

TAXONOMY OF HOUSE SPARROWS AND THEIR ALLIES IN THE MEDITERRANEAN BASIN

RICHARD F. JOHNSTON

Museum of Natural History and
Department of Zoology
The University of Kansas
Lawrence, Kansas 66044

Approximately 3600 years ago there occurred a significant movement of northern European agricultural man into southern European and Mediterranean regions (establishment of the Lake Dwellers in northern Italy, see Brea 1946 et seq.). Seemingly also with man came his newly-acquired commensal, the House Sparrow (*Passer domesticus*), which had been living with man in northern Europe since its presumptive origins in the Near East, perhaps some 5500 years earlier. Indigenous sparrows in Italy, probably also commensal in 1600 BC and almost certainly Willow Sparrows (conventionally considered a species by most taxonomists as *Passer hispaniolensis*), shared a common ancestry with House Sparrows but were phenotypically distinct. Interbreeding of the two phenetic kinds ensued, followed by establishment of populations of phenetic heterogeneity throughout the Italian peninsula. Similar instances of commingling of gene pools occurred in other places in and around the Mediterranean, but on the Balearic Islands only House Sparrows became established and on Sardinia only Willow Sparrows.

Later, only 300 to 400 years ago, there occurred persistent cold weather, the "Little Ice Age," sufficient to close Alpine passes for most of each year, with the result that the sparrows of the Italian peninsula were cut off from mainland European sparrows for many tens of generations. This short period of fairly stringent isolation presumably allowed the ongoing processes of selective reassortment of Italian sparrow genotypes to proceed toward relative stability more quickly than they would have otherwise, and upon re-establishment of Alpine contact gene flow between Italian sparrows and House Sparrows did not occur as freely as formerly.

These events, or some such similar set, have given us a remarkable complex of sparrows around the Mediterranean Sea, and their variable geographic, phenetic, and genetic characteristics provide a continual challenge to understanding present relationships (e.g., Brehm 1842; Chigi 1914; Meise 1936; Macke 1965). One of the most intriguing aspects of

the biology of these sparrows is that geographically disjunct populations may be phenetically much alike. This has suggested that they may also be genetically similar, but experimental verification of this hypothesis is lacking. It is known that the phenotypic feather coat of the sparrows has a highly polygenic basis (see below), and it is thus entirely possible that similar phenotypes can have different genotypes, and vice versa.

Polygenic control of gross phenotype may well be the expected condition, but we need not merely assume it for Mediterranean sparrows; Macke (1965; see also table 7) has shown that the F_1 of the cross, House Sparrow \times Willow Sparrow, may include a sampling of nearly the entire range of intermediate phenotypes, hence of genotypes. The importance of this finding cannot be exaggerated. It means at one level that wherever there is a restricted range of phenotypes (= genotypes) the action of selection or restricted founder gene-frequencies is strongly implied. But, if clines in phenotypes occur, then clines in gene-frequencies occur, and these can only be responses to differential selection pressures. It means also, but conversely, that we must be prepared to find populations in which a wide range of phenotypes occurs.

Consequent opportunities for "hybrid swarms" or for geographically-oriented spectra of phenotypes, or for intermediate conditions, have been only in part realized, owing variously to coincident gene frequencies in founder populations, selection of coincident characters, gene-flow, absence of gene-flow, etc. Current distribution of phenotypes and possible causal factors for such distributions are set forth below.

One of the aims of the initial phases of this study was detection of phenetic change in sparrows at localities where good samples were obtained by W. Meise 30 and more years ago. Persistent effort therefore is made to relate present findings to those of Meise (1936) and the chronological comparisons are an important part of this preliminary report.

TABLE 1. Scoring of characters on a hybrid index for male Mediterranean sparrows.

Character	Quality in House Sparrow and minimum point value	Quality in Willow Sparrow and maximum point value	Range in score
Color of back	Orange, rufous, buff, and black (0)	Pale buff, whitish, cream, and black (2)	0-2
Color of rump spots	Rufous, pale, or none (0)	Black (2)	0-2
Posterior margin of bib	Abrupt (0)	Spearpoint-shaped black streaks (2)	0-2
Flanks	Buffy or gray, but lacking shaft streaks (0)	Black or blackish shaft streaks (3)	0-3
Color of shoulder	Rufous with little black (0)	Black with little rufous (2)	0-2
Crown	Gray (0)	Rufous (6)	0-6
Totals:			0-17

MATERIALS

The total number of specimens is 2033, of which 882 (males) are housed in European museums and 1151, taken in 1965-66, are at the Museum of Natural History, The University of Kansas. Of the Kansas material, 918 specimens were prepared as conventional study skins, and of these 494 were males. This part of the study therefore includes reference to 1376 male specimens.

In field sampling no specimen was discarded for any reason; those chosen for preparation as skins or as skeletons were selected on a random basis. A working assumption in this report is that individuals taken at a locality were hatched there or close by. This assumption holds that meaningful, numerically significant migration does not occur in the populations sampled. Long-distance dispersal no doubt occurs, but it is impossible to distinguish between birds that have dispersed from another locality and some of the recombinant residents. To claim that this is possible (as have some earlier students) is to beg the question. The major consequence of such dispersal movement, since it is essentially random within major geographic units, should be to increase the apparent variability of characters in any sample.

METHOD OF ANALYSIS

The technique used here stems directly from that of Meise (1936), which was equivalent to the "hybrid index" then being used for the first time by Anderson (1936). This technique uses simultaneous comparison of several characters in the samples and it codes subjective estimates of non-quantified characters of pattern, shape, and color onto a convenient numerical scale. This kind of descriptive analysis is especially useful in evaluating the morphology of populations in which there are several, concordant variables (see Sibley 1954; Selander 1964). The work here treats House Sparrows as one end of a phenetic spectrum and Willow Sparrows as the other; "Italian" sparrows and other phenetic intermediates are intermediate in value.

In scoring on this hybrid index a given character is subdivided into several, graded conditions of expression, with specimens defining

the conditions and bearing arbitrary numerical values corresponding to the conditions. Several characters are scored (table 1), and the numerical index value for each specimen is the sum of the scores for all characters examined. Finally, for a given locality, mean scores are determined. This routine differs from that of Meise in 1936 in that fewer characters are scored, and it is not possible to make direct comparison of present values with those of Meise. However, a rough conversion to Meise's scale can be made by rendering present index values as per cent of the possible maximum and minimum scores (thus, 0 = 0% and 17 = 100%). Such conversions are included in tables 2, 3, and 4.

