Comparisons between the breeding biology of year-old and older females of the White Wagtail *Motacilla alba* in Central Finland

MATTI LEINONEN

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The breeding biology of year-old and older females was compared in a population of White Wagtails living along a water course in Central Finland. The year-old female can be distinguished from older ones by the colour of her crown, which is of the same grey shade as her back. The basic material comes from 309 nests. The study was carried out in 1967—72. Year-old females arrived later than older individuals. They bred more often in natural habitats and natural holes than older ones. There were no differences between the two age groups as to the onset of laying, clutch size or breeding success. Factors involved are discussed. Some year-old females did not breed. The author assumes that this is adaptive in that original nature does not offer enough suitable habitats, and, hence, some Wagtails are excluded from breeding. The influence of man has probably been of so short duration that no complete genetical change making the bird fit for the recent situation has taken place.

Introduction

In many passerines the age of the female influences its breeding. First-breeding year-old females often begin laying later than older females (e.g. in *Melospiza melodia,* NICE 1937; *Phoenicurus phoenicurus,* RUITER 1941, BUXTON 1950; *Sialia sialis,* LASKEY 1943; *Parus major,* KLUYVER 1951; *Sturnus vugaris,* DUNNETT 1955, BERTHOLD 1964; *Turdus merula,* SNOW 1958, 1969; *Passer domesticus,* SUMMERS-SMITH 1963, SEEL 1968; *Ficedula hypoleuca,* BERNDT & WINKEL 1967). They often produce smaller clutches (e.g. in *Phoenicurus phoenicurus,* RUITER 1941; *Parus major,* KLUYVER 1951, PERRINS 1965; *Ficedula hypoleuca,* CREUTZ 1955, BERNDT & WINKEL 1967, v. HAARTMAN 1967; *Ficedula albicollis,* LÖHRL 1957; *Anthus spinoletta,* COULSON 1956; *Turdus merula,* SNOW 1958, 1969; *Emberiza schoeniclus,* HAUKIOJA 1970). In some cases it has been established that losses during the nesting period are heavier among females breeding for the first time (e.g. in *Turdus merula,* SNOW 1958, 1969; *Alauda arvensis,* DELIUS 1965; *Parus major,* PERRINS 1965). It has even been assumed that the small clutch size of first-breeders is adaptive; they cannot take care of as many nestlings as older females (LACK 1954, BERNDT & WINKEL 1967, KLOMP 1970).

Among many passerines not all first year females breed, which may be due to the lack of suitable habitats or nest-sites (e.g. in *Phoenicurus phoenicurus,* RUITER 1941; *Motacilla flava,* DROST 1948; *Sturnus vulgaris,* BERTHOLD 1964; *Melospiza melodia,* TOMPA 1964; *Alauda arvensis,* DELIUS 1965; *Ficedula hypoleuca,* v. HAARTMAN 1967, WINKEL et al. 1970). Apparently in some passerine populations there are non-breeding year-old birds (v. HAARTMAN 1951, 1971, LACK 1954, ENEMAR 1959).

Most passerine species lack field marks, with the aid of which it is possible to determine the age of individuals. The White Wagtail, *Motacilla alba,* is an exception, as year-old females can be distinguished from older ones on the basis of the colour of their crown. I have studied the breeding biology of year-old females and compared it with that of older ones by using this field mark in age determination. As was mentioned earlier (LEINONEN 1973a), the Wagtail has been but little investigated, in spite of the fact that in large areas it belongs to the commonest bird species. For instance, LACK (1947, 1954, 1966) and KLOMP (1970) list a number of passerines in which the age of the female influences e.g. clutch size, but neither of them mentions the genus *Motacilla.*

The study was performed in the water course area of Keuruu, in Central Finland. The basic data were taken from 309 nests found in 1967—72. The study area and the breeding biology of the Wagtail have been described in more detail in an earlier publication (LEINONEN 1973a). In the spring of 1973 the arrival of the species was recorded at Tampere.

