WHITE-SPOTTING IN THE GENUS AMMOSPIZA AND OTHER GRASSLAND SPARROWS

By Frank Enders and William Post

This paper presents data on the prevalence of white-spotting phenotypes in the genus *Ammospiza*. We follow Hanson (1949) in nomenclature. Nero (1954) calls the same trait "random partial albinism". White-spotting involves the occurrence of white feathers, singly or in patches, in almost any part of the plumage. Soft-part colors are not affected.

White-spotting is of interest for (1) the comparison that the data allows with that on local populations of the Red-winged Blackbird presented by Nero (1954, 1960), and (2) the parallel prevalence of white-spotting in populations of the Sharp-tailed Sparrow (*Ammospiza caudacuta*) and the Seaside Sparrow (*A. maritima*) in northeastern North America.

PROCEDURES

We first noticed *Ammospiza* sparrows showing white-spotting in the fall and winter of 1967, when banding these sparrows at Oak Beach, Suffolk County, New York. We systematically searched for white in the plumage of *Ammospiza* sparrows handled there in the following spring and summer. In addition, we examined specimens of these and closely related grassland sparrows in the American Museum of Natural History, in the summers of 1968 and 1969.

All banding at Oak Beach was done in an area of *Spartina alterniflora* about twenty hectares in extent, including a narrow edge of *Phragmites communis* and *Spartina patens*. This area is part of an extensive unaltered salt marsh which is located on the north side of the Jones Beach parkway and borders Great South Bay. See Post and Enders (1969, 1970) for a more detailed description of the area.

Of the 427 Seaside Sparrows (*Ammospiza maritima maritima*) banded in the spring and summer of 1968, 104 were examined; 30 of the 138 Sharp-tailed Sparrows (*Ammospiza caudacuta caudacuta*) banded were examined. Birds were captured in mist nets from 2 March to 13 August, 1968.

Specimens in the American Museum of Natural History, New York, were examined (Table 1 and 2). These represent all of the available specimens of *Ammospiza maritima* and *Ammospiza caudacuta* at that museum.

We examined the plumage of each individual of *Ammospiza* and of the other taxa listed in Table 1 in the following sequence: (1) The plumage of the head, neck and back regions was blown apart. (2) The throat, breast and belly plumage was examined in a similar manner. (3) The wings and tail were spread and examined. Birds which turned out to have some white feathers were always carefully checked in order to determine the number and location of white feathers.

TABLE 1. SPARROWS EXAMINED IN DETAIL

	Number examined	% with any white (number) ±1.96S.D.*	% with one feather white (number)	% with noticeable white (number)
Ammospiza maritima maritima				
1) museum adult plumage	214	4.2(9) ±2.7	0.9(2)	2.3(5)
2) museum juvenile plumage	18	5.6(1) ±10.6	0	0
3) total museum (1+2)	232	4.3(10) ±2.6	0.9(2)	2.2(5)
4) adults examined at Oak Beach	104	17.3(18) ±7.3	5.8(6)	5.8(6)
A. m. macgillivraei museum, adults	74	1.4(1) ±2.6	0	1.4(1)
A. m. sennetti museum, including three juveniles	37	0		
A. m. fisheri museum, adults	37	0		
A. m. howelli museum, adults	2	0		
A. m. juncicola museum, adults	10	0		
A. m. peninsulae museum, adults	15			
Total museum *Ammospiza maritima* specimens	407	2.7(11) ±1.6	0.5(2)	1.5(6)
Total *Ammospiza maritima* examined	511	5.3(27) ±1.9	1.8(9)	2.3(12)
Ammospiza nigrescens museum, including three juveniles	77	0		
Passerherbulus caudacutus	84	0		
Passerherbulus henslowii	107	0		
Ammospiza caudacuta caudacuta				
1) museum adults	351	5.7(20) ±2.4	1.1(4)	4.0(14)
2) museum juveniles	30	0		
3) total museum (1+2)	381	5.2(20) ±2.2	1.0(4)	3.7(14)
4) adults examined at Oak Beach	30	26.7(8) ±15.8	13.3(4)	3.3(1)
A. c. subvirgata				
1) museum adults	59	3.4(2) ±4.6	3.4(2)	0
2) museum juveniles	7	0		
3) total museum (±2)	66	3.0(2) ±4.1	3.3(2)	0

These specimens were examined carefully, as described under Procedures, for the presence of any plumage aberrations.