Because House Sparrows show significant age variation in male plumage (Selander and Johnston 1967), index scores are different for adults and subadults from many localities. The extent to which such age variation can influence scores may be seen in the histograms of figure 2, where several localities are indicated. Determination of ages of specimens was made by examining the skull, with totally pillared bone being considered to represent adult age and any unpillared bone subadult age (Nero 1951). Such examination was possible only with specimens collected in the course of the present study, and none of the other specimens could be allocated to age by any comparable method. Index values for museum samples other than those for Kansas are therefore of both adults and subadults, in unknown proportions. Mean values for the Kansas samples are presented in tables here as weighted means calculated on the assumption of equal numbers of adults and subadults.

A further word on the nature of extant museum samples is necessary, so that one bias of the samples can be emphasized at the outset. As has been noted just above, there is a slight influence of age of individual on hybrid index

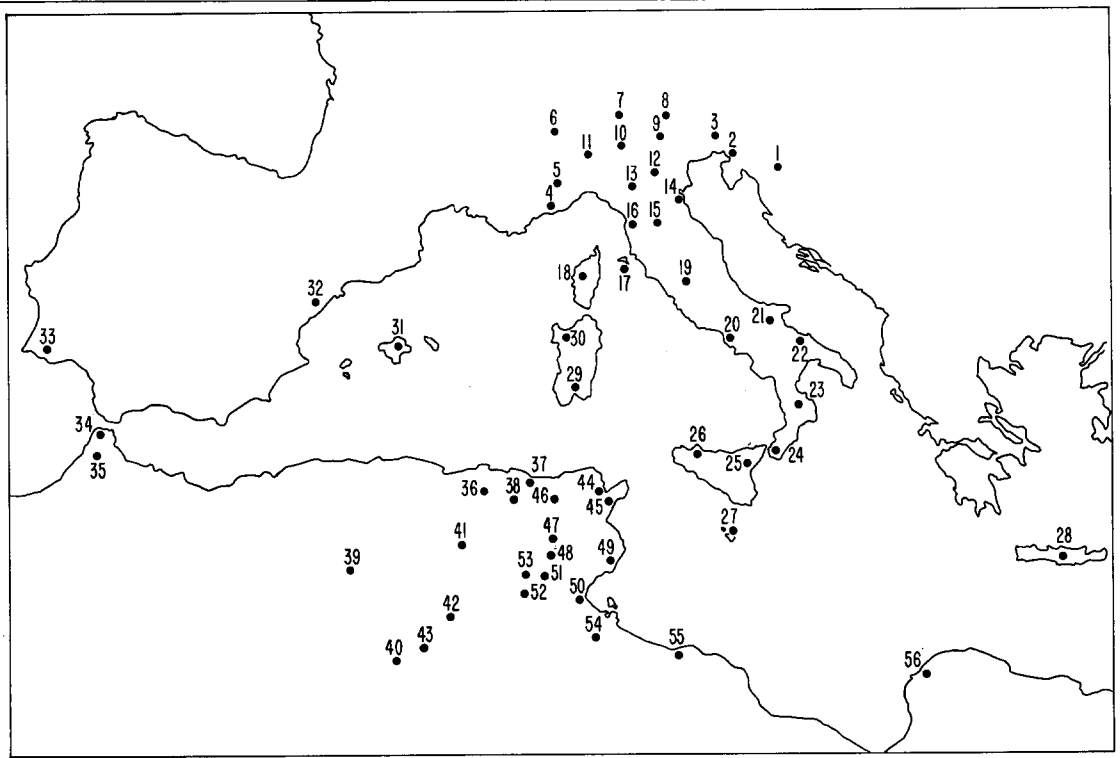


FIGURE 1. Sketch map of the Mediterranean basin, showing localities from which samples were taken for this study. The numerals indicate the following localities (with their hybrid index scores in parentheses): 1, Karlovac, Yugoslavia (0.5); 2, Trieste, Italy (3.0); 3, Udine, Italy (6.2); 4, Bordighera, Italy (3.0); 5, Cuneo, Italy (6.1); 6, Aosta, Italy (6.4); 7, Sondrio, Italy (6.2); 8, Bolzano, Italy (7.2); 9, Trento, Italy (6.4); 10, Bergamo, Italy (7.0); 11, Novara, Italy (7.2); 12, Mantova, Italy (7.3); 13, Parma, Italy (7.7); 14, Comacchio, Italy (7.7); 15, Firenze, Italy (7.5); 16, Pisa, Italy (8.0); 17, Elba, Italy (7.6); 18, Corsica, France (7.2); 19, Cantalupo Sabino (9.1); 20, Napoli, Italy (9.2); 21, Foggia, Italy (8.2); 22, Bari, Italy (10.3); 23, La Sila, Italy (10.4); 24, Reggio Calabria, Italy (10.1); 25, Catania, Paternò, and Randazzo, Sicily (12.4); 26, Palermo, Sicily (13.5); 27, Malta (12.9); 28, Crete (7.3); 29, Cagliari, Sardinia (14.9); 30, Sassari, Sardinia (15.1); 31, Balearic Islands (0.3); 32, Oropera Castellon, Spain (0.6); 33, Lagos, Portugal (0.6); 34, Morocco (1.4); 35, Morocco (15.3); 36, Constantine, Algeria (9.2); 37, Bône, Algeria (13.3); 38, Hamman Meskoutine, Algeria (11.6); 39, Laghouat, Algeria (14.0); 40, Menaad, Algeria (14.2); 41, Biskra, Algeria (8.5); 42, Touggourt, Algeria (8.6); 43, Ourgla, Algeria (6.4); 44, Tunis, Tunisia (14.2); 45, Hamman Lif, Tunisia (11.5); 46, Souk El Arba, Tunisia (7.7); 47, Kasserina, Tunisia (8.0); 48, Feriana, Tunisia (6.5); 49, Sfax, Tunisia (12.1); 50, Gabes, Tunisia (14.1); 51, Gafsa, Tunisia (11.8); 52, Tozeur, Tunisia (13.1); 53, Philippe Thomas, Tunisia (15.0); 54, Catahouine, Tunisia (12.4); 55, Tripolitania, Libya (15.0); 56, Cyrenaica, Libya (4.4).

score, so that Willow Sparrow-like subadults tend to score lower than adults. This can be accommodated in any study simply by separating subadults from adults whenever possible. Most older museum specimens do not have the kind of information on their labels allowing such allocation, and although it is possible to age specimens approximately by means of plumage characters, it is not permissible to do this if it is plumage characters themselves that are under study. Hence, the extant museum series have to be used as is.