Age of females

A year-old female can be distinguished from older ones by the colour of her crown, which is grey, the same shade as her back (v. HAARTMAN et al. 1971). Most handbooks fail to mention this difference. In older females the crown and the neck are dark grey, with individual variations up to black (cf. also DEMENT'EV & GLADKOV 1954). The colour change is probably induced by sex hormones (WINKEL et al. 1970, *Ficedula hypoleuca*).

The colour change of the crown after the first breeding summer was also established by observing colour-ringed Wagtails. From 1967 to 1971 255 nestlings were ringed. Of these five females were observed a year later, all of which had grey crowns. Four of these females were recorded in a later year. Three then had dark grey crowns, one a black crown. Of females with grey crowns and regarded as one year old when ringed, four were seen in a later year. In all of them the crown had changed from grey to dark grey. After the second year, the colour of the crown did not usually change, although in one case the crown darkened even further. Among old females about 70 % had dark grey crowns, and about 30 % black crowns.

In the male no corresponding colour changes were observed. Hence, this investigation concerns only females.

A female with a black crown could in most cases easily be distinguished from males. Males have bright white cheeks, while the cheeks of females are greyish with short, dark grey or black strips and/or patches. It was not possible in all instances to determine the age of a female due to e.g. rain, fog, hard wind, back light or vegetation cover.

From 1967 to 1972 403 different Wagtail females were observed in the study area, the age of 367 of which could be determined. According to these data 41.1 % of the females were one-year-old during the breeding season. In 1971—72, when data were most abundant and most evenly distributed throughout the study area, the proportion of one-year-old females was rather similar: in 1971 40.7 % (150 females) and in 1972 47.0 % (140 females). The difference is not statistically significant.

If the proportion of one-year-old birds in a balanced population is about 40 %, the mean life expectancy of females is about two years (e.g. v. HAARTMAN 1971). DROST (1948) estimated that at Helgoland the proportion of one-year-old birds in the breeding population of *Motacilla flava* was 68 %, which gives a life expectancy of about 1.5 years.

Arrival, territory occupation, nest-sites

The mean arrival date of the first Wagtails in the study area during the period of 1932—1972 was April 14. A great part of the population settled in their territories about a fortnight later (LEINONEN 1973a).

At Iidesjärvi in Tampere, the arrival of Wagtails was studied in the spring of 1973. Results can be summarized ar follows:

observation period	males	old females	one-year-old females
April 16 to 19	41	5	0
April 20 to 23	246	60	36
April 24 to 25	26	5	6

In an earlier paper (LEINONEN 1973a) the differences in the arrival dates of males and females have already been dealt with.

The female partner of pairs already occupying a breeding territory in May 1 to 5 of 1969, 1970 and 1972 ($n = 57$) was in 20.2 % of the cases one-year-old. Their proportion of the population at that time was therefore smaller than during the breeding season, the difference being statistically significant ($\chi^2 = 6.23$, $f = 1$, $P < 0.025$).

From the above it may be concluded that old females arrived at their breeding grounds earlier than one-year-old females, and that they occupied territories earlier, too.

Of the total Wagtail population of the Keuruu area 17.5 % bred in natural sites, the rest in artificial sites (LEINONEN 1973). Of one-year-old females no less than 29.4 % ($n = 82$) bred in natural holes, while the corresponding figure for older females was only 12.7 % ($n = 165$). The difference is statistically significant ($\chi^2 = 8.96$, $f = 1$, $P < 0.01$).

The result is quite similar, if those 131 territories are considered, in which the nest was not found. Of these 23 % were in natural habitats (LEINONEN 1973). 50 % of year-old females bred in natural habitats ($n = 46$); of the older ones, on the other hand, 15.6 % ($n = 64$) bred in natural habitats. The difference is highly significant ($\chi^2 = 13.46$, $f = 1$, $P < 0.001$).

