J. Orn. 134, 1993: S. 69–77

Hybridization between House and Tree Sparrow (*Passer domesticus, P. montanus*)

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Introduction

Interspecific hybrids among birds are expected to be rare in natural populations. Most examples of avian hybridization occur between parapatric taxa that interbreed along zones of contact (SHORT 1969, MOORE 1977, RISING 1983), while hybrids of widely sympatric species are more sporadic (MILLER 1955, SIBLEY & SHORT 1959, JÄRVINEN 1987). Although not exclusive, different mechanisms have been proposed to interpret the breakdown of isolating barriers between avian species: a) Sexual imprinting, in which young birds raised by another species may become imprinted and mate on maturity with individuals of the foster species (e. g. IMMELMANN 1979); b) Promiscuous behaviour, occurring in species in which the mating system is promiscuous or polygynous, and copulation is not necessarily preceded by a long period of pair formation (MAYR 1942); c) Mate restriction, in which the lack of conspecific mates may lead to pairing with a member of a similar species (e. g. SIBLEY 1954); d) Mis-identification, in which interbreeding occurs because of close similarities between the two forms in respect of morphology, behaviour and habitat (e. g. MURRAY 1971).

The House Sparrow *Passer domesticus* and the Tree Sparrow *P. montanus* are widely sympatric species between which hybrids have regularly been reported. It has been suggested (SUMMERS-SMITH 1988) that they originated from a common ancestor in the early Pleistocene, the House Sparrow in the Middle East, the Tree Sparrow in China, and that subsequent expansions have led to extensive sympatry. In the primary zones of allopatry the two species fill similar ecological niches, being virtual synanthropes, living close to man and breeding in holes in his buildings. Where they are sympatric they occupy different habitats, though still with some overlap, the House Sparrow occurring primarily in towns, villages and farmland, the Tree Sparrow in lightly wooded country with old trees, on the edges of cultivated land, in lines of trees and wooded gardens (LACK 1971). Both are multibrooded species with overlapping breeding seasons, and use the same type of nest sites. They are similar in voice and courtship behaviour (BERCK 1961–62). The House Sparrow is larger (typically 25–35 g, compared with 20–25 g) and is sexually dimorphic, whereas the Tree Sparrow is monomorphic with both sexes having a similar head pattern to that of the House Sparrow male.

If imprinting were the principal mechanism of hybridization in sparrows (CHEKE 1969), successful cross-fostering should occur when both species coexist. If it were the

result of promiscuous behaviour, we should expect broods in which some hybrids were found to be attended by homospecific pairs (i. e. both members of the pair the same species) and interspecific bonds to be loose or non-existant; on the contrary, both House and Tree Sparrow tend to form pairs that are maintained for life (SUMMERS-SMITH 1988). These two mechanisms would be expected to be more frequent where both species are widespread because of the increase of interspecific contacts. If mate restriction were the principal mechanism of hybridization, we should expect hybridization to occur when one (or both) species is locally rare, i. e. a situation in which conspecifics are grossly outnumbered by potential heterospecific mates. Finally, misidentification would be expected to be most likely at the boundary between sympatric and allopatric populations, rather than in sympatric areas where there tends to be some ecological separation.

In this paper we analyse both the field data from a long term study of mixed breeding-colonies of these two sparrows in northeast Spain and bring together all available information about hybridization, cross-fostering and related traits of their natural history in order to determine which of the alternative mechanisms of hybridization is most likely.

Material and Methods

Nests of House Sparrows (n = 386) and Tree Sparrows (n = 708) were studied in rural habitats in northeast Spain where the species coexist, both using nest boxes. Nests were inspected at least once a week, more often every 3—5 days in the seasons 1982—1991. Eggs were examined and identified by colour patterns and measurements, allowing for intra-clutch size variation (LOWTHER 1990, P. J. CORDERO & L. JOVER unpubl.). Nestlings were examined towards the end of the nestling period, when plumage development is almost complete, allowing apparent hybrids between House and Tree Sparrows to be determined by visual phenotypic examination of successful broods. This may underestimate cases of hybridization since we do not know the complete range of variability of young hybrids (e. g. CORDERO 1990 b). However, such hybrid young that were detected were found only in nests attended by both species, suggesting that they are true hybrids (CORDERO 1990 a).

