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## Nest-site and Evolution of Polygamy in European Passerine Birds

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### Introduction

The mating systems of birds can (v. HAARTMAN 1951, p. 256) be classified as monogamy, polygamy and promiscuity. Promiscuous birds do not marry; the sexes meet for copulation and then part. Polygamy may be called polygyny if the male is polygamous, polyandry if the female is so. Polyandry is exceptional among passerine birds of the north temperate zone. In the Pied Flycatcher, *Ficedula hypoleuca*, "stolen copulations" occurred if the male left his mate prematurely in search of a second territory (v. HAARTMAN 1951). Similarly, in the Chaffinch, *Fringilla coelebs*, neighbouring males copulated with females which for some reason had been deserted (MARLER, p. 98). (For other examples of occasional polyandry or polyandrous promiscuity, see ALLEN, HANN, HOWARD 1929, LASKEY, SCHÜZ.) Occasional polyandry may play a certain evolutionary role, as the risk that the female will copulate with strange males if her own mate is away may to some extent counteract polygyny. There are two major forms of polygyny, simul-

taneous (sometimes called harem polygyny) and successive (sometimes called restricted monogamy). These two types of polygyny are not always clear-cut. Thus, as a rule the second female of a polygynous male Pied Flycatcher starts laying only 5 or more days after his first female, but exceptionally there may be little or no interval. Also, other relevant dichotomies with respect to polygyny can be discerned, particularly monoterritorial and polyterritorial polygyny, the male in the latter case having his mates in different territories (Pied Flycatcher, v. HAARTMAN 1945, 1951, 1956; Whitethroat, *Sylvia communis*, ARMINGTON; Wheatear, *Oenanthe oenanthe*, ARO, JENNING, MENZEL). J. S. HUXLEY (1938) was ahead of his time in stressing the importance of polyterritoriality (the expression did not exist at that time) in the development of polygyny, but in fact relatively few polygynous species are clearly polyterritorial.

The evolution of non-monogamous mating systems is far from easy to understand, at least in species in which the sexes are about equally common.

Even in species with an unbalanced sex ratio among the breeding population, the excess of females may be a consequence rather than a cause of polygyny (SELANDER, p. 134). In nidicolous species polygamy or promiscuity may mean that the young will receive a smaller amount of food. A single female Pied Flycatcher or House Wren, *Troglodytes aedon*, may bring as many meals as a pair if the number of young is relatively small (c. 4 and 3, respectively, in these species); but if the number of young is larger each nestling receives fewer meals than when the two parents co-operate (v. HAARTMAN 1954, 1955; KENDEIGH, see v. HAARTMAN op.c.). As the size of meals has not been measured, it is possible that the food-supplying capacity of the single female is even more restricted than is indicated by the number of meals (cf. ROYAMA). In the Grey Starling, *Sturnus cineraceus*, a single adult bird was capable of nourishing maximally 3, a pair maximally 6 or 7 young (KURODA).

As a rule, natural selection ought to work against two or more females mating with the same male. At the same time, paradoxically, selection ought to favour polygyny in the male. CURIO (p. 64), it is true, suggests that brood losses of polygynous male Pied Flycatchers are so severe that selection would not favour polygyny (note that in this species the male assists in feeding the young, especially those of his first mate). However, polygynous males have a fair chance of getting both their broods fledged. The following figures show the number of fledged broods per polygynous male Pied Flycatcher in my study area (Lemsjöhölm in SW Finland) in 1941—49:

Two broods fledged	9 = 45 %
One brood fledged	9 = 45 %
No brood fledged	2 = 10 %

The average number of fledged broods per polygynous male was 1.35, against c. 0.76 per monogamous male in the same years (v. HAARTMAN 1951a, p. 37). Even if some of the young of the polygynous fathers do starve, the annual net result of reproduction ought to be superior among the polygynists. In the closely related Collared Flycatcher, *Ficedula albicollis*, the situation may be even more in favour of polygyny, as extra helpers often appear at those broods which have been deserted by the father (LÖHRL 1959). In Brewer's Blackbird, *Euphagus cyanocephalus*, WILLIAMS (p. 41) found an average of 1.04 fledged broods per monogamous male, and 1.71 per polygamous male.