Apparently in such areas as the Keuruu area, older females, arriving earlier in the spring, occupy the most attractive habitats and nest-sites first. These are often man-made and include buildings and different constructions. One-year-old females, which arrive later, more often have to settle in natural habitats and natural holes.

The higher social status of older females, may also influence the result. When competition for nest-sites occurs, they may drive away one-year-old females (e.g. SNOW 1958, *Turdus merula*). The following may serve as an example:

In the northern parts of the Keurusselkä area a female bred in the same territory from 1967 to 1971. In that territory on the other hand, the same male bred in 1969—1972. In the spring of 1970, however, a one-year-old female arrived in the territory, and mated with the male and began to lay eggs. On May 22, the old female was observed in the territory. She drove away the one-year-old female and mated with the male occupying the territory. The old female did not begin laying in a new nest until June 13. Next spring she returned again to the same territory and then laid her eggs at the normal time. The one-year-old female disappeared from the territory some days after the old one had arrived. During these few days the young female stayed in the territory but did not approach the building where her nest was located and where the old female attacked her violently. In the observed case the young female was further handicapped by the fact that the old female returned to her "own" territory and mated with her old mate.

The proportion of one-year-old females among those certainly breeding ($n = 179$) in the Keuruu area in 1971—72 was only 33.6 %. On the other hand, among females seen in the study area without possessing a territory at the time when most of the population had laid eggs, the proportion of one-year-old females was 69.6 %. The difference is statistically highly significant ($\chi^2 = 13.83$, $f = 1$, $P < 0.001$).

The large numbers of one-year-old females among Wagtails lacking territories could, theoretically at least, be

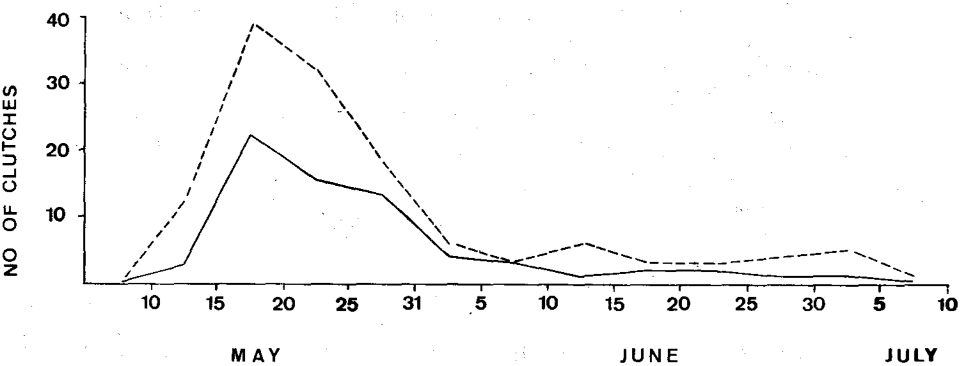

FIG. 1. Start of egg laying. Solid line = one-year-old females, broken line = older females.

due to late egg laying. This does not, however, hold true (see later). Probably some of the one-year-old females did not breed in the Keuruu area.

Egg laying, clutch size, breeding success

In the Keuruu area year-old females did not begin egg laying later than older individuals in 1967—72 (Fig. 1). No differences were found in the years when data were gathered evenly throughout the study area, viz. 1971 (n = 54) and 1972 (n = 68), either.

Nor were there differences in the onset of egg laying, when different-aged females breeding in similar habitats were compared. Year-old females nesting in natural holes (n = 22), began laying simultaneously with older individuals breeding in similar sites (n = 24). Also in artificial nest-sites year-old (n = 33) and older females (n = 79) began to lay eggs at the same time. In this comparison, nests where laying started in May, 1967 to 1972, were taken into account.

In Table 1 clutch sizes of different-aged females in 1967—72 are given. As can be seen, the clutches of year-old females were no smaller than those of older ones.

