EKOLOGIA POLSKA (Ekol. pol.)	34	1	63–73	1986

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ECOLOGICAL SEGREGATION BETWEEN SYMPATRIC SPANISH SPARROWS (*PASSER HISPANIOLENSIS* TEMM.) AND HOUSE SPARROWS (*PASSER DOMESTICUS* (L.)) DURING WINTER

ABSTRACT: The differences in food composition, habitat utilization, flocking behaviour and morphology of sympatric populations of two sparrow species have been analysed in an agricultural area of W – Spain. There is a clear spatial segregation between both species, the house sparrows remaining closer to human habitations. Associated flocking and feeding strategies are discussed.

KEY WORDS: Cultivated fields, Spanish sparrow, house sparrow, winter diet, sympatric sparrows, feeding ecology.

1. INTRODUCTION

It has been generally admitted that two closely related species sharing identical ecological requirements cannot coexist in a stable community in the same locality. The existence of interspecific isolating mechanisms, like differences in their distribution ranges, habitats or diets, has been demonstrated for many bird species (Lack 1971, MacArthur 1972, Cody 1974, Schoener 1974). The house sparrow and the Spanish sparrow are, phylogenetically, one of the most closely related bird species pairs (Sibley and Ahlquist – in press), showing partially overlapping distribution areas and even hybridizing in certain regions (Meise 1936, Johnston 1969, Summers-Smith and Vernon 1972). In the present paper I study the food composition, habitat utilization and morphology in an area where both species coexist during winter, trying to identify the mechanisms that alleviate interspecific competition.

2. STUDY AREA

The study was conducted in an irrigated farmland comprising round 15000 ha of corn, tobacco, cotton, and various other minor crops, near Coria in Cáceres, Spain (39°58′ N, 6°20′ W). The only forested areas are a few *Eucalyptus* and *Populus* plantations, and willow tree thickets along the river courses. There are two small villages, apart from dispersed farm houses and granaries in a density of about 5 per square km.

3. MATERIAL AND METHODS

112 Spanish sparrows and 103 house sparrows were captured with mist nets at roosting sites between October 1977 and March 1983. Immediately after collection, the stomach contents were removed, washed and dried at 70°C during 48 hours. Food elements were counted, weighed to the nearest 0.1 mg and identified with the aid of a 8 $-40\times$ binocular microscope and comparative collections. A sample of seeds was sown in a greenhouse to help identify some species. Grit was not included in the weight of the total stomach contents.

Trophic diversity was calculated with Shannon-Weaver's information function H'. Two criteria of trophic diversity were considered: H'_b, in relation to the biomass supplied by the different taxa, and H'_n, in relation to the number of individuals taken from each taxonomic group (species in the case of plant food and order in the case of animal food). Pielou's trophic evenness indices ($E = H'/H_{max}$) were also calculated for both number of elements (E_n) and biomass (E_b). In order to analyse the dietary overlap between both species, I used a qualitative index (number of classes eaten by both species/total number of classes identified) and the Morisita's (see Horn 1966) quantitative dietary overlap index:

$$\hat{C}_\lambda = \frac{2\sum_{i=1}^{n} x_i y_i}{\sum_{i=1}^{n} x_i^2 + \sum_{i=1}^{n} y_i^2}$$

where $\hat{C}_\lambda$ = dietary overlap (range 0 – 1, 1 meaning identical food composition); x_i and y_i = frequencies of a given class in the diets of both species compared.

Simultaneously, I recorded the size and species composition of each sparrow flock detected, the activity of the birds (resting or feeding), time of day, type of ground or perch, and estimated the distance from the flock to the nearest farm building. The ground and perch types considered are listed, respectively, in Tables 1 and 2. The relative extents of the different habitats were estimated recording the ground type at each of both sides of a 20 km transect through the study area.

The degree of mixing of both species in communal roosts was determined by mistnetting at random at the main roosting sites.

Additionally, biometrical data were also recorded in a number of individuals.