The fact that mating with a polygamous male may be unfavourable for the female should cause evolution of inhibiting mechanisms. There are such mechanisms (whether evolved *ad hoc* or not), but also mechanisms by which the male may evade this obstacle. A few examples may suffice. In the Long-Billed Marsh Wren, *Telmatodytes palustris*, the females are hostile towards each other and occupy parts of the male's territory as far from each other as possible (WELTER). Also, according to DIESELHORST, in the Yellow Bunting, *Emberiza citrinella*, the females of a polygynous male hold different territories within the male's territory; aggressiveness between the females seems to restrict the frequency of polygyny. In the Redstart, *Phoenicurus phoenicurus*, MÜHL found severe fighting between the established female and later arriving females within the territory of the male. In at least one case this resulted in the retreat of the late-comer, although in other cases polygyny developed. In the Red-winged Blackbird, *Agelaius phoeniceus*, NERO states that "sometimes in the early stages of female territory development, intolerance of females is so general that other females

have difficulty entering a male's territory". The male often interferes in the dispute between the females, "invariably attacking his original mate" thereby probably making it possible for the new female to settle. In spite of this, he may lose potential mates through the aggressiveness of the females. In the Pied Flycatcher the different territories of the male may be out of earshot of each other and separated by fields, meadows, territories of other males, etc. (v. HAARTMAN 1951, 1956); in many cases there will be no contact at all between the females in a triangle and therefore no opportunity for the first female to hinder the development of polygyny, or for the second female to avoid a mated male. In the Wheatear, the territories of the male may be up to 1400 m. from each other and separated by forest or open sea (JENNING, ARO); besides, MENZEL found that "when the first female approached the second one the male drove her off". If polygyny is polyterritorial and successive, there is obviously but little chance for a female to check the marital status of a potential mate.

In nidifugous species, in which the young are not fed by the parents, the drawbacks of non-monogamous mating seem less severe. However, it can hardly be without significance whether one or two parents incubate the eggs in turns, brood and shelter the young, lead them, attack predators, etc.

Under these circumstances it seems natural that monogamy should prevail among birds. It would be pointless even to conjecture what proportions of them are monogamous, polygynous, or promiscuous, as the mating system of many species can be established only after a considerable amount of work, and such work has been done only in a minority of species. "Every competent ornithologist can tell you that the private life of small birds is difficult to know" (JEAN ANOUILH: Colombe).

### Food supply and polygamy

Polygamy would be much easier to understand if the polygamous species were known to live in a *Schlaraffenland*\* with a surplus of easily obtainable food (v. HAARTMAN 1955). Much of the work done in recent years with the object of explaining the evolution of non-monogamous mating has sought to demonstrate a connection between food supply and polygamy.

ARMSTRONG (1955) found that the Wren, *Troglodytes troglodytes*, shows local variations with respect to polygyny. In St. Kilda, where the food supply is probably rather poor, without any seasonal peak in its abundance, Wrens are strictly monogamous; both parents feed the young and the breeding of individual pairs is scattered over a comparatively long period. In England and Holland, on the other hand, where there is a marked seasonal peak in food abundance, half the male Wrens are polygynous (cf. KLUIJVER *et al.*), and breeding is relatively synchronous.

SNOW suggested that the chief prerequisite for the evolution of group display in connection with promiscuity is that the female can find food for herself and the young quickly, as is the case with nectar- and fruit-eating, but not with insect-eating, nidicolous birds.

A comprehensive study has been carried out by CROOK on the African weavers, *Ploceinae*. Their mating system is clearly correlated with their habitat and food. In the forests, where the food supply is constant throughout the year, the breeding season is spread out, and the species living on insects or on a mixed diet of insects and seeds are monogamous. On savannah and grassland, on the other hand, where there is a temporary surplus of seeds after the

\* German fairy tale country where broiled pigeons flew into the mouths of the happy inhabitants.

short rainy period, the breeding season is timed so as to coincide with seed-production, and polygyny is the rule among the seed-eaters, whereas the species with a mixed diet are monogamous or polygynous.

Obviously, the correlation between seed-eating, a seasonal surplus of food and polygyny is a local African affair. In North America, however, as in Africa, passerines of the forest tend to be monogamous, those of "two-dimensional" habitats to be polygamous, as seen from a summary by VERNER & WILLSON (p. 144), here given in condensed form:

Habitat	No. of polygamous or promiscuous spp.
Marshes	6
Prairie and marsh	1
Savannah and marsh	1
Prairie	3*
Savannah	1
Scrub	1
Scrub and forest edge	1
Dense forest	1

\* Including *Spiza americana*, which was later shown to be polygynous (ZIMMERMANN).