*95% confidence interval, calculated using formula 8.7.1 in Snedecor and Cochran (1967).

TABLE 1. Continued
TABLE 1. SPARROWS EXAMINED IN DETAIL

	Number examined	% with any white (number) ±1.96S.D.*	% with one feather white (number)	% with noticeable white (number)
A. c. nelsoni museum, adults	103	1.9(2) ±2.7	1.9(2)	0
"Intermediate between *A. c. nelsoni* and *A. c. altera*", museum, adults	2	0		
A. c. altera museum, adults	6	0		
A. c. diversa, including those labelled "probably *diversa*" museum, adults	17	5.9(1) ±11.2	0	5.9(1)
Total museum *Ammospiza caudacuta* specimens	575	4.3(25) ±1.7	1.4(8)	2.6(15)
Total *Ammospiza caudacuta* examined	605	5.5(33) ±1.8	2.0(12)	2.6(16)

These specimens were examined carefully, as described under Procedures for the presence of any plumage aberrations.

*95% confidence interval, calculated using formula 8.7.1 in Snedecor and Cochran (1967).

Specimens of taxa listed in Table 2, on the other hand, did not have their feathers parted. Instead, these specimens were examined by looking at both the ventral and dorsal surfaces. It was hoped thereby to obtain an estimate of the incidence of noticeable white, the third column in Table 1, for available specimens of additional grassland sparrow taxa.

RESULTS

Extent of white plumage involved in white-spotting. — The extent of white varied from single partial white feathers to extensive patches of white feathers in almost every part of the plumage, including wing and tail feathers. Markings were not symmetrical. Elliott (1962) reported similar white-spotting in *Ammospiza* sparrows; however, he was observing birds through binoculars and probably noticed only extreme cases of white-spotting. Partial white feathers usually showed white in the distal portion of a feather. Most partial white feathers showed a color intermediate to the normal coloration in the proximal portion of the feather. The parts of the plumage that were white or whitish showed above-average wear, as Nero

TABLE 2. SPECIMENS EXAMINED FOR NOTICEABLE WHITE ONLY

	Number of museum specimens examined
Passerculus sandwichensis savanna	413*
P. s. beldingi	120
P. s. halophilus	16
Ammodramus bairdii	29
Ammodramus savannarum perpallidus	62

*Specimen AMNH number 762058, collected on October 12, 1906, at Mount Pleasant, S. C., was an albinoid.

(1954) has noted for such feathers of the Red-winged Blackbird (*Agelaius phoeniceus*).

Other than a single Savannah Sparrow, no individuals with abnormal coloration of the plumage were noticed in any grassland sparrow species, except *Ammospiza maritima* and *Ammospiza caudacuta* (Tables 1 and 2). The single albinoid (following the terminology of Nero, 1954) Savannah Sparrow (*Passerculus sandwichensis*) found had a washed-out whitish coloration that is quite distinct from the scattered white feathers found in the white-spotted *Ammospiza*. White-spotting is then unique to *Ammospiza maritima*, and *A. caudacuta*, among the grassland sparrows.

Sexual differences in the prevalence of white-spotting. — White-spotting was not disproportionately represented in either sex (Tables 3 and 4). The value of chi square calculated from the data in Table 4, to examine the possibility of a different rate of prevalence of white-spotting in the sexes of the Seaside Sparrow, is 0.5, not significant.

