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COLOR VARIATION AND NATURAL SELECTION IN ITALIAN SPARROWS

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The hybrid house sparrows of the Italian peninsula and adjacent islands (*Passer domesticus italiae* or *P. italiae*, among other names) show a considerable range in feather color and size phenotypes (MEISE, 1936; JOHNSTON, 1969a, 1969b). The variation in male display plumage throughout Italy covers most possibilities obtainable in crosses between the ancestral sparrows, *P. domesticus* and *P. hispaniolensis* (MACKIE, 1965; JOHNSTON, 1969a). However, in their proportional representation in population samples from northern Italy south to Sicily the feather phenotypes are clinally-ordered. This regularity in geographic variation of male plumage characters is not inconsistent with the past hybrid origin of the Italian sparrows, because the most *domesticus*-like phenotypes are found adjacent to the northern European distributional stronghold of *P. domesticus*, and vice-versa for the most *hispaniolensis*-like phenotypes. Nevertheless, interpopulation exchanges between Italian birds and either *domesticus* or *hispaniolensis* are not entirely free, and the possibility that the hybrid phenotypic gradient is maintained only by genic introgression is subject to question (JOHNSTON, 1969a, 1969b).

Alternatives to the idea that introgression (or « migration » of genes, or « gene flow ») is responsible for maintenance of the phenotypic gradients include effects of selection and mutation. Since it is most unlikely that differential mutation could be involved, selection is the only agency reasonably to be invoked (see EHRLICH and RAVEN, 1969). Such a conclusion, straightforward though it may be in most instances, is to some extent counterintuitive when it concerns a complex set of peninsular populations of hybrid origin. First, it requires a continuously-varying selective regime for a wide range of genically heterozygous phenotypes, and, second, it requires that the latitudinal selective gradient be expressed only in the

narrow corridor of Italy, and not on the adjacent mainland coastline of Yugoslavia, paralleling Italy to the east. To pursue this problem of alternatives this paper thus presents (1) a description of spectrophotometric analyses of pileum and flank feathers of both sexes of birds, (2) results of linear regression analyses of CIE brightness (Y) values of pileum and flank feathers against environmental variables of annual precipitation and isophane, and (3) discussion aimed at assessment of the adaptedness of hybrid phenotypes.

MATERIALS AND METHODS

Specimens used in this study are listed in table 1. The samples on which spectrophotometric scans were made are standard, round study skins taken in the autumn and winter of 1965, various size characteristics of which have already been reported (JOHNSTON, 1969b). All specimens are in the collections of the Museum of Natural History at The University of Kansas.

Spectrophotometric analysis. Pileum and flank feathers were scanned for relative reflectances at wavelengths from 400 m μ to 650 m μ , using a Bausch and Lomb Spectronic 505 spectrophotometer with reflectance bulb and beam condensers mounted in the transmittance sample chamber. Reflectance data were transformed to brightness Y via standard CIE techniques (see SELANDER and JOHNSTON, 1967). Statistics of central tendency were obtained from the data, providing mean brightness scores for each locality sample. Samples were assessed for statistical heterogeneity, or geographic variation, by means of Power's modification of Gabriel's sums of squares simultaneous test procedure (SS-STP), which indicates statistically homogeneous subsets on the ranked means (GABRIEL and SOKAL, 1969; POWER, 1969). Locality means were regressed on the independent variables of mean total precipitation and of isophane at each locality (cf. JOHNSTON, 1969b).

RESULTS

Female pileum. Brightness of the pileum shows highly significant geographic variation (table 2), such that samples from northern Italy tend to be darker than samples from the extreme Italian south and certain offshore islands (Sicily, Malta and Sardinia). The six palest readings are on samples from those islands and in the Calabrian highlands (Camigliatello Silano) of southern Italy. The ordering of means in table 2 does not strictly order the localities in a north-south gradient, but the overall geographic trend is clear. The extreme pallor of nape feathers in the Maltese females is such that if we were to speak of samples of similar relative pallor we could not legitimately include any from central or northern Italy.

Regression of pileum brightness on mean annual precipitation (fig. 1) shows considerable scatter, but the slope of the line is significantly different

TABLE 1 - Localities and Sample Sizes Represented in the Analysis.