Hybrids from the literature survey were detected by phenotypic characteristics (e. g. ROOKE 1957, RICHARDSON 1957, NYHOLM 1966) and, exceptionally, by genetic or chromosomal techniques (e. g. BULATOVA et al. 1972). It has been assumed that the area of record was the natal area since both House and Tree Sparrow are predominantly sedentary over most of their ranges (SUMMERS-SMITH 1988). The local breeding situation was recorded as described in the reference, or obtained directly from the author. In the absence of such detailed information, more general statements were taken from local avifaunas or breeding atlases. Cases in which both species are common and widespread include areas where they are sympatric and are well represented in numbers (A). Cases in which one (or both) species is rare include the following situations: one of them outside its normal breeding range (B1); one patchily distributed (the report coming from a non-breeding district) or a local rarity although both species widespread in the area (B2); local scarcity of one species because of sharp population decline (B3) and marked ecological separation, e. g. by altitude, differential habitat use or migratory behaviour (B4).

Grateful thanks are given to D. T. PARKIN for helpful comments on an earlier draft of the text.

Results

Hybrid phenotypes were identified in 1988 and 1989 in northeast Spain in a nest box attended by a male House Sparrow and a female Tree Sparrow (CORDERO 1990 a) from a sample of 1094 nests examined of which 899 had, at least, one successful brood (309 House Sparrows, 590 Tree Sparrows). Assuming inter-year nest independence, this gives a rate of hybridization close to 1 : 500. Hybridization occurred in the only breeding colony in which Tree Sparrows occupied all available nest sites.

House Sparrows laid eggs in 6 nest boxes (1.5 % of total House Sparrow nests, n = 386) which were abandoned by Tree Sparrows during laying or incubation; Tree Sparrows laid eggs in 6 nest boxes (0.8 % of total Tree Sparrow nests, n = 708) in which the reverse was the case (Table, columns 2 and 3).

Number of instances of nest usurpation. HS: House Sparrow, TS: Tree Sparrow. Interval shown is time between last date on which eggs or chicks of first occupant were present and the start of egg-laying by second species in same nest box.

Usurping species	Interval (days)	Stage in breeding of 1st nest occupant when nest abandoned: laying	incubation	fledging	post-fledging	total
HS	0— 7	1	1	1	3	6
	8—14	1	0	3	3	7
	15—21	1	1	1	3	6
	>21	0	1	1	2	4
	$\bar{x}$±sd	8.7±6.1	15.7±11.7	14.2±5.0	16.7±12.6	14.9±10.6
	Range	1—16	0—28	6—23	2—46	0—46
TS	0— 7	0	1	2	4	7
	8—14	0	0	1	3	4
	15—21	1	1	1	0	3
	>21	1	2	3	0	6
	$\bar{x}$±sd	29.0±8.0	30.7±21.1	20.9±12.4	8.9±5.7	18.9±15.2
	Range	21—37	6—58	6—40	3—22	3—58

Egg-dumping occurred in 0.5 % of the House Sparrow nests (2/386), but was not detected in the Tree Sparrow nests (n = 708). In neither case did the alien eggs hatch. In one nest box the Tree Sparrow started egg-laying a day before the House Sparrow. On the next visit, the eggs of both species were broken in the nest, and subsequently House Sparrows laid a new and successful clutch. In the other case, House Sparrows usurped a nest box in which Tree Sparrows were incubating a clutch of five eggs; the House Sparrows laid five new eggs on top of the Tree Sparrow clutch. They did not begin to incubate until the penultimate egg was laid and only House Sparrow eggs hatched because of the chilling of Tree Sparrow embryos. The remainder of the nests yielded normal clutches and broods with chicks showing uniform phenotypes. Cross-fostering was not detected or, at least, presumed heterospecific chicks from hypothetical mimetic eggs did not develop sufficiently to be fully identified.