4. RESULTS

4.1. TROPHIC DIVERSITY AND DIETARY OVERLAP

The winter diets of both species are basically granivorous (Table 1). The high overlap values indicate a high interspecific similarity in their compositions. The seeds of only three species, *Echinochloa crus-galli*, *Portulaca oleracea*, and *Digitaria sanguinalis*, all of them very abundant weed grasses in the study area, make up, respectively in Spanish sparrows and house sparrows, 80% and 82% of the total number of elements, and 75% and 50% of the biomass consumed. Trophic evenness values are therefore relatively low.

Table 1. Winter food composition, and trophic diversity, evenness and overlap of Spanish sparrows and house sparrows

Food elements and parameters compared	Spanish sparrow		House sparrow	
	no. of elements (%)	weight (%)	no. of elements (%)	weight (%)
1	2	3	4	5
Polygonum aviculare L.	0.03	0.06	0.08	0.12
P. persicaria L.	0.46	1.05	0.06	0.09
Chenopodium spp.	2.48	1.43	0.74	0.22
Amaranthus retroflexus L.	1.75	1.14	1.69	0.74
Portulaca oleracea L.	26.34	7.73	34.87	6.26
Cerastium spp.	8.01	1.97	6.60	1.91
Spergula arvensis L.	0.03	0.01	0.23	0.06
Trifolium sp.	0.08	0.04	0.14	0.05
Erodium sp.	0.02	0.07	0.00	0.00
Solanum nigrum L.	0.23	0.30	0.40	0.34
Nicotiana tabacum L.	4.30	0.38	5.13	0.34
Artemisia sp.	0.18	0.11	0.00	0.00
Triticum sp.	0.06	3.08	0.55	20.22
Poa sp.	0.57	0.28	0.11	0.04
Avena sterilis L.	0.00	0.00	0.01	0.15
Phalaris sp.	0.67	0.02	0.29	0.01
Digitaria sanguinalis (L.)	15.95	8.04	8.33	2.85
Echinochloa crus-galli (L.)	37.76	59.02	39.59	41.21
Zea mays L.	0.04	10.56	0.11	20.80
Other Gramineae	0.04	0.11	0.19	2.03
Typha sp.	0.09	0.01	0.00	0.00
Unidentified seeds	0.62	2.50	0.32	1.37
Arachnida	0.009	0.03	0.01	0.007
Dermaptera	0.002	0.05	0.00	0.00
Lepidoptera	0.002	0.08	0.01	0.07
Diptera	0.03	0.15	0.01	0.01
Coleoptera	0.04	0.69	0.02	0.16

1	2	3	4	5
Hymenoptera	0.16	0.54	0.46	0.90
Unidentified arthropods	0.05	0.50	0.03	0.04
Total no. of elements	42661		32362	
Total dry weight (g)		37.80		43.06
Diversity of number H'_n	1.70		1.56	
Diversity of biomass H'_b		1.58		1.69
Evenness E_n	0.51		0.49	
Evenness E_b		0.47		0.53
No. of identified classes	25		22	
Qualitative overlap		0.81		
Quantitative overlap in number $\hat{C}_{\lambda n}$		0.97		
Quantitative overlap in biomass $\hat{C}_{\lambda b}$		0.88		

The major interspecific difference is the higher energetic dependence of house sparrows on cereal food: wheat and corn seeds comprise 41% of total biomass ingested by this species, but only 13% of biomass ingested by Spanish sparrows.

The diversity of number of elements (H'_n) is slightly higher, but the diversity of energy dependence (H'_b) is slightly lower in the Spanish sparrow than in the house sparrow. Nevertheless, differences are very small.