Possible biases in data used to make estimates of prevalence of white-spotting. — No special attempt was made by us to capture or to record data from birds in the field which showed white-spotting; on some days we captured so many birds that all we were able to do was band and release them. Even so, there are probably biases in the collection of both museum and field data, which provide the estimates of prevalence of white-spotting which are presented in Table 1. Collectors might have been biased in favor of noticing and collecting "partial albinos" for museums. Might there not, on the other hand, have been some elimination of the "abnormal" white feathers by collectors or skinners?

As a check for bias in the data, after the field data had been gathered, we divided sparrows showing white-spotting into three non-overlapping categories: one white feather, intermediate white, and noticeable white feathers. Noticeable white includes any bird

TABLE 3. SEX OF WHITE-SPOTTED MUSEUM SPECIMENS

	Ammospiza maritima	*Ammospiza caudacuta*
males	6	10
females	4	6
sex unknown	1	9

with so many white feathers so placed that they could not have gone unnoticed even under conditions of rapid handling. E.g., a bird with three small white back feathers would not be noticeable, while one with three white primaries would be. The museum specimens were divided into the same categories. Then the possibility that the field data overestimates the proportion of noticeable white birds can be checked: we calculated an heterogeneity chi square between museum and field data for the nominate races (Table 5). Due to the small numbers in some categories, chi square is calculated between the categories "noticeable white" and "all others". The values obtained for chi square indicate that the field data has a significantly greater proportion of *A. c. caudacuta* individuals in the *not* noticeable category, while the difference for *A. m. maritima* is in the same direction, although not significantly so. Since there was not a greater proportion of white-spotted birds with noticeable white in the field data than in the museum data, we conclude that there was no bias toward recording birds with noticeable white in the field, compared to the museum collection. Thus, there is no unequivocal evidence available that field or museum data are biased.

Estimates of the prevalence of white-spotting. — Table 1 presents various estimates in the second column, along with the 95% confidence limits for each.

Geographic variation in the prevalence of white-spotting. — The estimates of the prevalence of white-spotting provided by the museum specimens show that the races of both species from northeastern

TABLE 4. SEX OF SEASIDE SPARROW EXAMINED IN THE FIELD, OAK BEACH

	Number examined	Number showing white-spotting
males	43	9
females	45	6
sex unknown	16	3

TABLE 5. AMOUNT OF WHITE PRESENT IN WHITE-SPOTTED *Ammospiza* OF NOMINATE RACES

	one white feather	some white feathers	noticeable white	noticeable	*not* noticeable	
A. m. maritima						
museum	2	3	5	5	5	$X^2=0.8$
field	6	6	6	6	12	$.3<P<.5$
A. c. caudacuta						
museum	4	2	14	14	6	$X^2=7.7$
field	4	3	1	1	7	$.005<P<.01$

United States have the highest prevalences. Neighboring races have lesser prevalences and the Gulf Coast races of the Seaside Sparrow show no white-spotting at all. The 95% confidence intervals of the estimates for neighboring races overlap, in both species, indicating a gradual change in the occurrence of white-spotting from one race to another.

No attempt was made to record geographical variation in the prevalence of white-spotting within races for museum specimens; from whatever locality many specimens had been collected (of a race showing white-spotting), a few white-spotted specimens were found. However, if one compares the estimates of the prevalence of white-spotting in the nominate races (=museum specimens) with the estimates for the Oak Beach populations of both species, then some geographic variation seems to be present within the nominate races.

The birds examined for white-spotting at Oak Beach included many that were captured or recaptured after May 30: 61% of the Seaside Sparrows examined, and 43% of the Sharp-tailed Sparrows. More than that were probably present at Oak Beach, since only a minority of the breeding individuals at Oak Beach were netted during the summer months. It is, then, a fairly safe assumption that the birds examined at Oak Beach are representative of the local breeding populations of each species. There is, then, a strikingly greater prevalence of white-spotting in both the Seaside and Sharp-tailed Sparrow populations at Oak Beach than in the rest of the nominate races of either species, using museum skins to provide an estimate of the overall prevalence of white-spotting in the nominate races. This difference between the prevalence of white-spotting in the Oak Beach populations of each species and the nominate races is significant at the five percent level, as may be seen by examining the 95% confidence limits in Table 1 for the Oak Beach and museum samples of each species.

