population of wing-clipped birds was built up to 30 individuals. Between February 26 and March 6, one individual disappeared, and heavy predation was evident in the days and weeks that followed. The rate at which birds were removed tended to vary and is graphically

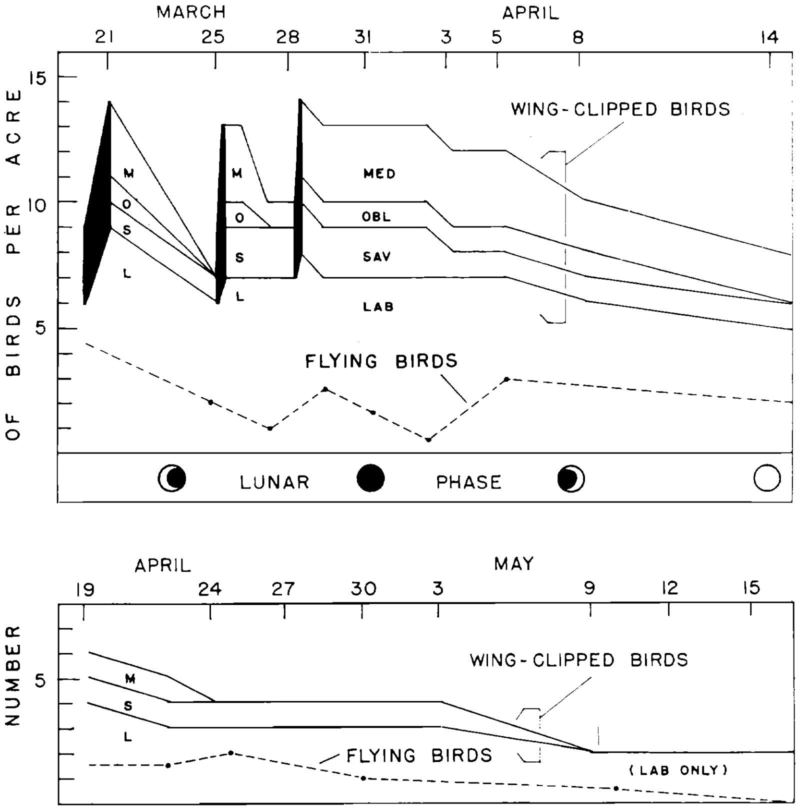


Fig. 6. Continued decline of population of flightless sparrows due to predation; increases in late March resulted from introductions, on three occasions, of a total of 15 wing-clipped individuals into enclosure. As indicated also in fig. 5, *labradorius* is removed at slower rate than other races. Population of fliers, as sampled in 3-412B, departed by mid-May; last two flightless birds disappeared by May 20.

shown in figures 5, 6, and 7. Although the main predator (or predators) was never seen, there was little doubt that it was one or more owls that caught the sparrows at night at the edge of the enclosure. There was no evidence that any sparrow was caught anywhere between the periphery and the center. Remains of prey, including feathers and parts of skulls, made it clear that the predator, after seizing its quarry, was prone to perch on certain of the posts that supported the barrier fence. Some sparrow feathers were found adhering to tops of posts; many others were found beneath or near posts both inside and outside the barrier and also in ground-level crevices between the outer and inner sheets of plastic. The two partial skulls that were found lacked the hind part of the cranium and resembled skulls taken from pellets of Short-eared Owls *(Asio flammeus)*. Although as many as four Short-eared Owls inhabited the 3-412 area in the winters of 1954-55 and 1955-56, so far as could be determined none was present anywhere in the Savannah River Plant area in the winter of 1956-57. Hence another kind of strigiform bird, perhaps a Barn Owl *(Tyto alba)*, which had been heard over 3-412 at night, or possibly a Screech Owl *(Otus asio)*, was suspected to be the raptor involved.

There was nothing to suggest a carnivore or other mammalian predator. In point of fact, in the course of five months of intensive work in the enclosure I found no signs (neither tracks nor scat) of any mammals except mice.