To understand what this means to hybrid index scores one has only to consider how Mediterranean sparrows have been collected in the past. All collections have more males than females preserved, clearly in excess of

the probable tertiary sex-ratio. This is so undoubtedly because it has been known for a hundred years and more that males show the variable phenotypes, not females. Field collectors have frequently been told to and often do collect only males since time and funds are limited, and only males show the important characters. Hence, that set of male phenotypes which are of low-contrast (and which may well appear to be female at even short distances), especially in fall and winter, tend to be poorly represented in field samples. Gunners try for the conspicuous males, and preparators select out the "taxonomically useful" males from random samples secured by nets or other means.

This results in old museum samples scoring

TABLE 2. Hybrid index scores for male Mediterranean sparrows: Italian peninsular and adjacent populations.

Locality and N	Hybrid index		% of maximum	Value of Meise
	Range	Mean		
*Karlovac (Yugoslavia), 8	0-3	0.5	3	
Trieste, 8	0-7	3.0	18	0
*Udine, 31	3-9	6.2	38	38.5
Bordighera, 16	0-6	3.0	18	35
Cuneo, 26	3-8	6.1	36	37.5
Aosta, 5	3-8	6.4	38	
Sondrio, 4	6-7	6.2	36	
Bolzano, 5	6-8	7.2	42	
Trento, 14	6-9	6.4	38	
*Bergamo, 25	3-10	7.0	41	
*Novara, 26	4-9	7.2	42	44
*Mantova, 25	6-10	7.3	43	44
*Parma, 61	6-10	7.7	45	44
*Comacchio, 62	4-11	7.7	45	
Firenze, 6	6-9	7.5	44	54
*Pisa, 9	6-11	8.0	47	65
*Elba, 11	6-9	7.6	45	
Corsica, 55	0-11	7.2	42	48
*Cantalupo Sabino, 28	7-11	9.1	53	65
Napoli, 9	8-10	9.2	54	
Foggia, 5	7-10	8.2	48	59
*Bari, 28	8-12	10.3	61	
*La Sila, 23	9-13	10.4	61	80
Reggio Calabria, 12	9-11	10.1	59	88.5
*Catania (Sicily), 27	7-16	11.8	69	81
*Paternò (Sicily), 20	10-16	12.4	73	81
*Randazzo (Sicily) 30	8-15	12.5	74	81
Palermo (Sicily), 29	10-17	13.5	80	81

* Samples taken in 1965-66 for present study.

slightly higher than would a random sample for southern Mediterranean localities. The best example of this occurring in the present study can be seen in the two samples from Sardinia. The one from the south was taken at night with nets and skins prepared according to random selection from the sacks of frozen specimens. The hybrid indexes of these birds are lower than those of birds from the north, and all but eight of the northern sample are specimens currently in European museums, probably subject to the bias in collecting and preserving described above. Probably also the high index values for birds from Palermo (western), Sicily, reflect the same bias. The best, albeit inadequate, way to compensate for this kind of sampling error is to compare extant museum collections only with adult samples taken by other means. If this is done with the present samples, some of the minor discrepancies of index values are minimized.

THE SAMPLES

Hybrid index scores are here listed as ranges and means and as percentages of extreme scores for 59 localities around the Mediterranean Sea (fig. 1 and tables 2, 3, and 4).

General remarks about localities and samples can be conveniently presented geographically.

The Po Valley samples. These five samples (Novara, Bergamo, Mantova, Parma, and Comacchio) from the broad northern valley region of Italy are remarkably uniform phenetically. From no other region in the zone of hybridization is there so little variation in mean score or so little range in scores about the mean at one locality. This region is the one to which taxonomists have referred when speaking of the "stabilized" Italian populations (cf. Mayr 1963:119). Characteristic individual variation in scores is shown for 10 males from Parma in table 5.

The submontane samples. There are six samples (Cuneo, Aosta, Sondrio, Bolzano, Trento, and Udine) included here. Hybrid indexes at these localities are not greatly different from those in the Po Valley. Yet, in each instance where a trustworthy sample has been examined, index values are lower in the submontane localities, which may be taken as evidence of introgression of genes from *P. domesticus*, working down the small valleys from montane zones of contact with Italian birds. The range in values about the mean is also larger than at Po stations, again suggesting genic introgression from House Sparrow populations. Characteristic individual variation in hybrid index scores is shown for Udine in table 5.

The northwestern Italian sample. The birds from Bordighera score low on the index, which reflects the hybrid nature of present populations there. The specimen sample and censuses taken in the field in April 1966 indicate that the old boundary line between House and Italian sparrows at Nice, France (Meise 1936), is no longer accurate. Such a boundary now might well be drawn at Ventimiglia, Italy. The field census there indicated about equal numbers of Italian, House, and hybrid sparrows. A superficial implication of this suggestion is that the boundary line between House and Italian sparrows has shifted in the short period from 1936 to 1966; but, if a shift has in fact occurred, it almost certainly involves a much greater time.

Meise saw but one specimen from the Riviera and relied heavily on the available distributional literature in deciding where the hybrid zone existed in that region. One citation dating to 1856 was of importance in placing the line at Nice (Meise op. cit.:647). Additionally, the specimens here evaluated from Bordighera, now in the museum in Milano, were taken in 1928. Thus, there is doubt, on the basis of adequate series of specimens, that the line

was a reasonable one initially. If it is assumed that a shift in phenotypes has occurred, the time period clearly does not involve 1928–1966, but it may include 1856–1928. It remains only to add that the field census of crown color taken in April 1966 showed hybrids extending at least from Menton, France (where House Sparrows predominate), to Imperia, Italy (where Italian sparrows predominate). It is likely that the zone is 25 miles wide at this point.

The persistent increase in human occupancy of the immediate coast of the Franco-Italian Riviera has favored movement of sparrows along the coast, and it is possible that this mobility is responsible for the width of the hybrid zone there. Because the zone, as defined chiefly by field censuses, has been the subject of extensive documentation in the regional European ornithological literature (citations below, under distributional comments), it is now known to run from the Riviera through the Alps, between 1000 and 1500 m elevation and around 5 to 10 miles in width, in a broad arc to the vicinity of Trieste.

The northeastern Italian sample. The small sample from Trieste matches the score for Bordighera on the west coast, but it is possible that the sample is biased in favor of rufous-headed Italian birds. Certainly today the House Sparrow predominates in Trieste, to judge by field censuses taken in April 1966; and, 30 miles inland to the east at Karlovac, Yugoslavia, a small sample of males is almost exclusively of House Sparrow phenotype. Occupancy of the rocky coast by man is much less dense than on the Franco-Italian Riviera, and sparrow populations are thin. But House Sparrows predominate in Trieste and Italian sparrows predominate at Monfalcone, to the northwest, just off the limestone escarpment. Hence, the zone is probably about 20 miles wide there, and the boundary between the two phenotypes may be drawn perhaps at 10 miles NW Trieste.