To a certain degree these figures may be biased, as bird behaviour may be easier to observe in an open habitat than in dense forest. I do not think, however, that this source of error invalidates the trend indicated by the list.

In two-dimensional habitats like marshes and prairies, all productivity resulting from solar radiation is concentrated into a narrow vertical belt, whereas in three-dimensional habitats (forests) productivity is spread over a broad vertical component. VERNER & WILLSON therefore concluded that food ought to be more concentrated in the former habitats.

At the same time, the authors (VERNER; VERNER & WILLSON) have stressed that ample food supply cannot as such explain the evolution of poly-

gyny. Another principle, which they call the polygyny threshold, may be involved. This means that the best and the poorest territories differ so much that a female in a good territory with little or no aid from her mate will be more successful in rearing the young than two mates working together in a poor territory. Thus it is the threshold, i.e. the difference in food supply between two alternative territories, that decides the choice of an unmated female between an already mated male and a lone one.

In polyterritorial species a polygyny threshold will probably play no essential role, as the females do not discover the marital status of the males. Instead, we may guess that the females will choose the better food supply, the better nest-site, the more colourful or less aggressive male, etc., irrespective of how superior these variables are.

#### European passerine birds

Only a few European passerines are known to show polygyny as a more or less regular phenomenon. By regularity, I do not mean that triangles are commoner than pairs. In the Pied Flycatcher, only 13 % of the females were mated to polygynous males (v. HAARTMAN 1951), which may seem almost negligible: in a population of 16 females only two would be involved in a triangle, corresponding to a single male. Nevertheless, polygyny is no accident in this species, as is shown by the fact that the majority of males (in my study area over 60 %, v. HAARTMAN 1956) tried to obtain a second territory about the time their first mate had started to lay or even earlier. The border between accidental and regular polygyny is naturally not sharp. Even in species in which polygyny seems to be accidental, it does not deserve to be neglected. The stronger the selection against polygyny, the rarer these accidents.

The Appendix lists all European passerine species in which polygyny, however rare, has come to my knowledge. In view of the incompleteness of our present knowledge, it seems likely that some species now included among the accidentally polygynous ones will in the future prove to be regularly polygynous. This may, for instance, be the case with the Redstart, as indicated by the observations of RUITER (concerning polyterritoriality) and MÜHL. Some (all?) members of the genus *Phylloscopus* (at least the Chiffchaff, *P. collybita*, and the Willow Warbler, *P. trochilus*) seem preadapted for polygyny in that the share of the male in feeding the young is almost negligible (cf. summary by v. HAARTMAN 1968). Why these species have not more often been established to be polygynous is difficult to understand. In the Bearded Tit, *Panurus biarmicus*, there are hints of a strange form of polygyny (TEN KATE), but KOENIG did not observe any cases of polygyny. The male Starling, *Sturnus vulgaris*, has repeatedly been established to be a polygynist, although never in large numbers. However, in the Starling polygyny seems to follow a certain pattern. If the brood is small the male may turn polygynous instead of feeding the young of his first mate (CARRICK). In the Rose-coloured Starling, *Sturnus roseus*, SEREBRENNIKOV considers polygamy to be the rule, but the life history of the species is insufficiently known.

Among the species generally considered polygynous, the status of the Corn Bunting, *Emberiza calandra*, (RYVES & RYVES) has recently been questioned (LACK 1968). But GYLLIN showed that polygyny occurred, although rarely, in Dorset, England, NORUP considered it common in Denmark, and KARVIK established quite a few cases in southern Sweden. It therefore seems likely that polygyny occurs in the Corn Bunting with a locally varying frequency.

The list does not indicate any prevalence of seed-eaters among the polygynous species. On the contrary, polygyny is practically unknown among European finches (Fringillinae and Carduelinae). To some extent this may be due to lack of knowledge. The finches are unusually easy to keep in cages, and so their "molecular" behaviour, the postures and their underlying motivation, has been subjected to exhaustive studies, whereas, with few exceptions, their "molar" behaviour, that is their behaviour as a whole, is less well known. But at least in Finland, feeding conditions for most finches are hardly likely to facilitate polygyny; besides, in some species the young are fed on a high proportion of insects.