Locality	Number of Specimens	
	Males	Females
Udine, Italy	11	10
Bergamo, Italy	12	10
Novara, Italy	16	12
Mantova, Italy	18	7
Comacchio, Italy	11	10
Parma, Italy	20	10
Pisa, Italy	9	10
Isola d'Elba, Italy	8	10
Cantalupo Sabino, Italy	17	10
Bari, Italy	16	10
Camigliatello Silano, Italy	19	20
Paternò, Sicilia	10	10
Randazzo, Sicilia	16	10
Catania, Sicilia	12	—
Cagliari, Sardegna	20	10
Olmedo, Sardegna	5	8
Gharghur, Malta	17	10
Totals	237	162

TABLE 2 - Variation in Brightness (Y) of Pileum in Female Mediterranean Sparrows (¹).

Locality	Mean Y	Inclusive Sets (¹)
Gharghur, Malta	111.30	
Randazzo, Sicilia	97.10	
Cagliari, Sardegna	96.80	
Camigliatello, Italy	92.70	
Paternò, Sicilia	91.70	
Olmedo, Sardegna	91.66	
Mantova, Italy	90.71	
Bari, Italy	90.40	
Isola d'Elba, Italy	89.80	
Parma, Italy	88.90	
Cantalupo Sabino, Italy	88.50	
Pisa, Italy	81.20	
Udine, Italy	80.70	
Bergamo, Italy	80.80	
Novara, Italy	79.58	
Comacchio, Italy	77.80	

(¹) Includes only samples from localities at which rufous-headed «italiae» or «hispaniolensis» males occur; specimens at The University of Kansas.

(²) SS-STP test; vertical lines connect statistically homogeneous groups of localities. Analysis of variance for overall heterogeneity gives an *F*-ratio of *F* = 9.029 (*P* = 0.00001).

from zero ($P = 0.014$), and about 36% of the variation in brightness can be attributed to variation in total annual precipitation. A significant negative regression of brightness on isophane ($P = 0.027$) was also obtained. The association is one of increasing pallor of nape feathers with decreasing precipitation and isophane.

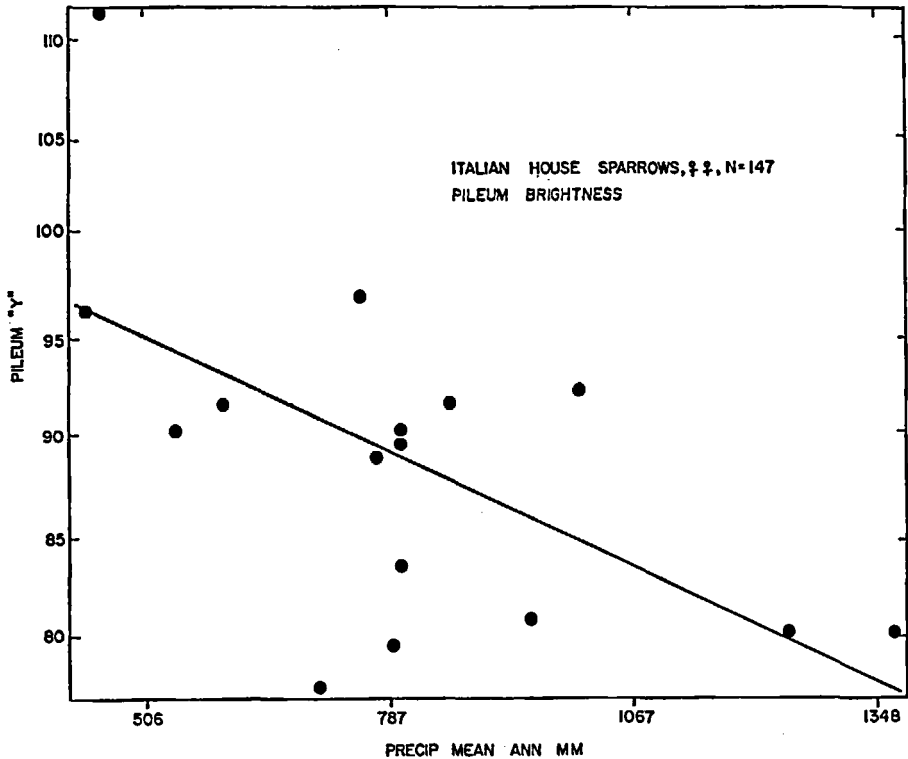


Fig. 1 — Bivariate plot of locality mean values of brightness of pileum feather color (Y) on mean annual precipitation, for female Italian sparrows. Equation for regression: $Y = 105.1 - 0.02X$ ($P = 0.0148$).