Northern Italian sparrows are nearly limited to the political confines of Italy. They climb up valleys running into the Alps, and reach perhaps 1000 m (3000 ft) in most places. Before coming to crests of Alpine passes the birds ordinarily meet gray-headed House Sparrows, and interbreeding with regular production of morphologic intermediates ensues. The phenotypic intermediates, both parental morphs, and backcross representatives are found in a narrow, irregular band in the Alps at around 900 to 1400 m (Wallis 1887; Chigi 1914; Meise 1936; Corti 1954; Schöll 1960; Niethammer and Bauer 1960; Löhrl 1963). Most of the inter-

mediate populations occur on southern Alpine slopes, that is, on the Italian side, but some Swiss and Austrian localities have a few brown-headed and chestnut-headed sparrows (Ris 1957; Niethammer 1958; Wettstein 1959; Schweiger 1959; Löhrl 1963). In one instance such intermediate birds reach 1510 m (4500 ft) in crossing the Paso di Resia (west of the Brenner Pass; Niethammer 1958); and intermediate populations occur at sea level at Ventimiglia and Trieste.

The north-central Italian samples. The localities for north-central Italy include Firenze, Pisa, Isola d'Elba, and Corsica. Index values for the four localities are essentially indistinguishable from those for localities near the Po. The Corsican sample is large, agrees with the value of Meise, and there is no reason to doubt the score simply because nearby Sardinian birds are "pure" Willow Sparrows. Indeed, Cheke (1966), who has done the only modern field work with Corsican sparrows, supports these values almost exactly, and the report of Löhrl (1959) constitutes the only record of occurrence of Willow Sparrow phenotype on Corsica. It is further surprising to find the Corsican birds so strongly resembling those from Elba and the Italian mainland, ties to which would seem to be weak owing to the water gap of nearly 35 miles between Corsica and Elba.

The south-central Italian samples. The localities of Cantalupo Sabino, Napoli, and Foggia are included here. The first, located some 50 miles ENE of Roma, is the only one for which a good sample was secured, but the other two samples are in fair agreement with it. Index values are intermediate between those of the Po Valley and Appennine samples and those found for southern Italy.

Note that for these generally central Italian samples the hybrid index conversion values do not match the values of Meise as closely as do those from northern Italy. This mismatch also is found in southern samples and others from southerly localities and it suggests that the two techniques of assessment are out of phase at the high or *hispaniolensis* end of the scale. The possibility that there has been a shift in phenotypes in central and southern Italy seems a less likely cause of the differences in index values, especially in view of the constancy of index values through time at one locality when judged by one means of scoring (see the scores for chronologically distinct Cretan and Maltese samples in table 3).

The southern Italian samples. Samples from Bari, La Sila, and Reggio Calabria show a great deal of consistency among themselves,

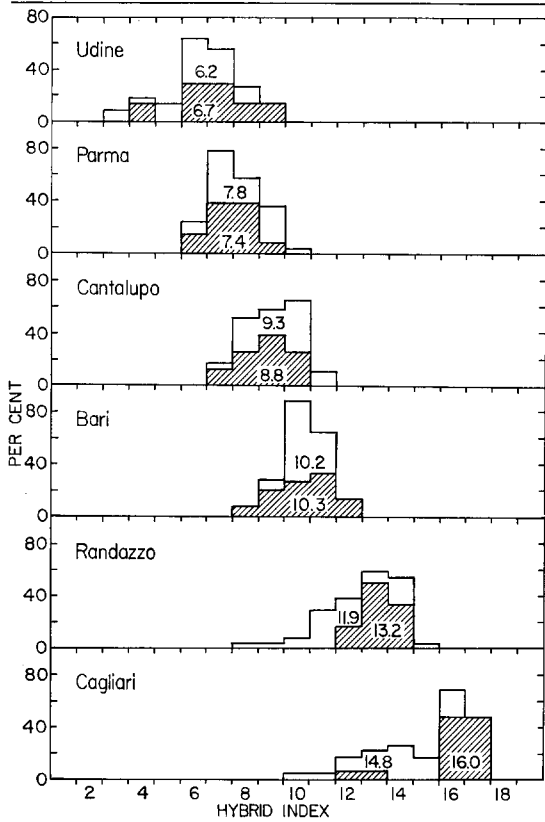


FIGURE 2. Histograms showing per cent frequencies of hybrid index scores for sparrows from six localities on the Italian peninsula, Sicily, and Sardinia. Cross-hatching indicates adults, clear indicates subadults, with each age group totaling 100 per cent.

in terms of both ranges and means. The consistency is of interest, for there is no ecologic unity from the east coast to Reggio Calabria. The index scores are about 17 per cent greater

for these samples than for Po Valley samples. The extent to which subadults and adults differ in index values is shown in figure 2.

The eastern Sicilian samples. Catania is on the eastern base of Mt. Etna, Paternò is on the southern flank, and Randazzo on the northwestern flank. There is a reasonable consistency in index values for the three samples, which average 12 per cent higher than values for Calabria, a short distance across the Strait of Messina. Most specimens from around Etna look much like Willow Sparrows, but the occasional first-year male lacking conspicuous flank streaks still strongly resembles a northern Italian sparrow.

The western Sicilian sample. The seeming distal end of the cline in hybrid index is reached at Palermo. Geographically the locality is the end of the line from northern Italy described in figure 3. Morphologically, I suspect that the sample available in museums is biased and hence has a slightly higher index value than a random sample from the same area would have. The suspicion of bias stems from a poor representation of low-contrast, first-year birds in the museums; in fact, there are many fewer than can be found in the Kansas samples from Sardinia, Malta, or eastern Sicily, which were obtained and prepared in strictly random fashion. Most of the skins from Palermo have been supplied over the years to museums by one commercial collector, and it is likely that he has been more interested in supplying handsome specimens of reasonably high-contrast plumage than in providing a nonbiased sample of the population.