Nor does there seem to be any obvious prevalence of marsh and grassland inhabitants among European polygynous passerines. Conditions do not seem to be so favourable in the Old World as in the New for these ecological groups. In Europe none of the marsh species are really abundant, like some American Icterids. However, in the European genus *Emberiza*, typical inhabitants of bushy terrain, grassland or reeds, there is a certain tendency towards polygyny. In the genus *Acrocephalus* polygyny was observed in two species, but not in *A. scirpaceus*, despite a thorough investigation (BROWN & DAVIES)\*. The Penduline Tit, *Remiz pendulinus*, which nests in bushy terrain by marshes, is perhaps the most genuine polygynist among European passerines.

The main correlation between way of life and mating system, as indicated by the Appendix, seems to be with the nest-site (cf. also v. HAARTMAN 1957). The Appendix may be summarized as follows:

\* Since this was written, C. K. Catchpole has informed me that he has good evidence of several cases of polygyny in this species (cf. also BELL, CATCHPOLE, and CORBETT).

	All species	Nests open	Nests roofed or in niches or holes
Total number of species	97 = 100 %	61 = 100 %	36 = 100 %
Polygyny established	43 = 44 %	19 = 31 % $\pm$ 5.9	23 = 64 % $\pm$ 8.0
Polygyny known to be common	5 = 5 %	1 = 1.5 %	4 = 13 %

Note. The significance of the difference  $64-31\% = 33\% \pm 6.9$  is high.

The total number of species is given in accordance with LACK's (1948, p. 38—41) list of mid-European passerines. Also, his classification of nest-sites has been followed with few exceptions.\* It would be meaningless to include other European species, as they have a northern, eastern, or southern distribution, and are likely not to have been thoroughly investigated. The percentage of commonly polygynous species (5%) coincides with the figure for North America (VERNER & WILLSON), whereas the number of accidentally polygynous species is much higher in Europe, perhaps owing to the greater number of amateur bird-watchers.

It can hardly be denied that there is a certain possibility of bias with respect to the occurrence of polygyny among hole-nesting species. Many of them are easy to attract with nest-boxes, and so may have been better studied than other species. However, polygyny seems to be especially frequent among birds with domed nests, which are hardly easier to study than other birds.

## Discussion

It has already been pointed out by STEINFATT and KLUIJVER *et al.* that, relatively speaking, a large number of the small birds known to be polygynous possess domed nests. Thus, according to KLUIJVER *et al.*, when the female is in search for food, the eggs are comparatively well protected against enemies

or cold, even if the male is not present. Also, one would think, both mates would not be needed to attack and distract enemies if the contents of the nest are invisible from the outside. NICE has shown that the nest losses in hole-nesting birds are much smaller than in birds nesting in the open. There are, of course, different means by which nest-security can be obtained. GILLIARD assumes that the promiscuity in combination with arena display evolved in the Cock-of-the-Rock, *Rupicola rupicola*, is a consequence of increased nest-security obtained through cryptic plumage in the female.

While the present study reinforces the idea that polygyny may evolve in connection with a well protected nest, the nest may also act in another and perhaps more important way. Nestlings need energy for two purposes, maintenance of life (including temperature regulation and activity) and growth. The relative importance of these two items of expenditure varies with the age of the nestlings (ROYAMA), being in the Great Tit, *Parus major*, larger for growth until about 13 days of age, and after that larger for maintenance. Following reduction in the speed of growth and/or the maintenance costs, a bird could afford either to have more young or to feed the young less often, i.e. to be polygynous. Thus there seems to be a certain freedom in evolution; the potentiality may be used in either way, and which course will be chosen depends upon additional factors, the nature of which is at present obscure. In the tits, for instance, which in most species have exceedingly large broods, there seems to

\* *Anthus spinoletta* and *Plectrophenax nivalis* have been recorded as hole-nesting, *Delichon urbica* as having a domed nest.

have been strong selection against polygyny. But, oddly enough, there is generally no clear correlation between clutch-size and polygyny (SKUTCH 1949, v. HAARTMAN 1954, 1955). This discrepancy has not so far been explained.