Blackish spotting on Ammospiza. — Wayne (1921) described blackish spotting on the ventral surface of the "partial albino" (=white-spotted) Sharp-tailed Sparrow specimens which he collected. All the Seaside and Sharp-tailed Sparrow museum specimens which showed white-spotting were examined a second time in 1969, in search of this plumage aberration. No such markings could be found, nor had we ever noticed any such marks on "partial albinos" which we observed in the field.

DISCUSSION

Elliott (1962) first remarked on the high prevalence of white-spotting ("partial albinism") in New York *Ammospiza* observed in the fall and winter of 1940-1941: "rather high for the limited population of several hundred . . . three Sharp-tails (*Ammospiza caudacuta*) and four Seaside Sparrows (*Ammospiza maritima*)" showed white-spotting. He did not mention any such white-spotting in the breeding populations of the two *Ammospiza* species in New York. In the form that white-spotting takes, and in its prevalence, our results for the two *Ammospiza* species are comparable to those of various authors for the Red-winged Blackbird (Nero, 1954, 1960), the Canada Goose (*Branta canadensis*) (Hanson, 1949), and the feral Rock Dove (Dunmore, 1968). It is remarkable that the prevalence of white-spotting both in the Seaside and in the Sharp-tailed Sparrow is highest in the nominate races, and, within those races, is still higher in the Oak Beach breeding populations.

Explanations for white-spotting. — Several hypotheses have been advanced as to the causes of white-spotting ("partial albinism"): (1) injury, (2) food, and (3) genetic traits (Gross, 1965). The first two would require that we call the occurrence of white-spotting a polyphenism (Mayr, 1966), the third, either a result of mutation rate only or else a genetic polymorphism (Ford, 1964). The data which we have presented above permit some conclusions as to the cause of white-spotting in the genus *Ammospiza:*

(1) *Mechanical injury.* — If one accepts the reasoning of Woolfenden (1956) that the Sharp-tailed Sparrow occurs in more abrasive vegetation, then one must expect it to suffer more injuries, and so to have a higher prevalence of white-spotting than does the Seaside Sparrow. However, the 95% confidence limits of the prevalence of white-spotting in the two species (Table 1) overlap considerably; hence, our data show no significant difference between the two species in prevalence of white-spotting. Furthermore, other grassland sparrows, which might be expected to incur the same amount of mechanical injury, do not show any white-spotting at all (Tables 1 and 2). This excludes mechanical injury.

Evidence that the occurrence of white-spotting is not due to an interaction of the effects of salt water and injury is provided by the fact that the other salt marsh sparrows examined show no white-spotting: Gulf and Florida races of the Seaside Sparrow, the Dusky

Seaside Sparrow (*Ammospiza nigrescens*), and the races *halophilus* and *beldingi* of the Savannah Sparrow (Table 1 and 2).

(2) *Food.* — Certain food items or nutrients might be present or absent in northeastern salt marshes. One must then relate the existence of white-spotting in the inland races of the Sharp-tailed Sparrow to the presence of those birds on the Atlantic coast during the spring molt. Since a white-spotted *Ammospiza caudacuta nelsoni* was collected in November, and this bird had presumably molted before migration, the hypothesis that food differences cause white-spotting cannot be so simple, for the Sharp-tailed Sparrow. It is also impossible for food differences alone to explain why some Seaside Sparrows should be white-spotted, and others not so: this species has feeding grounds that are held in common even during part of the breeding season (Post and Enders, unpub.). Also, birds of both species with and without this trait have been observed to intermingle freely throughout the year.