In the Keuruu area, a decreasing seasonal trend in clutch size was found (LEINONEN 1973a). Among many passerines the mean clutch size decreases partly because year-old females begin laying later and lay smaller clutches than older individuals (e.g. KLOMP 1970). From the above it may be concluded that in the Wagtail population living in the Keuruu area this factor cannot have any influence upon the observed trend.

In my study area 3.9 % of the eggs did not hatch (LEINONEN 1973a). In the clutches of year-old females the figure was 3.0 % (total number of eggs

TABLE 1. Clutch size of the White Wagtail as related to age of female in the Keuruu area in May 1967—72.

Age of female	Clutch size						
	4	5	6	7	$\bar{x}$	$S_{\bar{x}}$	N
One year	1	8	32	1	5.78±0.08		42
Older	2	18	69	—	5.75±0.05		89
Unknown	1	5	9	1	5.63±0.18		16

was 297), in the nests of older ones the corresponding figure was 3.9 % (697 eggs). The difference is not significant.

8.6 % of nestlings in broods where at least one nestling was fledged were lost (LEINONEN 1973a). In broods of year-old females the figure was 5.4 % (total number of nestlings was 230) and in broods of older females 8.2 % (534 nestlings). The difference is not significant.

Losses of total clutches and broods were not related to the age of the female.

In the above figures of egg or nestling losses of the total population, clutches laid by females of unknown age were also taken into account.

Although no statistically significant differences were found between the two age groups in respect of egg or nestling losses, the trend was the same in both cases: year-old females produced more fledglings. The difference, however, is more likely due to different nest-sites than to the age of the female. The effect of the nesting site on the breeding success is dealt with in another paper (LEINONEN 1973b).

Single egg losses in the nests located in natural holes with first eggs laid in May was 2.3 % for nests of year-old females (87 eggs) and 5.3 % for nests of older females (133 eggs). The difference is not significant. In nests located in artificial sites where laying commenced at the same time, losses were, for year-old females, 3.7 % (161 eggs) and for older ones 2.8 % (428 eggs). The difference is not significant.

Single nestling losses in nests located in natural holes where laying started in May were 3.0 % for year-old females (67 young) and for older females 3.2 % (94 young). The difference is not significant. In nests with first eggs laid in the same period and nests located in artificial sites the corresponding lossess for year-old females were 7.9 % (102 young) and for older ones 14.1 % (355 young). This difference is not significant.

From the above it can be seen that year-old females produced as many fledglings as older females did in similar nest-sites.

As to replacement and second clutches, the age of the female had no influence, as such clutches were laid approximately in equal numbers by different-aged females. The sample is, however, rather small: replacement clutches were recorded 15 and second clutches 20 times (LEINONEN 1973a).

The lengths of incubation and nestling periods may be affected by the time of egg laying, clutch size and nest-site. As to the first two factors, there are no possible differences that could be correlated with the age of the female in the Wagtail population of the Keuruu area. As to the last mentioned factor, the data are too scarce for nests placed in natural holes to permit comparisons.

On an average, the incubation period of year-old females was 12.5 ± 0.22 days (21 clutches), that of older birds 12.6 ± 0.20 days (42 clutches). The nestling stage lasted, in nests of year-old females, 13.9 ± 0.28 days (13 broods) and in nests of older females 13.6 ± 0.17 days (28 broods). The age of the female did not therefore affect either the length of incubation or the length of the nestling stage.

Discussion

From the above it can be seen that year-old females arrived in the Keuruu area and dispersed to their territories later than older individuals. However, they laid eggs simultaneously with older females, and laid as many eggs as older ones did, producing fledged young in equal numbers as older females. In the lengths of incubation and nestling stages there were no differences correlated to the age of the female. However, some of the year-old females did not breed.

Factors which may be involved are discussed in the following.