Thirty-three instances of apparent hybridization or suspected hybrids are available in the published literature or from personal communications (Appendix). 23 of the 32 reports (72 %) for which information is available are from areas where one (or both) of the parent species is locally rare, in most cases the Tree Sparrow. Most of the hybrid pairs were detected when the adults were attending cooperatively at the nest; in 6 of them (85 %) the female was a Tree Sparrow, the reverse of that reported by NAUMANN (1905).

Discussion

We do not know of any other interbreeding taxa among birds in which the females are as different as those of the House and Tree Sparrow. Species that hybridize may have different plumage patterns (WEST 1962, GILL & MURRAY 1972, JOHNSON & JOHNSON 1985) or size (MILLER 1955, BANKS & JOHNSON 1961), but most frequently it is the males that are different, while the females are very similar (e. g. SIBLEY 1957).

The striking difference in the plumage of the female sparrows has been adduced as grounds for imprinting. CHEKE (1969) suggested that cross-fostering could happen in the wild when sparrow species usurp each other's nest during egg-laying and take over any existing eggs. He reported a cross-fostering experiment in which he switched the clutches between House and Tree Sparrow nests. The following year he found a cross-fostered male House Sparrow attending a nest in which both Tree Sparrow eggs and hybrid nestlings occurred. However, the experiment consisted in switching whole clutches, a situation extremely unlikely to occur in nature. Rather, one might expect to find some eggs of one species among the clutch of the other or complete clutches of both species together, a situation that might lead to the discrimination of the eggs by the host species (see the case described above in which, after both species laid in the same nest, all the eggs were destroyed).

Preliminary results from our experiments on egg transfer were unsuccessful. Two eggs in two nests of the respective species were switched in late May 1991; in the first House Sparrow nest, the mixed clutch was destroyed by the birds; in the second, one House and one Tree Sparrow egg disappeared and only one House Sparrow egg hatched. One of the two nests of Tree Sparrows with transferred eggs was destroyed. In the other nest, the Tree Sparrows incubated five eggs (three Tree and two House Sparrow); all eggs hatched although the chicks died.

Natural egg transfer, although common in other birds, e.g. Tits, *Parus* spp. (HILDÉN 1983) is rare in the literature of sparrows. In spite of numerous investigations on the breeding ecology of these species, there is no convincing field data for egg transfer resulting in naturally cross-fostered young (though see BRUCKER 1985). The breeding of both species in the same nest box and season has been reported by other authors; normally, the second species starts egg-laying after the young of the first occupant have fledged (e. g. PINOWSKI 1967). Interspecific competion may result in nest site exchange (ANDERSON 1978), the more dominant House Sparrow being the most probable foster

species. The absence of successful natural cross-fostering in sparrows contrasts with the relatively high rate of hybridization (1 : 500) and the 33 apparent hybridizations or presumed hybrids reported in Appendix. The destruction of eggs or chicks by the sparrow species (mostly by House Sparrow) usurping alien nests (e. g. VEIGA 1990) is a strong argument supporting the lack of evidence for natural cross-fostering in sparrows.

DNA fingerprinting of broods and the pair attending the nest has suggested that up to 15 % of the young were not related to the male (PARKIN & WETTON 1991, WETTON & PARKIN 1991 a, b). S. A. FIRSOV (E. N. PANOV in litt.) has also found a high incidence of extra-pair copulations in the Tree Sparrow. On the other hand we have not obtained any evidence supporting the promiscuous behaviour mechanism of hybridization.