4.2. HABITAT USE

Statistically significant differences in habitat use exist between Spanish sparrows and house sparrows during both feeding ($\chi^2 = 123.3$, $p < 0.001$) and resting ($\chi^2 = 172.6$, $p < 0.001$, Table 2). Spanish sparrows select the corn fields as main feeding

Table 2. Relative extents (per cent of surface) and utilizations by both sparrow species (per cent of number of flocks) of the different ground types

Ground type	Relative extent	Spanish sparrow		House sparrow	
		resting	feeding	resting	feeding
Corn fields	48.2	4.0	61.4	2.9	13.2
Waste land and road sides	17.7	0.0	16.9	2.9	18.9
Pastures	11.6	0.0	7.2	1.4	7.5
Tobacco stubbles	7.3	0.0	4.8	0.0	1.9
Riparian vegetation	4.3	93.3	3.6	11.4	0.0
Cotton fields	3.0	0.0	2.4	0.0	0.9
Cereal stubbles	1.2	0.0	1.2	0.0	0.9
Other crops	3.0	0.0	1.2	0.0	0.9
Eucalyptus plantations	1.2	2.7	0.0	2.9	0.0
Grounds adjacent to farms, granaries or houses	2.5	0.0	1.2	78.5	55.7
Number of flocks		150	166	70	94

Table 3. Use of perch sites (percentage of flocks)

Perch type	Spanish sparrow	House sparrow
Ground	51.9	54.9
Shrubs (< 2 m)	19.6	2.4
Trees (> 2 m)	28.5	13.4
Buildings	0.0	29.3
Number of flocks	316	164

areas, while house sparrows prefer to feed on the grounds adjacent to farm buildings, waste land and road sides. As resting sites Spanish sparrows select the riparian vegetation, while house sparrows usually rest on the roofs of farm houses or on trees nearby.

There are also significant interspecific differences in the utilization of the various perch types considered ($\chi^2 = 164.0$, $p < 0.001$, Table 3). Spanish sparrows are more arboreal than house sparrows, perching most frequently on the willow trees along the river courses and avoiding the buildings.

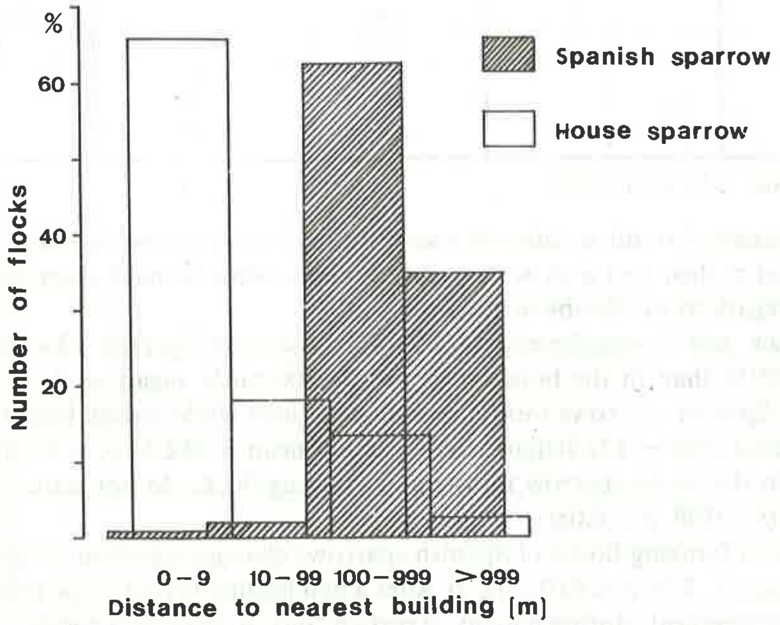

Fig. 1. Distribution of flocks in relation to distance to nearest farm building

There is a clear spatial segregation by distance to farm buildings (Fig. 1). The mean distances between foraging flocks and farms were 64 m for the house sparrow and 599 m for the Spanish sparrow, the difference being highly significant ($t = 20.6$, $p < 0.001$).

4.3. FLOCK SIZE AND COMPOSITION AND DAILY FEEDING PATTERN

Both species are gregarious throughout the whole year in the study area (Alonso 1982). Only occasionally they form mixed flocks (2% of all flocks observed). These were always Spanish sparrow flocks located relatively close to villages of farms, which were joined by a few (1 – 12) house sparrows. In contrast, I never observed a Spanish sparrow in a house sparrow flock.