BERTHOLD (1964) showed that the farther from their wintering quarters Starlings (*Sturnus vulgaris*) breed, the later they arrive at their breeding grounds, and the greater is the proportion of year-old individuals not breeding. Obviously year-old individuals had not time to recover after their stressing migration. After the first Wagtails have arrived in Finland in the spring, the species is soon dispersed throughout the country, usually sooner than most other early migrating species. The difference between the earliest arriving Wagtails and the main population is usually only from 7 to 10 days (v. HAARTMAN et al. 1971). Soon after spring migration Wagtails occupy territories. In the Keuruu area the time lag between the arrival of first Wagtails and the laying of first eggs was on average one month: April 14—May 13. Most of the population commenced laying on about May 20 (LEINONEN 1973a). Thus, there is a relatively long time lag between spring migration and onset of laying compared with many other migrating passerines (see also ROSENIUS 1926).

Territorial and mating displays were seen already in Wagtail flocks during spring migration. This behaviour continued after the birds had dispersed to territories. Apparently the nest-site was selected several days before nest-building began (LEINONEN 1973a). It is possible that year-old females during this rather long period were able to offset differences which favoured older females, as these arrived at their breeding grounds earlier.

Another factor probably involved in reducing differences between the two age groups with respect to the onset of egg laying is that the two groups nest in different sites. A larger proportion of year-old females than of older ones nested in natural holes. In natural holes nests were smaller and, hence, built within a shorter time than large nests located in artificial sites (LEINONEN 1973a). For instance, in *Delichon urbica* the time used in nest-building influences the timing of egg laying (LIND 1960).

A third factor tending to remove differences in the onset of breeding between the two age groups may be the rather unspecific habitat requirements of the Wagtail (v. HAARTMAN et al. 1971, LEINONEN 1973a). At least among typical hole-nesters competition for nest-sites is mostly resolved in favour of the older individual, and the younger one must spend a longer time finding a nest-site or it does not breed at all (*Phoenicurus phoenicurus*, RUITER 1941; *Parus major*, KLUYVER 1951; *Ficedula hypoleuca*, v. HAARTMAN 1967); alternatively, it must breed in a suboptimal habitat (*Parus major*, KLUYVER & TINBERGEN 1953; *Turdus merula*, SNOW 1958, 1969; *Ficedula hypoleuca*, BERNDT & WINKEL 1967).

Although in the Keuruu area Wagtails mainly breed in man-made habitats in artificial sites, the differences between man-made habitats and natural habitats in most cases were not great. When Wagtails bred on natural shores, they required open terrain and suitable holes for nests. Rather similar open terrain in small patches surrounds the summer-houses typical of the area. In the study area I have rarely seen intensive and long-lasting competition for nest-sites. When a territory became empty, e.g. when Wagtails abandoned their nest, it was not usually reoccupied, as is the case with typical hole-nesting passerines which suffer from lack of suitable nest-sites (e.g. *Ficedula hypoleuca*, v. HAARTMAN 1957).

Clutches of different-aged females were of equal size, in all probability partly because eggs were laid at the same time in both groups. On the whole, differences in the onset of breeding of females of different age as well as in their clutch sizes are not so great in many passerines (e.g. *Ficedula hypoleuca*, BERNDT & WINKEL 1967, v. HAARTMAN 1967; a list given by KLOMP 1970). In this respect passerines seem to follow a cline at one extreme of which is the Wagtail with no differences in the clutch sizes of year-old and older females. There are also other similar passerines, e.g. *Sialia sialis* (LASKEY 1943) and *Alauda arvensis* (DELIUS 1965). Different-aged females of *Passer montanus* begin egg laying at the same time (SEEL 1968).

In the Keuruu area other aspects of breeding biology, in which the two age groups might differ from one another, can better be interpreted by differences in nest-sites than by the age of the female. Breeding success was the same for different-aged females in similar nest-sites, and so were the lengths of incubation and nestling stages.