It is commonly thought that premating isolating mechanisms can be broken down in secondary contacts of related avian species if one (or both) of the forms is locally rare and conspecific mates are in short supply (e. g. SIBLEY 1954, MILLER 1955, WELLS et al. 1978, MARTIN 1980). For the House and Tree Sparrow, cases in which one of the species is rare form a high proportion of the examples of hybridization. In Europe the Tree Sparrow is generally the rarer species, is frequently patchily distributed and is in apparent decline (e. g. SUMMERS-SMITH 1989). Among other sparrow species the situation is very similar: the only known examples of hybridization between the Spanish Sparrow *P. hispaniolensis*, a dimorphic species similar to the House Sparrow, and the Tree Sparrow are from Malta, where the latter is rare and the Spanish Sparrow is common and widespread (SMITH & BORG 1976, SULTANA et al. 1975, SULTANA & GAUCI 1982). Also, hybridization between the House Sparrow and Somali Sparrow *P. castanopterus* has occurred in Somalia where the Somali Sparrow is the common widespread sparrow and the House Sparrow very rare (ASH & COLSTON 1981). Sparrow species show a strong attachment to the nest, and the nest normally provides the focus for pair formation, both for unmated males and for females that have lost their mates (SUMMERS-SMITH 1988). With both House and Tree Sparrows using the same type of nest site, mis-mating might occur (e. g. MARTIN 1980). Nest-site attachment is a probable reason for finding occasional individuals of one species (usually the Tree Sparrow) amid common heterospecific neighbours (House Sparrows) and interspecific competition may reduce the number of the subordinate species (Tree Sparrow). A female that has lost her mate may accept a mate of the wrong species, though it is surprising that a male House Sparrow accepts as a mate a female Tree Sparrow. It is probable that calls and behaviour, very similar in these two species, are more important than marked differences in plumage. Although imprinting and promiscuous behaviour cannot be excluded, and needs further experimentation, the available evidence suggests that mate restriction is the principal mechanism for mixed-pair formation and hybrid production in sparrows.

The study is continuing and DNA samples are being collected to establish formally the status of any future hybridization events.

Summary

An analysis is made of hybridization between the House Sparrow *Passer domesticus* and Tree Sparrow *P. montanus* based on a long-term breeding study in Spain and a survey of the published literature. The field study, in which hybrids were detected by phenotypes, gave a rate of hybridization close to 1 : 500. The majority of literature records of hybrids between these species are from areas where one is uncommon; there is no evidence for natural cross-fostering. We suggest that mate restriction is the most likely reason for mixed-pair formation and hybridization in these sparrows.

Zusammenfassung

Die Hybridisation zwischen Haus- und Feldsperling wurde in einer langfristigen brutbiologischen Studie in Spanien und auf der Grundlage eines Literaturüberblicks untersucht. In der Freilandstudie, bei der Bastarde phänotypisch registriert wurden, ergab sich eine Hybridisierungsrate nahe 1 : 500. Die Mehrzahl der Literaturangaben stammt von Gebieten, in denen eine Art nicht häufig ist (Appendix). Hinweise für Aufzucht von Jungen der jeweiligen anderen Art ergaben sich nicht. Sicher ist Partnermangel die wahrscheinlichste Ursache für Mischpaare und Verbastardierung beider Sperlingsarten.

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Appendix

Reported instances of hybridization between House and Tree Sparrows.

Reports refer to sight record of individual bird except where otherwise indicated. HS: House Sparrow, TS: Tree Sparrow, IT Italian Sparrow (*Passer hispaniolensis* (*domesticus*) *italiae*, HS x TS: hybrid between House and Tree Sparrow. A: Both species common, B1: one species outside normal breeding range, B2: one (or both) species patchily distributed or locally rare, B3: population of one species in sharp decline, B4: species separated ecologically.