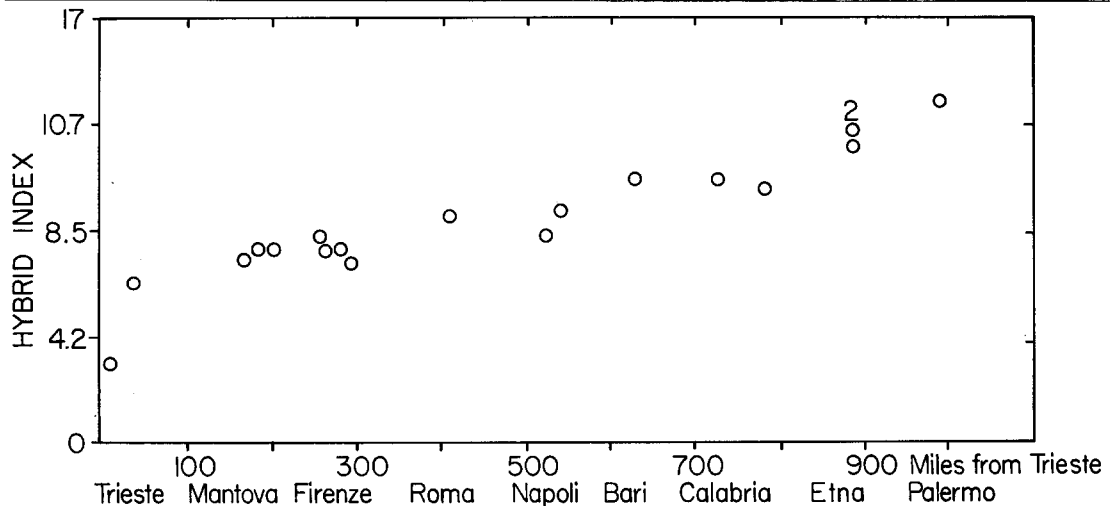


FIGURE 3. Mean hybrid index scores for sparrows from 19 localities on the Italian peninsula and Sicily; locality names below the abscissa give approximate geographic placement of the points in the scatter diagram.

TABLE 3. Hybrid index scores for male Mediterranean sparrows: insular populations.

Locality and N	Hybrid index		% of maximum	Value of Meise
	Range	Mean		
Sicily (west), 29	10-17	13.5	79	81
*Sicily (east), 77	8-16	12.1	71	81
Malta (1854-75), 13	10-15	12.1	71	80
*Malta (1965), 40	10-16	12.9	76	
Crete (1925), 48	3-12	7.3	43	50
Crete (1942), 16	6-9	7.1	42	
Crete (1960), 10	6-10	7.4	44	
*Sardinia (south), 58	10-17	14.9	88	99
Sardinia (north), 42	12-17	15.1	89	
Corsica, 55	0-11	7.2	42	48
Balearic Islands, 44	0-3	0.3	2	0
Canary Islands, 32	13-17	15.5	91	

* Samples taken in 1965 for present study.

The Maltese sample. Forty of the specimens were taken in December 1965 and provide an unusual opportunity to compare present color and pattern with those of birds some hundred years old. Thirteen specimens are available from the last century, and suggest that there has been no significant shift in index value in the past 100 years or so (table 3). The birds look much like the eastern Sicilian specimens, but are not so dark dorsally and have more reddish pigments present; the hybrid index values are as for Sicilian samples.

The Cretan sample. Three independent samples spanning 35 years in time have close agreement in hybrid index (table 3); 10 specimens from 1925 are listed in table 6 to illustrate individual variation in the colors and patterns used in assessing hybridity. Note how, in spite of essentially matching the index values from Udine and Parma (table 5), the scores are achieved by a high representation of pale backs relative to the mainland samples, which for their part have more red in the shoulders and rump as well as in the back.

The Sardinian samples. The northern and southern Sardinian samples show close agreement in hybrid index, and they may be taken as representative of "pure" *P. hispaniolensis* (tables 3, 5, and 6 and fig. 2). It should be emphasized that the southern Sardinian samples were taken randomly and specimens were selected to be prepared in random fashion. In a practical sense this means that many first-year males of low-contrast plumage were prepared, and it is no accident that of all the "pure" Willow Sparrow samples here treated, the southern Sardinian has the lowest index value. The lack of low-contrast, first-year males may be seen in the northern Sardinian and Canary Island samples, in which the lowest scoring individuals ranked at 12 and 13, respectively.

As has been remarked elsewhere, the Sardinian and Corsican samples are wholly out of agreement with each other. There must be very little gene-exchange between the two islands in spite of the short water gap at the Strait of Bonifacio (actually partly bridged by a string of small islands).

Perhaps this is not surprising to find in at least one instance, for a great amount of physiologic distinction accompanies the morphologic distinctions of Willow Sparrows from House Sparrows. First, there is differential distribution of blood groups, even within the Italian population (Bocchi et al. 1960). Second, almost nowhere in montane regions of distributional overlap does the Willow Sparrow occur altitudinally as high as the House Sparrow (see, e.g., Kumerloev 1961:268-269). Similarly, Voous (1960), although he does not mention altitude, notes that the northern boundary to the breeding distribution of the Willow Sparrow is roughly coincident with the 75°F July isotherm, whereas the northern boundary for the House Sparrow in Europe is close to the plot of the 50°F July isotherm. Hence, with the House Sparrow being largely resident and the Willow Sparrow largely migratory, the former is clearly adapted to cooler summer maxima and winter minima than the latter. In the western part of its range, the Willow Sparrow is nearly confined in summer to the Mediterranean vegetation belt, a peculiar kind of vegetation found in a few places in the world where summers are warm and dry and winters are warm and wet. Possibly the abrupt northerly confinement of the Italian sparrow to its peninsula reflects some of the thermoregulatory adaptations of its Willow Sparrow forebears.

The Canary Island sample. This sample is included here (table 3) mainly to provide an index value for a population of Willow Sparrows that have had little, if any, contact with House Sparrows. It is likely, as has been noted above, that low-scoring subadult birds have not been saved in the museum series available today.

The Balearic Islands (Mallorca) sample. This sample is here included (table 3) chiefly to provide an example of index values for a population of House Sparrows that have little contact with Willow Sparrows, and which, nevertheless, live in strictly Mediterranean environmental conditions. The manner in which the individuals vary on scores is shown in table 5.

The Moroccan sample. The distribution of scores for sparrows from Morocco is such that two distinct populations are clearly involved.

TABLE 4. Hybrid index scores for male Mediterranean sparrows: North African populations.