Why do some year-old females fail to breed? As mentioned in the introduction, young birds of several passerines do not breed owing to the lack of suitable territories or nest-sites (see also e.g. v. HAARTMAN 1971). In the Keuruu area the habitats most attractive to the Wagtails were partly open shores with suitable nest-holes. Such places were not frequent, as in most places the vegetation reached the shoreline, and the edge of the forest was close by (see LEINONEN 1973a). When man settled in the area, he changed the environmental conditions by increasing open areas, and thus increased the breeding Wagtail population. Apparently, however, there are not enough suitable habitats, in relation to the size of the population, as some year-old Wagtails do not breed. In addition, the species is probably genetically adapted in that part of the young birds are not able to breed (v. HAARTMAN 1971). The influence of man has been so short that no complete genetical change making the bird fit for the recent situation has taken place.

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Selostus: **Nuorten ja vanhojen västäräkkinaaraiden pesimisbiologia Keski-Suomessa.**

Yksivuotiaan västäräkkinaaraan voi erottaa vanhemmista yksilöistä harmaan, selän värisen päälaen perusteella. Tätä hyväksi käyttäen on Keski-Suomessa sijaitsevalla Keuruun reitillä selvitetty vv. 1967—72 yksivuotiaiden naaraiden osuutta västäräkkipopulaatiossa ja vertailtu yksivuotiaiden ja vanhempien naaraiden pesimisbiologiaa. Perusaineistona on 309 pesälöytöä.

Yksivuotiaat naaraat saapuvat pesimisalueelle myöhemmin kuin vanhemmat yksilöt. Ne pesivät vanhempia useammin luonnonhabitaateilla ja luonnonkoloissa. Muninnan alkamisessa, pesyekoossa, haudonta- ja poikasvaiheen pituudessa ja poikastuotossa ei kuitenkaan ole eroja ikäryhmien välillä. Kirjoittaja arvelee, että pitkä aika kevätmuuton ja muninnan alkamisen välillä (noin yksi kuukausi) tasoittaa niitä eroja, joita on olemassa vanhempien naaraiden hyväksi niiden tullessa aikaisemmin pesimisalueelle. Muita tasoittavia tekijöitä voivat olla pienemmän pesän rakentaminen luonnonkoloihin kuin tekoainekseen ja pesäpaikkojen runsaus ihmisen toiminnan alaisella rannalla.

Kaikki yksivuotiaat naaraat eivät pesi. Kirjoittaja arvelee syyksi tähän, että alkuperäisessä pesimisympäristössä on ollut puutetta pesäpaikoista. Tällöin osa yksivuotiaista on jättänyt pesimättä. Kulttuurin vaikutus on ollut siksi lyhytaikainen, että se ei ole ehtinyt aiheuttaa täydellistä geneettistä muutosta lintujen sopeutumisessa uusiin olosuhteisiin.

References

BERNDT, R. & WINKEL, W. 1967. Die Gelegegrösse des Trauerschnäppers (Ficedula hypoleuca) in Beziehung zu Ort, Zeit,