Female flank. Relative brightness of flank feather color shows no meaningful geographic variation (anova F -ratio = 1.67 with 15 and 146 degrees of freedom; $P = 0.062ns$). Heterogeneity in flank brightness exists, but intralocality variances are large enough that no statistically significant subsets exist. There is, of course, no meaningful regression relationship with any environmental variable.

TABLE 3 - Variation in Brightness (Y) of Pileum in Male Mediterranean Sparrows.

Locality	Mean Y	Inclusive Sets (¹)
Gharghur, Malta	96.71	
Camigliatello Silano, Italy	92.82	
Catania, Sicilia	88.42	
Cagliari, Sardegna	86.60	
Paternò, Sicilia	85.80	
Udine, Italy	85.27	
Olmedo, Sardegna	85.20	
Isola d'Elba	84.88	
Pisa, Italy	83.83	
Mantova, Italy	80.88	
Cantalupo Sabino, Italy	80.82	
Bari, Italy	80.25	
Randazzo, Sicilia	79.10	
Novara, Italy	79.00	
Bergamo, Italy	77.83	
Parma, Italy	73.70	
Comacchio, Italy	70.64	

(¹) SS-STP test; vertical lines connect statistically homogeneous subsets of localities. Analysis of variance for overall heterogeneity gives an F -ratio of $F = 5.185$ ($P = 0.00001$).

TABLE 4 - Variation in Brightness (Y) of Flank in Male Mediterranean Sparrows.

Locality	Mean Y	Inclusive Sets (¹)
Mantova, Italy	262.94	
Cantalupo Sabino, Italy	238.82	
Comacchio, Italy	238.64	
Gharghur, Malta	237.71	
Bari, Italy	227.69	
Novara, Italy	226.69	
Isola d'Elba, Italy	220.63	
Parma, Italy	219.55	
Bergamo, Italy	217.17	
Catania, Sicilia	216.67	
Udine, Italy	214.18	
Camigliatello Silano, Italy	211.95	
Pisa, Italy	205.00	
Randazzo, Sicilia	202.63	
Paternò, Sicilia	201.20	
Cagliari, Sardegna	188.80	
Olmedo, Sardegna	182.60	

(¹) SS-STP test; vertical lines connect statistically homogeneous subsets of localities. Analysis of variance for overall heterogeneity gives an F -ratio of $F = 3.946$ ($P = 0.00002$).

It is unexpected to find no meaningful variation in flank color of females; almost certainly the relatively great amount of variation within locality samples is responsible for this peculiarity. And, it is likely that the large variances have been induced by the spectrophotometric scanning technique. Two sources of gross error are present. First, the preparation of skin specimens was conventional, with standard, stuffed, flat-backed, round-chested specimens resulting. These specimens are esthetically pleasing to the human eye but they are inadequate in allowing flank feathers to be laid flat for the spectrophotometric eye. Second, position of scan on the flank is critical, such that relatively trivial variation in placing specimens in the scanning port greatly increases variation between specimens in reflectance readings. The operational difficulty in «reading» the precisely analogous spot on each specimen is increased by using round skins. Parenthetically, work in our laboratory now is confined to scans of flat skins, and we obtain greatly reduced variance statistics in this manner.

Male pileum. Relative brightness of male pileum shows significant geographic variation, as is evident in table 3. There is a strong tendency for samples from southern Italy and offshore islands to be paler than samples from the north, a direct parallel to the pattern found in females. In fact, the palest samples in each sex are from the same localities, as are the darkest.

There are no significant regression relationships between male pileum brightness and precipitation or isophane.

Male flank. Relative brightness of male flank color shows significant geographic variation, the outlines of which are presented in table 4. For this character the trend is reversed from those previously discussed, and the palest readings are on samples from northern Italy. Reversal of the trend in brightness of male flanks is a straightforward expression of the degree of flank-streaking, a character of *P. hispaniolensis* almost wholly lacking in *P. domesticus*. Thus, given the hybrid nature of most populations sampled, the clinal trend in flank brightness is only expected, with the two Sardinian samples («pure» *hispaniolensis*) making the darkest scores.