Locality and N	Hybrid index		% of Value of	
	Range	Mean	maxi- mum	Meise
Spain				
Oropera Castellon, 14	0-3	0.6	4	0
Portugal				
Lagos, 7	0-1	0.6	4	0
Morocco, 16	0-7	1.4	8	0
Morocco, 7	10-17	15.3	90	100
Algeria				
Constantine (winter), 8	4-14	10.2	60	62
Constantine (spring), 14	2-17	9.2	54	62
Bône, 8	9-17	13.3	78	85
Hamman Mes- koutine, 11	3-17	11.6	68	50
Laghouat, 8	0-17	14.0	82	30
Menaad, 4	8-17	14.2	83	
Biskra (spring), 16	1-17	8.5	50	59
Biskra (winter), 24	4-16	13.0	76	
Touggourt, 17	6-14	8.6	51	61
Ourgla, 9	0-11	6.4	38	
Tunisia				
Tunis (1886-1909), 12	10-16	13.3	78	96
Tunis (recent), 15	11-17	14.2	83	96
Hamman Lif, 17	4-16	11.5	67	
Souk El Arba, 3	4-10	7.7	45	
Kasserina, 6	4-13	8.0	47	
Feriana, 5	1-11	6.5	38	30
Sfax, 13	6-16	12.1	71	
Gabes, 9	11-17	14.1	83	
Gafsa, 10	5-17	11.8	69	30
Tozeur, 6	11-16	13.1	77	
Philippe Thomas, 5	14-17	15.0	88	
Catahouine, 5	11-16	12.4	73	
Libya				
Tripolitania, 11	9-17	15.0	88	
Cyrenaica, 9	0-9	4.4	26	

Some hybridization, or movement by hybrid individuals into Morocco, is indicated by the distributions, but there is no suggestion of introgression by either parental entity.

The Algerian samples. The most striking thing about the index scores from Algeria is the enormous range shown by most samples. For this reason the birds here have been relegated to the status of "hybrid swarm" by authors in the past. There is no clear definition of "hybrid swarm" by any of these authorities, but they apply the term to populations of variable phenotype, which suggests genetic heterozygosity, causes of which in the present instances may well be owing to factors other than extensive, closed-system backcrossing with no phenotypic selection. At least one other factor could be unilateral introgression of Willow Sparrow genes, a possibility suggested on the following bases. In interior Algeria (and Tunisia) each oasis has its own phenetic kind of sparrow. Since these oases are and have been spatially isolated from one another and from the coast, they must have

TABLE 5. Individual variation in six characters of color and pattern in male Mediterranean sparrows from Mallorca and northern Italy.

Specimen number	Character scores						Hybrid index
	Rump	Bib	Back	Shoulders	Flank	Crown	
<i>Mallorca (Balearic Islands)</i>							
BM 34118466	0	0	0	0	0	0	0
51132971	0	0	0	0	0	0	0
51132969	0	0	0	0	0	0	0
415305226	0	0	0	0	0	0	0
51132970	0	0	0	0	0	0	0
415305228	0	0	0	0	0	0	0
1483119	0	0	0	0	0	0	0
415305225	0	1	0	0	0	0	1
415305224	0	0	0	1	0	0	1
071220391	0	1	0	0	0	0	1
Totals	0	2	0	1	0	0	3
<i>Udine</i>							
KU 53542	0	1	0	0	0	3	4
53516	0	0	0	0	0	6	6
53517	0	0	0	0	0	6	6
53518	0	0	0	0	0	6	6
53519	0	0	0	0	0	6	6
53532	0	0	0	0	0	6	6
53531	0	1	0	0	0	6	7
53541	0	1	0	0	0	6	7
53526	0	1	0	1	0	6	8
53537	1	1	0	1	0	6	9
Totals	1	5	0	2	0	57	65
<i>Parma</i>							
KU 53808	0	0	0	0	0	6	6
53813	0	1	0	0	0	6	7
53820	0	1	0	0	0	6	7
53821	1	0	0	0	0	6	7
53838	0	1	0	0	0	6	7
53824	0	1	0	1	0	6	8
53841	0	1	0	1	0	6	8
53850	1	0	0	1	0	6	8
53852	1	0	1	0	0	6	8
53845	1	1	0	1	0	6	9
Totals	4	6	1	4	0	60	75

been independently colonized by sparrows in the past. There is no reason to expect that founder populations would have had coincident gene-frequencies, and they probably had different frequencies in each instance. Coming to the important point, the Willow Sparrow is, and has been, migratory throughout North Africa, reaching the desert oases in variable numbers. Evidence of how strongly the local oases can be affected by influx of Willow Sparrows can be seen in table 4. For Biskra, mean index values in winter are much higher than in the breeding season, although the range in spring is perhaps broader than that in winter. The winter and spring values for Constantine, a coastal locality, show no such marked differences. It is likely that some of the overwintering birds occasionally get caught up in the sociality of the oasis sparrows and remain with

TABLE 6. Individual variation in six characters of color and pattern in male Mediterranean sparrows from southern Italy and insular localities.

Specimen number	Character scores						Hybrid index
	Rump	Bib	Back	Shoulders	Flank	Crown	
<i>Bari</i>							
KU 54020	0	1	0	1	0	6	8
54022	0	1	0	1	1	6	9
54021	1	1	0	1	1	6	10
54023	1	1	1	1	0	6	10
54026	1	1	1	1	0	6	10
54014	1	1	1	1	1	6	11
54015	1	1	1	1	1	6	11
54024	1	1	1	1	1	6	11
54027	1	2	1	1	1	6	12
54032	2	1	1	1	1	6	12
Totals	9	11	7	10	7	60	104
<i>Crete</i>							
Bonn 57790	0	0	0	0	0	3	3
57791	0	0	1	0	0	3	4
57797	0	0	1	0	0	6	7
57794	0	1	0	0	0	6	7
57792	0	1	0	0	0	6	7
57795	0	2	0	0	0	6	8
57789	0	1	1	1	0	6	9
57793	0	1	1	0	0	6	8
57788	0	1	1	0	0	6	8
57796	0	1	1	1	0	6	9
Totals	0	8	6	2	0	54	70
<i>Malta</i>							
KU 51075	1	1	1	1	1	6	11
54178	0	1	1	1	2	6	11
54179	1	1	1	1	1	6	11
54198	0	1	1	1	2	6	11
51074	1	1	1	1	1	6	11
51076	1	1	1	1	1	6	11
54176	0	2	1	1	2	6	12
54187	1	1	2	1	2	6	13
51073	2	1	2	1	2	6	14
54194	2	1	2	2	2	6	15
Totals	9	11	13	11	16	60	120
<i>Sardinia (south)</i>							
KU 51093	1	1	1	2	2	6	13
51091	2	2	2	2	2	6	16
51100	2	2	2	2	2	6	16
54232	2	2	2	2	2	6	16
54241	2	2	2	2	2	6	16
54247	2	2	1	2	3	6	16
51089	2	2	2	2	3	6	17
54227	2	2	2	2	3	6	17
54237	2	2	2	2	3	6	17
54246	2	2	2	2	3	6	17
Totals	19	19	18	20	25	60	161

them to breed. If so, there would be a regular addition of Willow Sparrow genes to oasis gene pools. This might be enough in itself to maintain the conspicuous degrees of phenotypic and presumably genotypic heterogeneity. However, it is likely that selection has operated to reduce certain gene frequencies, and the heterogeneity probably results from the continual introduction of alien genes into a

pool otherwise tending toward a more stable condition. This is a plausible hypothesis in view of the great phenotypic range in the F_1 of the cross House Sparrow \times Willow Sparrow, as shown by Macke (1965; see also table 7). Thus, the broad phenetic range at many of the Algerian and other desert stations could be owing to genetic introgression and not the kind of closed-system backcrossing that the term "hybrid swarm" suggests.