Biotop und Alter. Vogelwelt 88:97—136.
BERTHOLD, P. 1964. Über den Fortpflanzungszyklus südwestdeutscher Stare (Sturnus vulgaris L.) und bedingende Faktoren der Brutreife beim Star. Vogelwarte 22:236—275.
BUXTON, J. 1950. The Redstart. — Collins, London.
COULSON, J. C. 1956. Mortality and egg production of the Meadow Pipit with special reference to altitude. Bird Study 2:119—132.
CREUTZ, G. 1955. Der Trauerschnäpper (Muscicapa hypoleuca Pallas): eine Populationsstudie. J. Orn. 96:241—326.
DELIUS, J. D. 1965. A population study of Skylarks, Alauda arvensis. Ibis 107:466—492.
DEMENT'EV, G. P. & GLADKOV, N. A. et al. 1954. Birds of the Soviet Union. V. — "Sovetskaya Nauka", Moskva. English ed. Israel Program for Scientific Translations, Jerusalem.
DROST, R. 1948. Populationsstudien an der Englischen Schafstelze, Motacilla flava flavissima Blyth, auf Helgoland. Vogelwarte 15:18—28.
DUNNETT, G. M. 1955. The breeding of the Starling Sturnus vulgaris in relation to its food supply. Ibis 97:619—662.
ENEMAR, A. 1959. On the determination of the size and composition of a passerine bird population during the breeding season. Vår fågelvärld, Suppl. 2:1—114.
HAARTMAN, L. VON, 1951. Der Trauerfliegenschnäpper. II. Populationsprobleme. Acta Zool. Fenn. 67:1—60.
— 1957. Adaptation in hole-nesting birds. Evolution 11:339—347.
— 1967. Clutch size in the Pied Flycatcher. Proc. XIV Intern. Orn. Congr. 155—164.
— 1971. Population dynamics. In FARNER, D. S. & KING, J. R. (ed.): Avian biology, 1:391—459. — Academic Press, New York.
HAARTMAN, L. VON, HILDÉN, O., LINKOLA, P. & TENOVUO, R. 1971. Pohjolan linnut värikuvin. XI. — Otava, Helsinki.
HAUKIOJA, E. 1970. Clutch size of the Reed Bunting Emberiza schoeniclus. Ornis Fenn. 47:101—135.
KLOMP, H. 1970. The determination of clutch-size in birds. A review. Ardea 58:1—124.
KLUYVER, H. N. 1951. Population ecology of the Great Tit, Parus m. major L. Ardea 39:1—135.
KLUYVER, H. N. & TINBERGEN, L. 1953. Territory and the regulation of density in titmice. Arch. Neerl. Zool. 10:265—289.
LACK, D. 1947. The significance of clutch-size. Ibis 89:302—352.
— 1954. The natural regulation of animal numbers. — Clarendon Press, Oxford.
— 1966. Population studies of birds. — Clarendon Press, Oxford.
LASKEY, A. R. 1943. The nesting of Bluebirds banded as nestlings. Bird-Banding 14: 39—43.
LEINONEN, M. 1973a. On the breeding biology of the White Wagtail Motacilla alba in Central Finland. Ornis Fenn. 50:53—82.
— 1973b. Influence of the habitat and nest site upon the breeding biology of Motacilla a. alba (L.) in Central Finland. Ann. Zool. Fenn. 10:500—506.
LIND, E. A. 1960. Zur Ethologie und Ökologie der Mehlschwalbe, Delichon u. urbica (L.). Ann. Zool. Soc. Vanamo 21:1—123.
LÖHRL, H. 1957. Zur Brutbiologie der Bachstelze. Vogelwelt 78:155—157.
NICE, M. M. 1937. Studies in the life-history of the Song Sparrow. I. A population study of the Song Sparrow. Trans. Linn. Soc., New York 4:1—247.
PERRINS, C. M. 1965. Population fluctuations and clutch-size in the Great Tit, Parus major L. J. Anim. Ecol. 34:601—647.
ROSENIUS, P. 1926. Sveriges fåglar och fågelbon. — Gleerup, Lund.
RUITER, C. J. S. 1941. Waarnemingen omtrent de levenswijze wan de Gekraagde Roodstart, Phoenicurus ph. phoenicurus (L.). Ardea 30:175—214.
SEEL, D. C. 1968. Breeding seasons of the House Sparrow and Tree Sparrow Passer spp. at Oxford. Ibis 110:129—144.
SNOW, D. W. 1958. The breeding of the Blackbird Turdus merula at Oxford. Ibis 100: 1—30.
— 1969. An analysis of breeding success in the Blackbird, Turdus merula. Ardea 57: 163—171.
SUMMERS-SMITH, D. 1963. The House Sparrow. — Collins, London.
TOMPA, F. 1964. Factors determining the numbers of Song Sparrow, Melospiza melodia (Wilson), on Mandarte Island, B. C., Canada. Acta Zool. Fenn. 109:1—73.
WINKEL, W., RICHTER, D. & BERNDT, R. 1970. Über Beziehungen zwischen Farbtyp und Lebensalter männlicher Trauerschnäpper (Ficedula hypoleuca). Vogelwelt 91:161—170.

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