There is no meaningful regression of male flank brightness on precipitation or isophane. The trend in darkness owing to flank streaking is really quite clear (MEISE, 1936; JOHNSTON, 1969a), but an inverse cline in degree of background brown color of flanks obscures any regression effect. This situation is especially evident in samples from Udine and Pisa (northern and central Italy), which have considerable melanin deposition

in flank feathers, and virtually no flank streaking; these two samples are not distinguishable from the Sicilian samples on the basis of raw brightness scores (although they look nothing alike to the human eye).

DISCUSSION

Independent support for the hypothesis of selective maintenance of color gradients. Ordered geographic variation of character variables inevitably suggests ideas of selection-maintained differential character states, and this is especially true if, as in the present instance, a reasonable regression relationship can be detected between some independent environmental variables and the character states. The argument is almost always an appeal to reason, because we know little about the interactions between the putative genetic basis of the character states and the environment. However, there are two logical lines that can be pursued in the present case, each making some contribution supporting the probability that selective maintenance of color phenotypes exists in the Italian house sparrows and their insular allies.

First, we should note that the kind of color variation found in Italian sparrows is found also in other populations of *Passer domesticus*. Perhaps the most dramatic instance is for North American populations of house sparrows, introduced to the continent slightly over 120 years ago. Most of the birds brought to the United States came from England (BARROWS, 1889), but in the course of their spread, ultimately to occupy most of the continent, color phenotypes of differential brightness have developed such that few North American samples now precisely resemble the English birds. These color phenotypes do bear relationship to environmental gradients associated with longitude and latitude, and these relationships are most pronounced with temperature, humidity, and precipitation. The data on brightness of female breast feather color are here presented in the same format used above for Italian samples (table 5), and are regressed against number of days of precipitation annually at each locality sampled (fig. 2). The relationships thus laid bare show that there is highly significant geographic variation in breast feather brightness, with relative darkness occurring at northerly and inland stations with high precipitation schedules and relative pallor occurring at southerly and desert localities with low precipitation schedules.

The parallel between pileum brightness in Italian sparrow females and breast brightness in North American females is striking and shows

TABLE 5 - *Variation in Brightness (Y) of Breast of Female House Sparrows From North America* ⁽¹⁾.

Locality	Mean Y	Inclusive Sets ⁽²⁾
Phoenix, Arizona	262.80	
Death Valley, California	261.70	
Del Rio, Texas	258.00	
Progreso, Texas	255.80	
Bastrop, Texas	249.80	
Houston, Texas	247.20	
Oakland, California	246.80	
Sacramento, California	246.20	
Mexico City, Mexico	244.30	
Gainesville, Florida	243.60	
Vancouver, British Columbia	241.50	
Montréal, Quebec	241.50	
Las Cruces, New Mexico	238.60	
Oaxaca de Juárez, Oaxaca	234.70	
Los Angeles, California	233.40	
Edmonton, Alberta	231.60	
Ann Arbor, Michigan	231.30	
Detroit, Michigan (1963)	226.60	
Salt Lake City, Utah	225.30	
Detroit, Michigan (1965)	222.20	
Camilla, Georgia	216.80	
Birmingham, Alabama	215.50	
Pittsburgh, Pennsylvania	207.70	
Middlebury, Vermont	206.60	

⁽¹⁾ Data from SELANDER and JOHNSTON, unpublished.

⁽²⁾ SS-STP test; vertical lines connect statistically homogeneous subsets of localities. Analysis of variance for overall heterogeneity gives an F -ratio of $F = 10.358$ ($P = 0.0042$).

that we could reasonably have expected one of these relationships given that we knew about the form of the other. The North American regression of brightness on precipitation is especially instructive, because we know that it has come about within considerably less than the past 120 years, which would be less than 120 generations of sparrows. And, there is no possibility of genic introgression being implicated in the ordering of these phenotypes. Two ordered sets of color samples, one in Italy and the other in North America, are unlikely to have come about by chance, and this provides some support for the idea that the color gradients are one consequence of differential selection in accord with environmental variation.