In spring there was, however, limited predation by one or more snakes. On April 3, at 3:30 p.m., some six feet from the west edge of the enclosure, I came upon a Coachwhip *(Masticophis flagellum)* in a coiled position. On being disturbed, the snake moved somewhat, rearranging its coils, whereupon I saw that it held in its mouth the anterior part of one of the wing-clipped Savannah Sparrows (Al-RGR). Since it was my objective to allow free rein to predators, I did not molest the snake, tried not to disturb it further, and after a minute or so gradually withdrew. At 3:55 I returned to the spot, approaching stealthily, and found the snake had gone and had left the bird, whose moist anterior was now covered with ants. Parts of the sparrow, a female, proved to be salvageable. Although I did not see a snake in the enclosure again, it is possible that in April and May snake predation contributed appreciably to the decline of the beta-confined population.

Measure of intensity of predation.—We can express the intensity of predation in terms of percent mortality (or survival) of the prey population through a given period, or we can think not only in terms of the prey population but also in terms of the predator, or predator population, and additionally in terms of the individual members of the prey population. From the latter, somewhat broader (if unconventional) viewpoint, it is patent that a 50 percent reduction, in N days, of a population of 30 sparrows is more important and should be weighted more heavily than a 50 percent, in N days, of a population of, let us say, 6 sparrows. A formula expressing an index of intensity of predation (IIP) which seems valid as applied to the situation with which I dealt is

$$\mathrm{IIP} = \sqrt{\left(\frac{Nb}{Nn}\right)\left(\frac{1}{S}\right)} \qquad (2)$$

where Nb = number of birds taken per period, Nn = number of nights in the period, and S = survival rate of the population in the period (= number of birds present at end of period/ number of birds present at start of period). In other words, the formula represents, for a given period, the geometric mean of (1) the calculated number of birds removed per night and (2) the reciprocal of the rate of survival of the initial population for that period. With this formula, 14 index values were computed for as many periods from early March to May 20 (when the last two sparrows disappeared). A comparison between IIP values and percent mortality is presented in figure 7. As long as the prey population is relatively large, the two kinds of indices are seen to be similar (they tend to form mirror images), but after the population has dwindled to few birds, as it had from late April to May 20, the mortality values tend to increase and finally reach 100 percent.

If we interpret the evidence in figure 7 in terms of IIP values, we note marked fluctuations in the intensity of predation. The high peaks occurring on moonlit nights in March are associated with a flightless prey population which averaged more than 18 birds; the lower peak, coinciding with a comparable moonlit period in April, is associated with a flightless prey population which averaged about 8 birds. Using

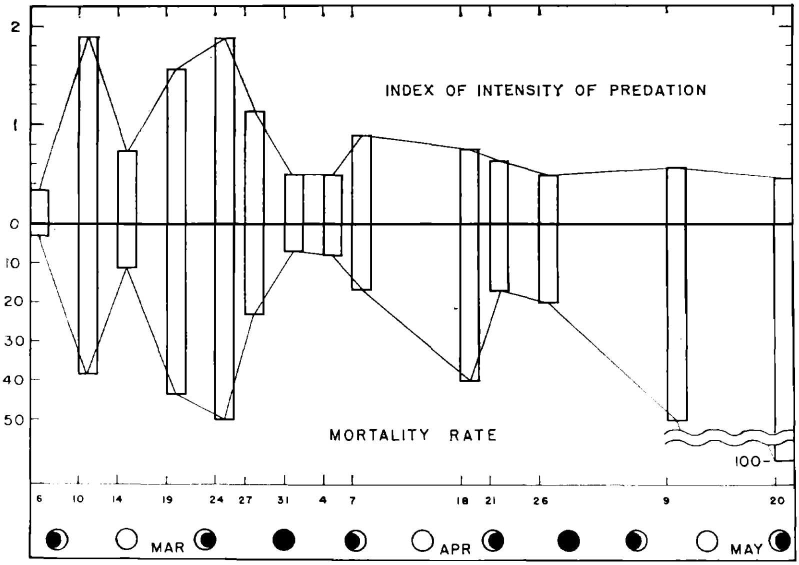


Fig. 7. Comparison of measures of impact of predation on enclosed population of wing-clipped Savannah Sparrows in relation to seasonal period and phase of moon. See text for discussion of "index of intensity of predation."