Table 4. Degree of mixing of Spanish sparrows and house sparrows in communal roosts during the non-reproductive season *

Month	Number of roosts examined	Total of birds	Number of birds captured	Per cent contribution of male house sparrows to total number of males
July	2	20000	73	0
August	1	40000	84	4.7
September	1	60000	130	36.7
October	3	60000	219	36
November	2	4000	237	18.7
December	1	950	57	0
January	1	197	31	0
February	2	457	28	0
March	1	2500	82	0

* Data from Alonso (1982)

Both species also utilize different roosts during winter (Table 4): house sparrows usually roost at their nest sites or very close to them, while Spanish sparrows roost in larger aggregations on shrubs or thickets.

The flock size is significantly larger in the Spanish sparrow (2 – 4000 birds, mean = 289.9) than in the house sparrow (1 – 300 birds, mean = 36.4) ($t = 9.04$, $p < 0.001$). Spanish sparrows form larger aggregations while resting (mean = 417.9 birds, standard error = 122.9) than while foraging (mean = 232.4, *s.e.* = 57.0) ($t = 2.75$, $p < 0.01$). In the house sparrow resting and foraging flocks do not show significant differences ($t = 0.89$, $p > 0.05$).

The size of foraging flocks of Spanish sparrows changes significantly throughout the day ($F_{5,200} = 3.36$, $p < 0.01$, Fig. 2). After a first feeding period in the morning, the birds tend to aggregate during midday at certain "day or secondary roosts" (Ward 1965, 1971) on riparian vegetation thickets. During the afternoon the flocks disperse again in search for food. Thus, the size of those day roosts changes significantly throughout the day ($F_{4,93} = 2.64$, $p < 0.05$, Fig. 2). The flock size also varies significantly in the house sparrow ($F_{5,155} = 3.52$, $p < 0.01$), but this species do not form such large aggregations during midday. Thus, foraging and resting flocks have not been separated in Figure 2.

There are two daily periods of high feeding activity in both species (Fig. 3).

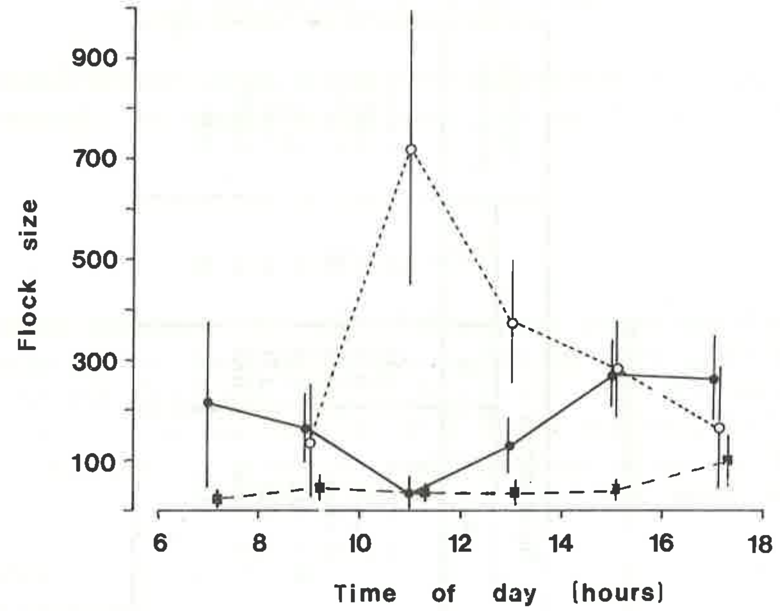

Fig. 2. Daily variation of flock size: Spanish sparrow foraging flocks (solid line); Spanish sparrow aggregations at "day roosts" – see text – (dotted line), and house sparrow flocks (dashed line)