The other logical line stems from considerations of population genetics. Referring only to the Italian birds, note that they normally exist at rea-

sonably high population densities and probably maintain relatively large effective population sizes. Rates of exchange of individuals between populations are doubtless modest (to judge from studies of dispersal in England; SUMMERS-SMITH, 1968), and in any event such exchange would provide relatively small fractional contributions to population gene pools each generation. Under these circumstances, if the Italian birds represent

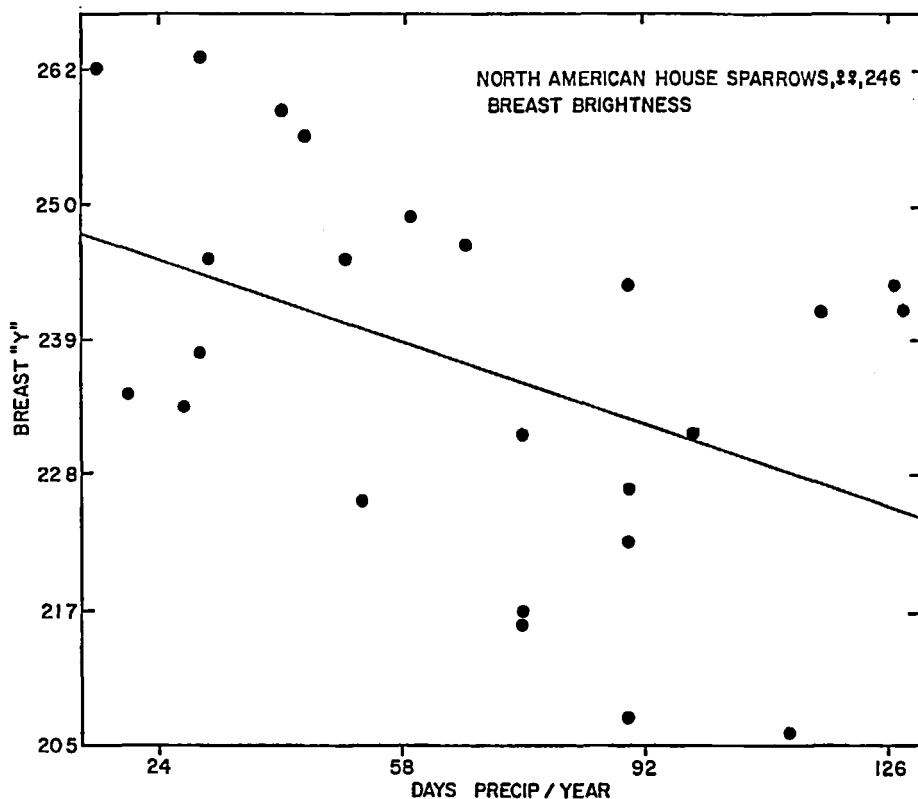


Fig. 2 — Bivariate plot of locality mean values of brightness of breast feather color (Y) on mean number of days of precipitation annually, for female house sparrows from North America. Equation for regression : $Y = 25.1 - 0.20X$ ($P = 0.032$).

the *continuing* consequences of hybridization between a northerly parent and a southerly one, we should expect to find a noticeable break in gene frequencies, and the color phenotypes with which they should be associated, somewhere on the Italian peninsula. This is not evident in the specimen

information available for study (*). We can conclude there is little present evidence of continuing genic introgression in Italian sparrows.

Possible selective agency. Visually-orienting-predators are likely to be the most important of the possible agencies of color selection. The most significant of these predators would be men with guns and bird-hunting hawks and owls. Some of the hawks can be extremely effective at catching sparrows (TINBERGEN, 1946), and it would take only a little differential in catching darker or lighter sparrows to affect proportional representation of color classes in a population. Although this argument relies on a predator taking conspicuous individuals, light ones on a dark background, or vice-versa, once a color class becomes established at a locality, any individual that is odd in color may well receive a disproportionate share of the attention of a bird hawk (MUELLER, 1968).

The classical experimental studies of SUMNER (1935) and DICE (1947) are germane to this line of speculation even though they pertained to predator selection on confined samples of other kinds of vertebrates: conspicuous individuals are more readily taken than less conspicuous individuals. The inferential case, established in part by intuition, would seem to be reasonably robust. It would be feasible to obtain testable predictions from this hypothesis on causes of color gradients in sparrows, and perhaps now it is a responsible thing to do.