this measure, we conclude that the evidence points up that intensity of predation is dependent to no small extent on the density of the prey population. It seems that a density-dependent effect is demonstrated. On the other hand, if we interpret figure 7 from the standpoint of percent mortality, we find that once the predator has struck, its rate of removal of prey tends to be high with a large or crowded prey population, somewhat lower with an intermediate population, and high with a very small population. This suggests that there is an optimum size in which the prey population suffers a minimum rate of mortality. If the top half of the graph based on IIP values (fig. 7) is employed, intensity of predation is scarcely higher with a prey population of intermediate size (April) than with one of smaller size (May). If one should combine the two approaches (IIP and percent mortality) in some way, as by an additive procedure, one would again be impressed with the apparently reduced intensity of predation on an optimum-sized prey population. We are left with the suggestion that the density-dependent relationship is not a simple one; it is affected not only by periodic phenomena, such as the phase of the moon, but also by the particular method employed in analyzing the intensity with which the predator reduces the prey population.

Vulnerability of prey population in relation to migratory unrest.—As noted already (see fig. 5), by mid-March the population of Savannah Sparrows had been halved, and by March 20 it had declined to nine birds (30 percent of the starting population). Some of the heaviest predation occurred in a moonlit period in which flying sparrows were leaving the field *en masse*—migrating out of the 3-412 area. All the migratory egress, presumably northward, took place at night. It is highly probable that this nocturnal activity among the fliers served to augment, if not actually to elicit, actions which amounted to more or less oriented, nocturnal, migratory unrest among the wing-clipped sparrows. It is believed that such unrest (which evidently continued to some extent through April and May) was the main reason why the nocturnal predator or predators caught the birds at such a rapid rate, especially in the periods of moonlight. Further evidence supporting this view is that three-fourths of the total mass of feather remains (which I gathered up carefully, mapped as to exact position, and weighed in milligrams) were along the *north* edge of the enclosure, just inside the barrier. (Most of the rest of the feathers were along the edge on the southwest side.) Hence there can be little doubt that a large amount of the predation on the confined birds was directed against individuals engaged in nocturnal, migratory unrest, most of which was oriented in a northerly direction. Observations in the early morning and late afternoon revealed no evidence of crepuscular predation.

Isolated instances of migratory unrest were observed in the daytime in certain individuals among the wing-clipped birds. These birds would attempt now and again to fly in the absence of any observable, external stimulus. In such an attempt, a bird would usually beat its clipped wings and rise as much as a foot off the ground. I called this action the "voluntary upflutter." Such instances of diurnal unrest (which sometimes occurred near the barrier) were not observed before the latter part of March but were witnessed a number of times in April and May.

Selective predation on different geographic races.—From graphical evidence (figs. 5 and 6) there is a strong indication that individuals of the race *labradorius*, in their ability to survive for relatively long periods under more or less hazardous conditions, showed marked superiority over those of the races *mediogriseus*, *oblitus*, and *savanna*. In table 12 is presented statistical evidence that this difference is highly significant. The X^2 values were obtained by use of the formula

$$X^2 = \frac{n\ (ad - bc)^2}{(a+b)\ (c+d)\ (a+c)\ (b+d)} \qquad (3)$$

Here individual animals of two races, A and B, are subjected to selection through a given period, the numbers of individuals preyed upon being, respectively, a and b and the numbers left or not taken being c and d; n represents the combined total. This formula has been used by others (as Dice, 1949). From table 12, it appears that the race *labradorius*, if compared with the others taken separately or taken together, enjoyed, as it were, a selective advantage over the other races. At present it is not possible to say what factors are influential in bringing about this difference. Still, certain racial attributes which may show correlations or even have direct effects have come to light. These will be discussed briefly.