LACK (1948, 1968) has tried to show that the growth-rate in the young of hole-nesting species is slowed down as a consequence of their safer nests. This is probably so, although not to the extent LACK suggests when he uses the nestling period as an indication of growth-rate (young hole-nesters usually stay in the nest for a considerable time after reaching peak weight, see v. HAARTMAN 1954, SKUTCH 1967). According to LACK, the slower growth-rate has enabled the hole-nesting birds to have larger broods (cf. however the diverging opinion of RICKLEFS). It would also make polygyny possible. Likewise, more efficient heat insulation would reduce the energy requirement of the young and thus enable the species to increase its brood-size or to become polygynous. In case of both slower growth-rate and more efficient insulation the *Schlaraffenland* effect would be indirectly reached.

The idea that efficient heat-insulation of the nest might be important for the evolution of polygamy was put forward by ROYAMA on theoretical grounds. Measurements of the insulation of domed or hole-nests on the one hand, and open nests on the other are lacking. PALMGREN & PALMGREN made experiments on the insulation of passerine birds' nests, but their method only allows comparisons between open, cup-shaped nests. Long-tailed Tits, *Aegithalos caudatus*, however, were shown to have well insulated nests, as would be expected. Further, wind was shown strongly to reduce the insulation of open nests; with nests in holes the effect will probably be close to nil. Even small temperature differences during the development of the young may have notable

consequences. For instance, IRVING & KROG reckon it possible that "an increase of only 1°C. in temperature in nests might shorten the time for nestling growth by . . . 10 per cent."

A restricted number of nest-sites is sometimes thought to be a factor favouring the evolution of polygyny. ORIANs concluded that species with widespread feeding areas but restricted nest-sites tend towards polygyny. In the Dickcissel, *Spiza americana*, ZIMMERMANN found that the territories of bachelor males lacked acceptable nest-sites, whereas those of mated males, irrespective of whether monogamous or polygynous, offered enough favourable sites. Somewhat similar situations were found in the Red-winged Blackbird (LINSDALE) and Yellow-headed Blackbird, *Xanthocephalus xanthocephalus* (WILLSON).

In the Collared (LÖHRL 1951) and Pied (v. HAARTMAN 1956) Flycatcher, males sometimes occupy such poor nest-holes that they have no chance of getting a mate. In spite of this, I hesitate to consider lack of nest-sites the major factor leading to polygyny in hole-nesting birds. In the Pied Flycatcher, the ownership of two acceptable nest-holes is a prerequisite for polygyny but actually leads to polygyny only in a minority of cases. At the same time, some males with a good nest-hole may remain unmated. Further, it should be observed that species with domed nests tend to be polygynous as frequently as hole-nesters or more so.

From a purely statistical analysis of the species showing or not showing polygyny, one cannot hope to arrive at a final explanation of this phenomenon. So diverse, in fact, is polygyny that the combination of factors favouring or counteracting it will differ from species to species, except perhaps among closely related species, in which the mating systems is identical, thanks to homology.

## Summary

Recent studies have stressed the importance of superfluous food (*Schlaraffenland* effect) in the evolution of polygamy. Among European passerines, however, little correlation was apparent between feeding habits or food milieu and polygamy. On the other hand, comparatively large numbers of polygynous European species had domed nests or nested in holes.

The causes of this correlation are discussed. (1) The assistance of the male in driving off enemies or covering the eggs may be of less importance if the nest is safe. (2) Safety of the nest makes evolution of slower growth in the nestlings possible; further, good insulation reduces the maintenance costs of the nestlings. Both these factors reduce the food-requirement of the nestlings and should enable the species concerned to increase their brood size or become polygynous. (3) The restricted number of nest sites may to some extent facilitate the evolution of polygyny among hole-nesters, but cannot be called upon to explain polygyny among birds with domed nests.

Selostus: Pesäpaikat ja polygamian kehittyminen eurooppalaisilla varpuslinnuilla.

Viimeaikaiset tutkimukset ovat painottaneet ylenmäärin runsaan ravinnon vaikutusta polygamian kehittämisessä ("*Schlaraffenland*-efekti"). Eurooppalaisilla varpuslintulajeilla ei kuitenkaan ole selvää korrelaatiota polygamian ja toisaalta ruokailutapojen tai ympäristön välillä. Eurooppalaisista polygynisistä lajeista on sen sijaan suhteellisen suurella osalla katettu pesä tai kolopesä.