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SUMMARY

Aspects of color of the feathers in Italian sparrows, *Passer domesticus italiae* or *P. italiae*, can be quantified by reflectance spectrophotometry. Clinal geographic variation in CIE brightness (Y) values for pileum and flank feathers exists at a highly

(*) However, there is a phenetic break and by inference a genetic break of this very sort between grey headed *P. domesticus* and rufous-headed *P. hispaniolensis* through the Alps in a great semicircle from the Franco-Italian Riviera on the west to Trieste on the east. This zone of conspicuous hybridity should be studied in detail; it is very likely that such study would demonstrate the basic affinities of *italiae* with *hispaniolensis*, rather than with *domesticus* as most taxonomists presently infer.

significant level. There is a strong tendency for population samples from northern Italy to be darker than samples from southern Italy and adjacent Mediterranean islands. Brightness of pileum in females shows significant regression relationships to aspects of environmental brightness associated with precipitation schedules.

There is a parallel regression of brightness values of breast feathers of female house sparrows from North America. This relationship together with those in Italian sparrows suggests that the ordered variation is an adaptive response to environmental selective pressures. The idea that genic introgression from northern European *P. domesticus* and from Mediterranean *P. hispaniolensis* is responsible for the clinal variation in color phenotypes down the Italian peninsula and into Sicily is examined and discarded.

RIASSUNTO

Aspetti del colore delle penne del passero d'Italia, *Passer domesticus italiae* o *P. italiae* possono essere quantizzati mediante spettrofotometria in luce riflessa. Esiste una variazione clinale geografica per i valori di chiarezza delle penne del pileo e dei fianchi altamente significativa. Vi è una forte tendenza, per le popolazioni dell'Italia settentrionale, ad essere più scure di quelle dell'Italia meridionale e delle adiacenti isole mediterranee. La chiarezza del pileo delle femmine mostra significativi rapporti di regressione relativamente ad aspetti di chiarezza ambientale associati ai dati delle precipitazioni. Una parallela regressione nei valori di chiarezza si trova riguardo alle penne del petto nelle femmine nordamericane. Questa relazione e quelle sui passeri italiani suggeriscono l'esistenza di una ordinata variazione come risposta adattativa a pressioni selettive ambientali. L'idea che la variazione clinale nei fenotipi colorati lungo la penisola italiana e in Sicilia dipenda da introgressione genica proveniente dal settentrionale *P. domesticus* e dal mediterraneo *P. hispaniolensis* viene considerata e respinta.

REFERENCES

- BARROWS W. B., 1889 - *The English sparrow* (*Passer domesticus*) in *North America...* U. S. Dept. Agric. Div. Econ. Ornith. Mamm., Bull. 1.
- DICE L. R., 1947 - *Effectiveness of selection by owls of deer mice* (*Peromyscus maniculatus*) *which contrast with their background*. Contr. Lab. Vert. Biol. Univ. Michigan, No. 34.
- EHRlich P. R. and RAVEN P. H., 1969 - *Differentiation of populations*. Science, 165: 1228-1232.
- GABRIEL K. R. and SOKAL R. R., 1969 - *A new statistical approach to geographic variation analysis*. Syst. Zool., 18: 259-278.
- JOHNSTON R. F., 1969a - *Taxonomy of house sparrows and their allies in the Mediterranean basin*. Condor, 71: 129-139.
- JOHNSTON R. F., 1969b - *Character variation and adaptation in European sparrows*. Syst. Zool., 18: 206-231.
- MACKE T., 1965 - *Gelungene Kreuzung von Passer domesticus und hispaniolensis*. J. Ornithol., 106: 461-462.
- MEISE W., 1936 - *Zur Systematik und Verbreitungsgeschichte der Haus- und Weidensperlinge*, *Passer domesticus* (L.) und *hispaniolensis* (T.). J. Ornithol., 84: 631-672.

- MUELLER H. C., 1968 - *Prey selection : oddity or conspicuousness ?* Nature, 217 : 92.
- POWER D. M., 1969 - UNIVAR, a FORTRAN IV program for IBM 7090/94 computer.
Version of July, 1969. Unpublished manuscript.
- SELANDER R. K. and JOHNSTON R. F., 1967 - *Evolution in the house sparrow. I. Intra-population variation in North America.* Condor, 69 : 217-258.
- SUMMERS-SMITH D., 1963 - *The house sparrow.* Collins, London.
- SUMNER F. B., 1935 - *Evidence for the protective value of changeable coloration in fishes.* Amer. Nat., 69 : 245-266.
- TINBERGEN L., 1946 - *Der Sperwer als Roofvijand van Zangvogels.* Ardea, 34 : 1-213.
-