One possible source of influence can be dispensed with. The fact that the dark races *oblitus* and *labradorius* appeared to remain later in spring than the races *mediogriseus* and *savanna* was suggested by our study in 1955-56 (Norris and Hight, 1957: 48, 50). However, the best aggregate sample of data on relative abundance of the races (based on two years of work) is included in table 5 and figure 3, and this sample suggests that whereas *oblitus* may be relatively more abundant in spring than in midwinter, this is scarcely true of *labradorius* (which makes up 20.6 percent of the sample in January and February, and 19.6 percent in March and April). Had *oblitus*, rather than *labradorius*, exhibited the greatest resistance to predation, I might have hypothesized that because the former race tended to tarry in spring, the appearance in this race of nocturnal, migratory unrest was delayed with the result that its members tended to survive for longer periods than those of the other races. But so far as present data indicate, such a hypothesis is not applicable to *labradorius*, whose northward egress appears phenologically to correspond to that of most of the other races.

Table 12. Significance of Seminatural Selection Against Three Races of Savannah Sparrow as Compared to the Race *labradorius*

	Races Considered Separately (Mar. 20)			*Mediogriseus, oblitus*, and *savanna* Considered Together		
Measure of Significance	*mediogriseus*	*oblitus*	*savanna*	March 20*	April 8	April 24
x^2	2.9	3.6	3.6	6.4	4.8	3.4
P	.09	.06	.06	$<$ .02	.03	.07
Combined P		$<$ .02			$<$ .01	

* Starting populations are compared to those on March 20 and on two later dates.

Hence it is believed that factors other than "delayed unrest" were responsible for the greater capacity for survival exhibited by wing-clipped birds ascribed to this race.

It is of interest to note that *labradorius* averages largest in weight and wing length and that its color is relatively dark, its pattern having a liberal supply of black and rich browns. The other races are either lighter or grayer. Since predation took place at night, however, interracial differences in color probably had little effect on susceptibility to predation. Preliminary comparison of dorsal coloration of sparrows with color of substrate (involving the use of the Munsell Book of Color, 1929) gave no indication that *labradorius* was more "protectively" colored than the others. The present, semiexperimental study did not yield the clear-cut results that Sumner (1934) and Dice (1949) obtained in their experiments, in which it was demonstrated that animals whose colors matched their backgrounds were not as subject to predation as were those showing contrast with their backgrounds.

From the standpoint of behavior, *labradorius,* as compared with the other three races, was intermediate in conspicuousness (or tameness); it was decidedly less conspicuous than *oblitus,* decidedly more so than *mediogriseus.* In social position, however, *labradorius* ranked ahead of the others. Its larger size was probably a factor here. Although this race showed the lowest degree of diurnal peripheral tendency, it does not necessarily follow that its nocturnal peripheral tendency was less than that of the other racial groups.

Ecological longevity of confined sparrows.—Not only by means of X^2 but also by means of an "index of ecological longevity" (IEL) applied to the population of wing-clipped birds can we show a notably high rate of survival for *labradorius.* The latter index also affords some idea of relative survival in *mediogriseus, oblitus,* and *savanna.* For each individual, ecological longevity was computed by the formula

$$\mathrm{IEL} = \frac{\left(\Sigma\left[Ns_p \cdot \frac{1}{s_p}\right]\right)^2}{\Sigma Ns} \qquad (4)$$

where ΣNs = total number of nights (the sum of those in several, successive, arbitrary periods) survived by an individual (the mean maximum error incurred in calculating this value was about 7 percent); Ns_p = number of nights survived by the individual in a given period; and $\frac{1}{s_p}$ = reciprocal of the rate of survival of the wing-clipped population during that period. After an individual's several periodic values $(Ns_p \cdot \frac{1}{s_p})$ are summed, squared, and divided by ΣNs, one obtains an index of ecological longevity which is weighted in accordance with the mean, albeit fluctuating, *degree of hazard* to which the confined population has been exposed during the sojourn of that individual. Two examples may be given: YA1-YR, the first bird to be preyed upon, lived in the enclosure through 25 nights, during which there were no losses in the surrounding population of confined birds; for each period, then, $\frac{1}{s_p}$ is unity, $\Sigma[Ns_p \cdot \frac{1}{s_p}]$ equals ΣNs, hence IEL equals ΣNs. By contrast, A1Y-OR, which was introduced into the enclosure on February 3, survived 69 nights during which there were heavy losses in the surrounding, confined population; for each period, $\frac{1}{s_p}$ is greater than unity (ranging from 1.03 to 3.22), $\Sigma[Ns_p \cdot \frac{1}{s_p}]$ exceeds ΣNs, hence IEL is greater than ΣNs. The formula (4) appears to give due weight both to absolute longevity and to the varying degree of averted hazard. I believe it would be misleading to take only the former concept of longevity into consideration when one of the most striking characteristics of the beta-confined population was the accentuated predation pressure which was brought to bear upon it.