(3) *Genetic explanations.* — Some authors have suggested that mutation rate alone explains the occurrence of white-spotted ("partial albino") birds (Gross, 1965). For the Red-winged Blackbird (Nero, 1954, 1960), the Canada Goose (Hanson, 1949), and the feral Rock Dove (Dunmore, 1968), it has been shown that individuals showing white-spotting occur at a rate above that possible as a result of mutation only, namely, five per cent prevalence. In these species it has thus been shown that white-spotting or "random partial albinism" probably represents a genetic polymorphism (Ford, 1964). Since estimates of the prevalence of white-spotting in the *Ammospiza* sparrows rise above five per cent (Tables 1), white-spotting cannot be the result of recurrent mutation only, in both species of sparrow. There is, then an argument, by exclusion of alternative hypotheses, that white-spotting in the *Ammospiza* sparrows represents a genetic polymorphism.

Although we have no direct proof that it is inherited, white-spotting has been present in the *Ammospiza* frequenting the Oak Beach area for thirty years since Elliott's observations, and it is present among the earliest Long Island specimens that we have seen (1890's). This also excludes the possibility that white-spotting is the result of recent pollution in the New York region (which includes various mutagenic chemicals). Information on the pedigrees of white-spotted *Ammospiza* is not available; such data would be very useful.

Selective factors maintaining white-spotting. — Sage (1963) pointed out that the highest prevalence of white-spotting ("partial albinism") occurs in birds which are both sedentary and social in their breeding habits. Invoking the lack of gene flow that is related to a sedentary, colonial life as a causative factor for the *exhibition* of white-spotting would help explain why much white-spotting occurs in the goose, blackbird, and *Ammospiza* sparrows, since all these species occur as chains of semi-isolated populations, due to the spatial isolation of suitable marshy habitats. But, it should be clear that even though such inbreeding may result in a greater prevalence of the trait in a particular population, nonetheless, it does not, by itself, explain what is maintaining the trait in the gene pool of these species, i.e. what is maintaining at least a selective neutrality for the trait. One must postulate some selective factor that favors the white-spotting; this could involve selection for a linked advantageous trait rather than direct selection for the white-spotting trait. Dunmore (1968) has observed changes in the prevalence of white-spotting in a Rock Dove population that suggested that the white-spotting phenotype increased in prevalence during the winter. In our own data, from the parallel amount of white spotting both in the nominate races and in the Oak Beach populations of the two *Ammospiza* species, it seems clear that there is a relation between an elevated incidence of white-spotting and some factor peculiar to the salt marshes of northeastern North America.

One might speculate that white-spotting provides disruptive coloration to birds against a visually hunting predator on snow-covered ground in the winter. It is our experience that in some winters quite a few *Ammospiza* of the nominate races are present on the northern breeding range, although it is not clear yet how regularly or successfully *Ammospiza* overwinter in marshes that experience regular snowfall.

SUMMARY

The prevalence of white-spotting ("random partial albinism") phenotypes was measured for museum speciment of various grassland sparrow species. No white-spotting was found in species examined from the genera *Ammodramus*, *Passerculus*, and *Passerherbulus*. For both of the *Ammospiza* species (*Ammospiza maritima* and *Ammospiza caudacuta*) there were several per cent white-spotted individuals, with the highest prevalences (approximately five per cent) occurring in the nominate races of both species, in northeastern North America. Within the nominate races, still higher prevalences were recorded for *Ammospiza* banded at Oak Beach, N. Y.: 95% confidence intervals for the prevalence of white-spotting were 10.0 to 24.6% for *A. m. maritima* and 10.9 to 42.5% for *A. c. caudacuta*. Simple injury, food, and genetic explanations of white-spotting are considered, and the simple injury and food hypotheses are rejected: the simplest available explanation for white-spotting in these *Ammospiza* sparrows is that it is a genetic polymorphism maintained by a selective pressure that acts on both *Ammospiza* species in the northeastern United States. Inbreeding of localized populations of each of the two species of sparrows may make the white-spotting trait more evident; but this alone cannot explain the geographic coincidence of high prevalences of white-spotting in both species both at Oak Beach and in the races of northeastern North America.

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Department of Zoology
North Carolina State University,
Raleigh, N. C. 27607

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