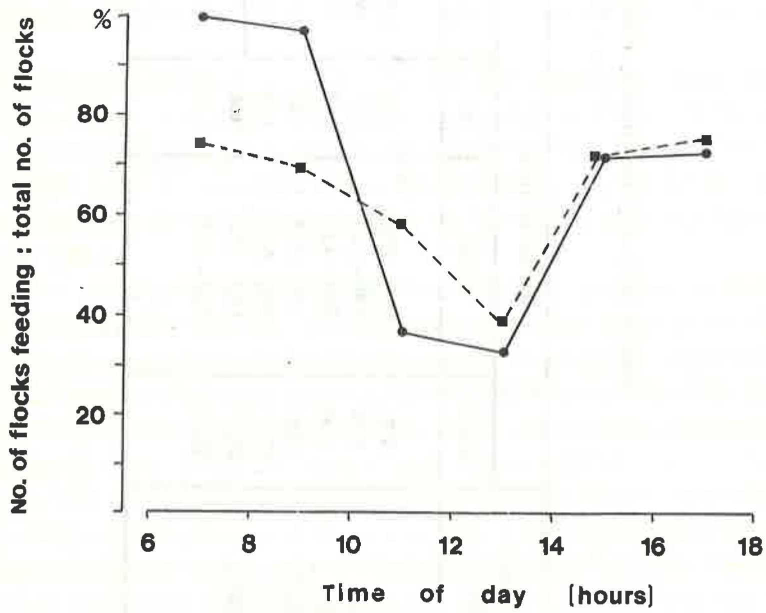

Fig. 3. Daily variation of the feeding intensity in the Spanish sparrow (solid line) and the house sparrow (dashed line)

Table 5. Biometrical data (mm) and weight (g) of winter samples of both sparrow species
*** = $p < 0.001$, ** = $p < 0.01$

Parameters compared	Spanish sparrow				House sparrow				t-test value of difference
	mean	range	σ_n	n	mean	range	σ_n	n	
Bill length	9.77	9.00 – 10.96	0.34	120	9.34	8.44 – 10.30	0.36	52	7.31 ***
Bill height	8.54	7.98 – 9.16	0.27	46	7.99	7.28 – 8.50	0.30	32	8.29 ***
Bill width	8.60	7.84 – 9.16	0.33	31	8.03	7.56 – 8.64	0.23	25	7.19 ***
Wing length	79.40	75.0 – 83.5	1.41	167	79.77	76.5 – 83.5	1.48	63	1.71
Tail length	57.77	54.0 – 63.2	1.59	116	58.76	55.0 – 62.0	1.71	43	3.30 **
Tarsus length	19.54	18.3 – 20.5	0.66	23	18.92	17.5 – 20.66	0.65	41	3.58 ***
Weight	28.46	25.0 – 33.5	1.45	185	28.47	25.2 – 31.0	1.36	64	0.05

4.4. MORPHOLOGICAL RELATIONSHIPS

Both species are very similar in their body measurements and weight (Table 5). Spanish sparrows have larger bills and longer tarsi, and shorter tails than house sparrows.

5. DISCUSSION

Interspecific differences in the bill size of sympatric populations of two closely related species have been usually interpreted as a result of selection against competition for food resources (Vaurie 1951, Schoener 1965; Hespenheide 1966, 1973, Pulliam and Enders 1971, Newton 1972, Allaire and Fisher 1975). Bill size has been also used by ecologists as indicator of prey size, longer-billed birds generally taking larger food items than smaller-billed birds (Hespenheide 1966, Newton 1967, Willson 1971, Pulliam 1983). Although it is possible that the bill size difference between both sparrows originally developed as a consequence of divergent feeding habits, the slight interspecific differences in food selection observed in this study do not match the bill size differences measured: the smaller-billed house sparrows take higher proportions of the largest seeds – wheat and corn – than Spanish sparrows.

Rather, the results indicate that the spatial segregation is the mechanism utilized by both sparrow populations to alleviate interspecific competition for food. The difference in tarsus length could be probably related to differential space use habits between both sparrows.

House sparrows are man commensals probably since the origin of the species (Summers-Smith 1963, Johnston and Klitz 1977). In my study area they are strongly sedentary and do not separate much from the buildings where they have their nests. In contrast, many Spanish sparrows spend the late summer, autumn and winter in the study area, far from their breeding sites, and leave it in spring (Alonso 1982).

Surely as a consequence of the preference of house sparrows to remain in close proximity to farms and granaries, their diet includes a higher proportion of cereal seeds, which are usually taken from the food for livestock. This higher consumption of cereal food by house sparrows has been observed in many different parts of the species' range, where their diet has been compared with that of the tree sparrow, *Passer montanus* (L.) (references in Grün 1975, Wiens and Dyer 1977).