The Tunisian samples. The general picture of hybrid index scores and of phenetic variation seen in Algeria is duplicated in part in Tunisia (table 4). The coastal samples score higher than inland samples and are very close to "pure" Willow Sparrows in certain instances. Inland samples prove exceedingly individualistic, and the hypothesis concerning introgression in oasis populations presented just above would seem to apply equally for Tunisian samples.

The Libyan samples. Birds from Tripolitania are not easily distinguished from Willow Sparrows, and there is no phenetic heterogeneity in this sample. The small sample from Cyrenaica, although clearly allied with the House Sparrow, shows evidence of gene exchange with Willow Sparrows.

PROVISIONAL CONCLUSIONS ON HYBRIDIZATION

It is clearly possible to describe these many samples of sparrows from around the Mediterranean Sea without using the terms "hybrid" or "hybridization." In fact, use of the terms here has been deliberately kept to a minimum, because their presence dilutes stress placed on infraspecific character variation. Yet historically the sparrows of Italy and adjacent regions have been considered to be "hybrids," and indeed it is certain that they have come about as a result of extensive gene flow between phenetically dissimilar sets of populations.

If it is possible to use the terminal part of the last sentence as a definition of hybridization, then sparrows of the Mediterranean basin can have many hybrid populations referred to them. In any event, this is the view adopted here (and essentially by Bigelow 1965) and on which the following summary statement is based.

"Italian sparrows" are of hybrid origin; the parental stocks are the House Sparrow and the Willow Sparrow. Because there is little gene-exchange between Italian, insular, and North African populations, each population heretofore called "Italian sparrow" is highly

TABLE 7. Individual variation in six characters of color and pattern in F₁ males of House Sparrow × Willow Sparrow.

Til Mücke Specimen number	Character scores						Hybrid index
	Rump	Bib	Back	Shoulders	Flank	Crown	
981	0	0	0	1	0	3	4
673	0	0	0	1	0	6	7
578	2	1	0	1	2	6	12

likely to have had an independent hybrid origin with limited genetic contact since then. These populations may certainly be closely related, especially phenetically, but they do not necessarily share common ancestors in the way that their phenotypes superficially suggest.

The general view of hybridization provided 30 years ago (Meise 1936) is supported by new series of specimens and by older series not used by Meise totaling 1376 skins of males.

In Italy the gradient from House Sparrow-like birds in the north to Willow Sparrow-like birds in the south is strictly clinal. The different morphological kinds, although originating through hybridization, are maintained today probably by differential selection. An alternative hypothesis, to the effect that introgression of genes of House Sparrows from the north and Willow Sparrows from the south is responsible for the cline, is not supported by considerations of geographic isolation or of experimentally-produced hybrids. First, there is the conspicuous, tertiary hybrid contact in the Alps between House Sparrows and Italian sparrows. It is highly restricted in extent, and can only mean that the hybrids are selected out on either side of the hybrid zone. Second, to the south the sea provides extrinsic isolation for peninsular and insular populations; indeed, all along the peninsula the evidence of geography suggests that the Italian birds are strongly isolated from both parental stocks. Third, Mücke's F₁ hybrids show a broad range in phenotypes, scoring 4, 7, and 12 on the system used here (table 7). This is to say that one looks like a northern hybrid from Bordighera or Trieste, the second looks like a Po Valley bird, and the third like a Sicilian. From this great range in phenotypes in the first generation an even greater range would be obtainable in the second generation and additional backcross generations. If strong modal phenotypic tendencies are apparent in extensively backcrossed generations, as they are in Italian samples, almost certainly this reflects the action of selection. Weak modes,

such as those recorded here for North African oasis populations, may well represent results of additional phenomena, as discussed above.

In Morocco and Libya, House and Willow Sparrows do not often cross. Interior Algerian and Tunisian populations probably show their distinctive phenotypes as a result of differing founder gene-frequencies, plus persistent low-grade immigration of Willow Sparrows within a matrix of weak modal selection for color and pattern.

There is no persuasive evidence that there have been significant phenotypic shifts in the past 100 years, except perhaps on the Franco-Italian Riviera, where previous assessments of phenotypes have been suboptimal.

One practical matter remains for comment. The hybrid birds have been badly treated by systematists in the past (Arrigoni 1929; Peterson et al. 1954; Dementiev and Gladkov 1954; Vaurie 1959; Moltoni 1962), and a stable nomenclature would be a useful thing. Since all the hybrid populations have resulted from events long since gone, and since today most of them (excepting perhaps North African oases, which could use additional study) are in poor genetic contact with the parental species, they might profitably be referred to species status. They are also in poor genetic contact with one another, but their easily recognized phenetic intermediacy is a strong argument for referring them to a single species. One other alternative is to place them, as at present, in one of the parental species; another is not to name them at all. Neither would be so useful as using full species status. The available name is *Passer italiae* (Vieillot 1817).

SUMMARY

Sparrows of the Mediterranean basin are referred to three nominal entities, the House Sparrow, the Willow Sparrow, and the Italian Sparrow. There has been little phenetic change in any population sample since Meise's study (1936), and no change in certain insular populations for longer periods of time. This, in view of the fact that the Italian peninsula populations show clinal hybrid-character variation, suggests that these populations are phenetically stable under present environmental conditions.

Considerations of isolation and associated reduction of gene exchange show that the occurrence of large-scale hybridization is now a thing of the past, and suggest that the Italian sparrows behave essentially as species. An available name for these populations is *Passer italiae* (V.), which could also serve nomen-

claturally for all populations that show a clear hybrid phenotype (Crete, Malta, Corsica, North African oases, etc.).