Kirjoituksessa käsitellään tämän korrelaation syitä: (1) Koiraan apu vihollisten poisajamisessa tai munien peittämisessä saattaa olla vähemmän tärkeää, jos pesä on turvallinen. (2) Pesän turvallisuus tekee poikasten hitaamman kasvuvauhdin evoluution mahdolliseksi, ja hyvä eristyskyky vähentää poikasten lämmönhukkaa. Molemmat tekijät vähentävät poikasten ravinnontarvetta ja suovat lajille mahdollisuuden nostaa pesyekokoa tai kehittyä polygamiseksi. (3) Pesäpaikkojen rajoitettu määrä saattaa jossakin määrin helpottaa polygynian kehittymistä kolopesijöillä, mutta ei selitä polygyniaa lajeilla, jotka pesivät katetuissa pesissä.

## Appendix: Polygyny in European passerine birds

(Commonly polygynous species printed with letters spaced out)

### Species with open nests

*Lullula arborea*, RYVES, according to WITHERBY *et al.*

*Corvus frugilegus*, ADAMS, LYE, YEATES

*Panurus biarmicus*, TEN KATE, FEINDT & JUNG

*Turdus merula*, KOCHS, LIND, STEINBACHER

*Saxicola rubetra*, WILCOCK

*Luscinia megarhynchos*, CLIDIUS

*Acrocephalus arundinaceus*, KLUIJVER 1949, 1955

*Acrocephalus schoenobaenus*\*, BROWN & DAVIES

*Sylvia atricapilla*, GROEBBELS

„ *communis*, ARMINGTON

*Anthus campestris*, NORUP

„ *trivialis*, NORUP

*Motacilla flava* (?), DROST

*Lanius collurio*, CHANSE & OWEN (according to NETHERSOLE-THOMPSON), DURANGO 1958

\* Concerning *Acrocephalus scirpaceus*, cf. note on p. 5.



- Pyrrhula pyrrhula*, NETHERSOLE-THOMPSON  
*Fringilla coelebs*, KAUER, MARLER  
*Emberiza citrinella*, DIESELHORST, MAYER-GROSS  
 „ *calandra*, GYLLIN, KARVIK, NORUP, RYVES & RYVES  
 „ *hortulana*, DURANGO 1948  
 „ *schoeniclus*, BELL, BELL & HORNBY, HAUKIOJA  
*Calcarius lapponicus*,\* SCHAANNING
- Species nesting in niches
- Hirundo rustica*, LÖHRL 1962, MOHR, RICHARDSON  
*Luscinia svecica*, PEIPONEN  
*Eritbacus rubecula*, LACK 1946  
*Muscicapa striata*, GOSNELL, SUNKEL  
*Motacilla alba*, NICHOLS (according to NETHERSOLE-THOMPSON)
- Species with roofed nests
- Aegithalos caudatus*, NETHERSOLE-THOMPSON, WOLDA  
*Remiz pendulinus*, BURCKHARDT, MERKEL, STEINFATT  
*Troglodytes troglodytes*, ARMSTRONG, KLUIJVER *et al.*  
*Phylloscopus trochilus*, HARTLEY, HOWARD 1907—14
- Phylloscopus collybita*, GEISSBÜHLER, HURRELL, STEINFATT  
 „ *sibilatrix*, COX, LEHMANN, SVÄRDSON
- Species nesting in holes
- Riparia riparia*, STONER  
*Corvus monedula*, ARMINGTON  
*Parus major*, GOOCH  
   *caeruleus*, NETHERSOLE-THOMPSON  
 „ *ater*, NETHERSOLE-THOMPSON  
*Oenanthe oenanthe*, ARO, JENNING, MENZEL  
*Phoenicurus phoenicurus*, KIERSKI, MÜHL, ROSENSON  
 „ *ochruros*, GUTSCHER  
*Ficedula hypoleuca*, CREUTZ, CURIO, v. HAARTMAN  
 „ *albicollis*, LÖHRL 1949, 1951, 1959  
*Sturnus vulgaris*, CARRICK, FREITAG, KESSEL, MARKKULA, MORTENSEN, SCHÜZ, WALLRAFF  
 „ *roseus*,\* SEREBRENNIKOV  
*Plectrophenax nivalis*, TINBERGEN  
*Passer domesticus*, DAANJE, PEARSE, SUMMERS-SMITH

\* Not included in the summarizing table, p. 6, as the species does not belong to the mid-European avifauna.

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