In table 13 mean indices of ecological longevity are compared with mean indices of conspicuousness for the four races. Note that the relatively long-lived *labradorius* (in particular) and *savanna* have moderate degrees of conspicuousness; the least conspicuous race *mediogriseus* has the shortest ecological longevity while the most conspicuous, *oblitus*, is also relatively short-lived. If there is a functional relationship between ability to survive under adverse conditions and degree of conspicuousness, it would seem that a *moderate* degree of conspicuousness or tameness is advantageous to the group.

Suggestive support for this tentative conclusion is provided by data from the Grasshopper Sparrow *(Ammodramus savannarum)*, of which four were kept in the enclosure with the Savannah Sparrows. (These four sparrows were not mentioned earlier because they rarely associated with the Savannahs, and then only fortuitously, and they otherwise had very little effect on the Savannah Sparrow population.) The Grasshopper Sparrows were exceedingly shy and secretive and hence were quite inconspicuous. Unlike Savannahs they would hide on occasion. Even so, observations in the enclosure were frequent enough to indicate that these shy sparrows lived, on the average, for periods that were less than those characterizing *mediogriseus*. Like *mediogriseus*, although in far more exaggerated fashion, they proved unable to adjust to life under beta-confinement. When flushed, a Grasshopper Sparrow would almost invariably dash madly through the vegetation until lost from sight. None of these sparrows utilized food and water at the center of the enclosure, although once, from the blind, I saw one paying

Table 13. Comparison of Races of the Savannah Sparrow with Respect to Ecological Longevity and Conspicuousness (Data Based on Flightless Birds)

	mediogriseus		*labradorius*		*savanna*		*oblitus*	
Characteristic*	No. Indiv.	Av. Value	No. Indiv.	Av. Value	No. Indiv.	Av. Value	No. Indiv.	Av. Value
Index of Ecological Longevity (IEL)	13	38	15	116	8	85	9	67
Index of Conspicuousness (IC)	8	0.79	13	0.92	8	1.06	8	1.29

* Formulae for numerical values are provided and explained in text.

a short, surreptitious visit to this area. This relative inflexibility in the behavior of the Grasshopper Sparrow and, to a lesser extent, in that of *mediogriseus* was apparently one important source of their undoing. At the other extreme, individuals of *oblitus* possibly "went too far" in their adjustment to the conditions of the enclosure—including their strong tendency toward being conspicuous or confiding. The adaptations shown by *savanna* and especially by *labradorius* seemed to strike balances that were more nearly optimum. To anthropomorphize, it was as if the seminatural conditions tended to favor "survival of the ambivert."

SUMMARY

In the Savannah River Plant area, on the Upper Coastal Plain of South Carolina, the Savannah Sparrow *(Passerculus sandwichensis)* is the most abundant bird inhabiting old fields in the nonbreeding period (late September to early May). Its density in winter may average four or five birds per acre, or more—up to 30 per acre—in particularly favorable fields. The short-term home range of a Savannah Sparrow was estimated to be about eight acres, but there was evidence that individuals exhibited greater vagility over a several-week period. In such a period, then, a substantially larger number of sparrows would frequent a given area than would frequent it at any particular moment or short interval of time. The above-given density values refer to short-term populations.

The wintering populations include five subspecies or races: the "light races" *mediogriseus, savanna,* and *nevadensis,* and the "dark races" *labradorius* and *oblitus.* These breed in different geographic regions, the dark ones as far north as the Ungava Peninsula and Hudson Bay. Data on the relative abundance of the races based on 1758 identifications (mostly of birds netted for banding and examined in the hand) made in the winters of 1955-56 and 1956-57, are presented for different seasonal periods. A case is made for the practice of making sight identifications, with binoculars, of the five races in question. This practice, which seems quite valid, serves to supplement and extend the other studies in "field taxonomy," which refers, in part, to the identification of infraspecific categories in live birds handled under field conditions.