Probably due to the low density of farm buildings, house sparrows form only relatively small colonial groups (Alonso 1982). As they forage close to the farms, they aggregate in smaller units and roost isolated or in small groups. This is an efficient strategy when exploiting and defending predictable food resources, i.e., waste cereal near granaries or cereal seeds in livestock food (see Davies 1976). In contrast, Spanish sparrows exhibit a higher gregarious and mobile behaviour, that probably enables them to exploit locally or temporally abundant food resources more efficiently (W i e n s 1976). This duality in the foraging strategies has been also observed in other instances where two related granivorous species coexist in the same area (references in W i e n s and J o h n s t o n 1977).

ACKNOWLEDGMENTS: I am very grateful to family Rodríguez for their hospitality during the field work and to R. Outerelo, C. Gómez and M. Carrasco for animal and seed identification. This research was made possible by a FPI grant from the Ministerio de Educación.

6. SUMMARY

In the present study the differences in food, habitat selection, flock size and biometrical features between sympatric Spanish sparrows, *Passer hispaniolensis*, and house sparrows, *Passer domesticus*, are analysed in a cultivated area of W-Spain during the winter season.

Although diet composition is very similar in both species, in the house sparrows the nutritional requirements are more distributed between weed seeds and cereal grain (Table 1). This is a consequence of a different habitat selection in both species: while Spanish sparrows feed mainly on weed seeds in corn stubble fields near river thickets, house sparrows remain in the vicinity of farms and granaries, the distance to buildings being the principal ecologically segregating factor (Table 2, Fig. 1).

The small biometrical differences (Table 5) suggest the existence of divergent trophic adaptations, and the differences in daily routine and social structure, with a more gregarious behaviour in the Spanish sparrow (Fig. 2), are surely adaptive to the social and feeding strategies of both species.

7. POLISH SUMMARY

W pracy oceniono różnice w składzie pokarmu, wybiórczości środowiskowej, wielkości stad, w wymiarach ciała w okresie zimowym między sympatrycznymi gatunkami: wróblem hiszpańskim (*Passer hispaniolensis*) a wróblem domowym (*Passer domesticus*), żyjącymi w krajobrazie rolniczym zachodniej Hiszpanii.

Chociaż skład pokarmu jest bardzo podobny u obu gatunków, wróbel domowy zjada tyle samo nasion chwastów co ziarn zbóż (tab. 1). Jest to wynikiem różnic w wybiórczości środowiskowej obu gatunków. Wróbel hiszpański odżywia się głównie nasionami chwastów na ścierniskach kukurydzy położonych w pobliżu zarośli nadrzecznych. Wróbel domowy przebywa w pobliżu gospodarstw i spichrzów. Odległość od zabudowań jest głównym ekologicznym czynnikiem segregującym oba gatunki (tab. 2, rys. 1).

Małe różnice biometryczne (tab. 5) sugerują istnienie różnic w adaptacjach troficznych. Różnice w dziennym obszarze aktywności i strukturze socjalnej przy większej towarzyskości u wróbla hiszpańskiego (rys.2) są jedynie przystosowaniami do strategii socjalnej i pokarmowej obu gatunków.

8. REFERENCES

1. A l l a i r e P. N., F i s h e r C. D. 1975 – Feeding ecology of three resident sympatric sparrows in Eastern Texas – Auk, 92: 260–269.
2. A l o n s o J. C. 1982 – Contribución a la biología del Gorrión Moruno, *Passer hispaniolensis* (Temm.) en la Península Ibérica y sus relaciones ecológicas con el Gorrión Común, *Passer domesticus* (L.) – Ph.D. Thesis, Univ. of Madrid, 316 pp.