ACKNOWLEDGMENTS

In Italy I worked with a home base at the Università di Parma, Parma, and many courtesies by officials there made the work go smoothly. In other ways also I received much help, and must thank Dott. E. Callegari, Dott. G. C. Carrada, Prof. F. Caterini, Prof. C. Conci, Dr. C. De Lucca, Dott. E. A. Di Carlo, Prof. P. Dohrn, Prof. G. Fornaciari, Dott. S. Frugis, Dott. M. Guerra, Signora N. Guerra, Prof. G. Magni, Prof. A. Micallef, Prof. E. Moltoni, Sig. C. Morandini, Sig. A. Pasquali, Sig. R. Pirino, Sig. A. Priolo, Prof. G. Reverberi, Prof. S. Ruffo, Prof. B. Schreiber, Prof. R. E. Scossiroli, Prof. R. Stefani, Prof. B. Terio, Dott. A. Tornielli, Prof. A. Trischitta, Sig. E. Turano, and Prof. A. Valle for their considerable help. I must especially single out Prof. Danilo Mainardi, who was practically indispensable to my work.

In England I used the facilities of the Edward Grey Institute and the University of Oxford. These were thorough and complete, as were the help and counsel of Dr. D. Lack, Mr. R. Moreau, and Dr. C. Perrins.

Specimens of sparrows were examined in the following museums through the courtesies of their respective curators: Museo Civico di Storia Naturale di Milano, Dott. Edgardo Moltoni; Museum National d'Histoire Naturelle, Paris, Dr. Jean Dorst; British Museum (Natural History), London, Dr. Ian Galbreath; Museum Alexander, Koenig, Bonn, Dr. Gunther Niethammer; Naturmuseum Senckenberg, Frankfurt/M., Dr. Joachim Steinbacher; Zoologisches Museum, Berlin, Dr. Erwin Stresemann.

Field and museum studies in Europe in 1965-1966 were supported by a grant of funds from the NSF (GB 4006).

LITERATURE CITED

- ANDERSON, E. 1936. Hybridization in American tradescantias. *Ann. Missouri Bot. Gardens* 23: 511-525.
- ARRIGONI, E. 1929. *Ornitologia Italiana*. Hoepli, Milano.
- BIGELOW, R. S. 1965. Hybrid zones and reproductive isolation. *Evolution* 19:449-458.
- BOCCHI, G., D. MAINARDI, AND C. ORLANDO. 1960. Gruppi sanguigni e ibridazione interspecifica in pesci e ucelli. *Rend. Ist. Lombardo Accad. Sci. Lett.* 94:63-74.
- BREA, B. 1946-56. Gli scavi nella caverna delle Arene Candide. I. Gli strati con ceramichi. *Ist. di Studi Ligure, Bordighera*.
- BREHM, C. L. 1842. Einige Bemerkungen über Sperlinge und über die Zeichnung verwandter Vogelarten. *Isis von Oken*, p. 884-902.
- CHEKE, A. S. 1966. Sparrows in Corsica and Sardinia. *Ibis* 108:630-631.
- CHIGI, F. 1904. *Passer hispaniolensis* (Tem.), *Passer italiae* (Vieill.), *Passer domesticus* (L.). *Boll. Soc. Zool. Ital.* 1904:127-146.
- CHIGI, F. 1914. Il *Passer domesticus* (Lin) le sue forme e i suoi rapporti con le specie congeneri. *Boll. Soc. Zool. Ital.* 23:1-47.
- CORTI, W. R. 1954. Beobachtungen auf der Fahrt durch die Schweiz, Hochsavoiën, Isere- und Rhone-Tal bis Arles. *Anz. Ornithol. Ges. Bayern* 4:120-132.
- DEMENTIEV, G. P., AND N. A. GLADKOV. 1954. *Ptitsy Sovetskogo Sojuza*. Vol. 5. Moscow.
- KUMERLOEVE, H. 1961. Zur Kenntnis der Avifauna Kleinasiens. *Bonner Zool. Beitr.* 12:1-318.
- LÖHRL, H. 1959. Beitrag zur Avifauna Korsikas. *J. Ornithol.* 100:79-83.
- LÖHRL, H. 1963. Zur Höhenverbreitung einiger Vögel der Alpen. *J. Ornithol.* 104:62-68.
- MACKE, T. 1965. Gelungene Kreuzung von *Passer domesticus* und *hispaniolensis*. *J. Ornithol.* 106: 461-462.
- MAYR, E. 1963. *Animal species and evolution*. Harvard Univ. Press, Cambridge.
- MEISE, W. 1936. Zur Systematik und Verbreitungsgeschichte der Haus- und Weidensperlinge, *Passer domesticus* (L.) und *hispaniolensis* (T.). *J. Ornithol.* 84:631-672.
- MOLTONI, E. 1962. Saggio sull'avifauna del Lago Trasimeno (Umbria). *Riv. Ital. Ornithol.* 32: 153-234.
- NERO, R. W. 1951. Pattern and rate of cranial ossification in the House Sparrow. *Wilson Bull.* 63:84-88.
- NIETHAMMER, G. 1958. Das Mischgebiet zwischen *Passer d. domesticus* und *Passer d. italiae* in Süd-Tirol. *J. Ornithol.* 99:431-437.
- NIETHAMMER, G., AND K. BAUER. 1960. Das Mischgebiet zwischen *Passer d. domesticus* und *Passer d. italiae* im Tessin. *Ornithol. Beob.* 57:241-242.
- PETERSON, R. T., G. MOUNTFORT, AND P. A. D. HOLLAND. 1954. *A field guide to the birds of Britain and Europe*. Collins, London.
- SCHÖLL, R. W. 1960. Die Sperlingsbesiedlung des Pustertales/Südtirol und seiner nördlichen Seitentäler. *Anz. Ornithol. Ges. Bayern* 5:591-596.
- SCHWEIGER, H. 1959. Über das Vorkommen des Rotkopfsperlings (*Passer domesticus italiae* Vieill.) Südkärnten. *J. Ornithol.* 100:350-351.
- SELANDER, R. K. 1964. Speciation in wrens of the genus *Campylorhynchus*. *Univ. California Publ. Zoöl.* 74:1-305.
- SELANDER, R. K., AND R. F. JOHNSTON. 1967. Evolution in the House Sparrow. I. Intrapopulation variation in North America. *Condor* 69:217-258.
- SIBLEY, C. G. 1954. Hybridization in the red-eyed towhees of Mexico. *Evolution* 8:252-290.
- RIS, H. 1957. Zum Vorkommen des Haussperlings in Kanton Wallis. *Ornithol. Beob.* 54:195-197.
- VAURIE, C. 1959. *The birds of the Palearctic fauna*. Witherby, London.
- VOOUS, K. H. 1960. *Atlas of European birds*. Thos. Nelson, N. Y.
- WALLIS, H. M. 1887. Notes upon the northern limit of the Italian sparrow *P. italiae*. *Ibis* 1887:454-455.
- WETTSTEIN, O. 1959. Ergänzende Nachrichten über das südalpine Mischgebiet der Haussperlinge. *J. Ornithol.* 100:103-104.