From early January to May, 1957, special attention was given to a seminatural population of sparrows which included all the races except *nevadensis* (the least common). The birds in this population were wing-clipped, color-banded, and kept inside a low plastic fence enclosing one acre of old-field vegetation (where natural food, chiefly seeds of the grass *Digitaria,* was particularly abundant). The area of the circular enclosure exceeded the "home range" of any one of the confined birds, and it is proposed that the term *beta-confinement* be used to distinguish between this situation and that referring to birds in small enclosures or cages (alpha-confinement). In the enclosure the nonflying birds mingled freely with flying individuals of the same species. The density of fliers in the enclosure showed unusually sharp fluctuations which were thought to represent a "crowding effect." By means of the Petersen-Lincoln index (ratio of number of nonfliers to fliers

as obtained by random counts) it was possible to estimate repeatedly the density of fliers in the enclosure and to compare results with those of other methods, notably a transect method, employed in adjacent areas. Density values due to the two methods were very nearly the same. Whereas measures of spatial relations of sparrows in the enclosure suggested near-random patterns of distribution, it is possible that improved methods of investigation will reveal in many instances significant degrees of contagiousness involving twosomes, threesomes, or larger assemblages of birds.

Aspects of behavior of color-banded sparrows were observed from a blind near supplies of food and water, which were provided intermittently at the center of the enclosure. The presence of a rather loose social hierarchy soon become apparent; among the dominant individuals, certain males belonging to dark races were especially well represented. Many sparrows, however, displayed no signs of hostility, and nowhere, either within the enclosure or without, was there indication of social or ecological segregation among the different races. Of the confined birds, some of the measurable characteristics of individuals and racial groups were peripheral tendency (tendency to occupy relatively peripheral parts of the enclosure), conspicuousness (tantamount to tameness or "viewability" by the human observer), and ecological longevity (absolute longevity under beta-confinement weighted in accordance with degree of danger imposed by predators, during an individual's sojourn, on the surrounding, confined population).

The wing-clipped birds, numbering 30 at the end of February, suffered heavy predation by an owl or owls in early and middle March. In their capacity to survive for relatively long periods under such hazardous circumstances, individuals of the race *labradorius* showed marked superiority over those of the other races. There was no evidence that any race was more "protectively" colored than the others. The most "successful" race *labradorius* was characterized by individuals that were relatively large-sized, socially dominant, and moderately conspicuous. There was evidence that the heaviest predation on the nonflying population was density-dependent and took place in moonlit periods during which many of the sparrows were engaged in northward-oriented, nocturnal, migratory unrest. The last of the flightless birds was taken about May 20. Two methods of describing the impact of a predator or predators on a prey population are considered; a formula expressing the "index of intensity of predation" is suggested inasmuch as it seems especially applicable to the predator-prey relations involved in the present study.

It is believed that seminatural, beta-confined populations of birds—particularly small species that inhabit ground or low-herb strata—offer a wide range of possibilities for observation and experimentation. Such studies will help to bridge the gap which exists, at least in some ecologists' minds, between "natural" and "experimental" populations.

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COMMENTS ON THE MIGRATION OF STARLINGS IN EASTERN UNITED STATES

By David E. Davis

The origin of migration of birds is shrouded in mystery primarily because it began so long ago. However some clarification may be obtained from the study of the Starling *(Sturnus vulgaris)*, which has developed migratory patterns since its introduction into the United States. Unfortunately since the exact source of the introduced birds is not known, it is impossible to know whether they belonged to a migratory or to a sedentary race. In any case the pattern of spread (Kessel 1953) does not suggest the prompt beginning of extended migration but rather spread by diffusion, probably by subadults principally. It has been clear for sometime (Kessel 1953) that some starlings are residents while others migrate. In Britain (Bullough 1942) characters to distinguish resident and migratory birds have been found, but in North America none of the characters reported by