3. Cody M. L. 1974 – Competition and the structure of bird communities – Monographs in population biology. 7 – Princeton Univ. Press, Princeton, 318 pp.
4. Davies N. B. 1976 – Food, flocking and territorial behaviour of the pied wagtail (*Motacilla alba yarrellii* Gould) in winter – J. anim. Ecol. 45: 235–254.
5. Grün G. 1975 – Die Ernährung der Sperlinge *Passer domesticus* (L.) und *Passer montanus* (L.) unter verschiedenen Umweltbedingungen – Int. Stud. Sparrows, 8: 24–103.
6. Hespenheide H. A. 1966 – The selection of seed size by finches – Wilson Bull. 78: 191–197.
7. Hespenheide H. A. 1973 – Ecological inferences from morphological data – Ann. Rev. Ecol. Syst. 4: 213–229.
8. Horn M. S. 1966 – Measurement of overlap in comparative ecological studies – Am. Nat. 100: 419–424.
9. Johnston R. F. 1969 – Taxonomy of house sparrows and their allies in the Mediterranean basin – Condor, 71: 129–139.
10. Johnston R. F., Klitz W. J. 1977 – Variation and evolution in a granivorous bird: the house sparrow (In: Granivorous birds in ecosystems, Eds. J. Pinowski, S. C. Kendeigh) – Cambridge Univ. Press, Cambridge – London – New York – Melbourne, 15–51.
11. Lack D. 1971 – Ecological isolation in birds – Harvard Univ. Press, Cambridge, Massachussetts, 404 pp.
12. MacArthur R. H. 1972 – Geographical ecology: patterns in the distribution of species – Harper and Row, New York, 287 pp.
13. Meise W. 1936 – Zur Systematik und Verbreitungsgeschichte der Haus- und Weidensperlinge, *Passer domesticus* (L.) und *Passer hispaniolensis* (Temm.) – J. Orn. 84: 631–672.
14. Newton I. 1967 – The adaptive variation and feeding ecology of some British finches – Ibis, 109: 33–98.
15. Newton I. 1972 – Finches – Collins, London, 288 pp.
16. Pulliam H. R. 1983 – Ecological community theory and the coexistence of sparrows – Ecology, 64: 45–52.
17. Pulliam H. R., Enders F. 1971 – The feeding ecology of five sympatric species of finches – Ecology, 52: 557–566.
18. Schoener T. W. 1965 – The evolution of bill size differences among sympatric congeneric species of birds – Evolution, 19: 189–213.
19. Schoener T. W. 1974 – Resource partitioning in ecological communities – Science, 185: 27–39.
20. Sibley C. G., Ahlquist J. E. (in press) – The phylogeny and classification of the Passerine birds, based on comparisons of the genetic material, DNA – Proc. XVIII Int. Cong., Moscow, 1982.
21. Summers-Smith D. 1963 – The house sparrow – Collins, London, 285 pp.
22. Summers-Smith D., Vernon J. D. R. 1972 – The distribution of *Passer* in Northwest Africa – Ibis, 14: 259–262.
23. Vaurie C. 1951 – Adaptive differences between two sympatric species of nuthatches (*Sitta*) – Proc. 10th Int. Orn. Cong. 163–166.
24. Ward P. 1965 – Feeding ecology of the black-faced dioch *Quelea quelea* in Nigeria – Ibis, 107: 173–214.
25. Ward P. 1971 – The migration patterns of *Quelea quelea* in Africa – Ibis, 113: 275–297.
26. Wiens J. A. 1976 – Population responses to patchy environments – Ann. Rev. Ecol. Syst. 7: 81–120.
27. Wiens J. A., Dyer M. I. 1977 – Assessing the potential impact of granivorous birds in ecosystems (In: Granivorous birds in ecosystems, Eds. J. Pinowski, S. C. Kendeigh) – Cambridge Univ. Press, Cambridge – London – New York – Melbourne, 205–266.
28. Wiens J. A., Johnston R. F. 1977 – Adaptive correlates in granivorous birds (In: Granivorous birds in ecosystems, Eds. J. Pinowski, S. C. Kendeigh) – Cambridge Univ. Press, Cambridge – London – New York – Melbourne, 301–340.
29. Willson M. F. 1971 – Seed selection in some North American finches – Condor, 73: 415–429.