No	Locality	Record	Status	Reference
1	Bolbec, France	collected —. 12. 1887	both common (A)	SUCHETET 1892 (in HARTING 1895)
2	Aiglegill, England	Spring 1892	TS rare (B2)	MACPHERSON 1919
3	Bury St Edmunds, England	collected 13. 1. 1894	both common (A)	TUCK 1894
4	Fordham, England	collected	ditto (A)	NICHOLS 1919
5	Wrocław, Poland	2 Hybrid broods	ditto (A)	SAXENBERGER 1925 (in MEISE 1951)
6	Zwickau, Germany	collected —. 4. 1928	HS ♂ rare for some years (B2)	pers. comm. (in MEISE 1934)
7	Lübeck, Germany	breeding pair ♂ HS — ♀ TS 1930	both common (A)	RUTHKE 1930
8	Portland, England	trapped 27. 9. 1955	TS rare (B2)	ROOKE 1957
9	Norfolk, England	trapped 19. 4. 1956	TS locally rare (B2)	RICHARDSON 1957

No	Locality	Record	Status	Reference
10	Bergen, Netherlands	breeding pair ♂ HS — ♀ TS 1959 or 1960	both common (A)	MONSEES 1962, G. J. VAN DEN BERG & D. GROENENDIJK in litt.
11	Fair Isle, Scotland	14. 8. 1962	TS rare (B1)	DAVIS 1963
12	Valais, Switzerland	breeding pair: ♂ TS —♀ IS 1965	bred at 1750 m TS rare at this altitude (B4)	PACAUD 1966
13	Białowieza, Poland	collected 13. 12. 1965	both locally rare (B2)	RUPRECHT 1967
14	Norra Ralta, Sweden	26. 12. 1965 to 15. 1. 1966	TS rare (B2)	NYHOLM 1966
15	Gurain, Belgium	trapped 20. 7. 1966	both common (A)	TRICOT 1968
16	Isles of Scilly	1968, full year	TS rare (B1)	PENHALLURICK 1978
17	Dzhambul, Tadschikistan	2 collected 3. 5. 1970	sharp ecological separation (B4)	STEPHAN & GAVRILOV 1980
18	ditto	♀ collected 16. 5. 1972	ditto (B4)	ditto
19	Dushanbé, Tadschikistan	collected	ditto (B4)	BULATOVA et al. 1972
20	Fair Isle, Scotland	30. 9. 1977 to 2. 10. 1977	TS rare (B1)	WATERSON 1978
21	Tisvilde, Denmark	—. 12. 1977 to —. 3. 1978	both common (A)	ANDERSEN 1978
22	Busalkort, India	1972	TS rare (B2)	PRICE 1979
23	Ereğli, Turkey	Pair coition: ♂ HS — ♀ TS 22. 6. 1978	TS rare (B2)	ALBRECHT 1983
24	Bolton Abbey, England	breeding pair ♂ HS x TS — ♀ TS 17. 6. 1979	TS in decline (B3)	HUME 1983
25	Fair Isle, Scotland	—. 10. 1980 up to 5 hyb.	TS rare (B1)	ARNOTT 1981
26	Hilfield Park, England	1. 6. 1982	TS in decline (B3)	GLADWIN and SAGE 1986
27	Slovenia	—	—	GROSELJ 1985—86
28	Falsterbo, Sweden	trapped 16. 10. 1984	both common (A)	PERSSON 1985
29	Prat de Llobregat, Spain	breeding pair ♂ HS — ♀ TS 1988	HS rare at colony though common in area (B2)	CORDERO 1990a
30	ditto	1989, ditto	ditto (B2)	CORDERO (unpub.)
31	Schiermonnikoog, Netherlands	—. 5. 1989	TS uncommon, in decline (B3)	BERG and GROENENDIJK 1991 and in litt.
32	Aalsmeer, Netherlands	23. 1. 1990 to 26. 2. 1990	TS locality rare (B2)	EIGENHUIS 1990
33	Welwyn Garden City, England	2. 10. 1990	TS rare (B2)	J. CORFIELD (pers. comm.)