On the Breeding Biology of the White Wagtail *Motacilla alba* in Central Finland

MATTI LEINONEN

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The breeding biology of a White Wagtail population living along a water course area in Central Finland was investigated from 1967 to 1972. Basic material for the study was derived from 309 nests found. Breeding behaviour was studied from hiding huts. Further data were gathered during visits to other nests.

The spring arrival of the Wagtails to the study area was investigated, as well as their dispersal to territories, choice of nest-sites, nest building, and nest constructions in different nest-sites. Egg laying in the study area and in southern Finland were compared. The annual variations in the onset of egg laying were compared with May temperatures. The average clutch size was compared with data from southern Finland, and the clutch sizes in different years were compared. Clutch size shows a seasonal decrease. Clutch sizes in second and repeat clutches were also studied. Hatching and fledging success of the White Wagtail were compared with open nesters and hole nesters. Breeding success was studied also in respect to the time of egg laying and clutch size. Incubation was studied, especially the length of attentive and inattentive periods, the share of sexes in incubation, and the time spent daily in incubation. The length of incubation and nestling stages were determined. Hatching, brooding, feeding, nest sanitation, fledging, and dispersal of the brood were investigated, as well as the weight development of the young. The numbers of second and repeat nests were taken under consideration, especially their occurrence within the same territory as the first one.

1. Introduction

There are many bird species living even in settled areas, and hence easily studied, which have not been studied in any detail yet. Such studies are necessary as they enable general conclusions

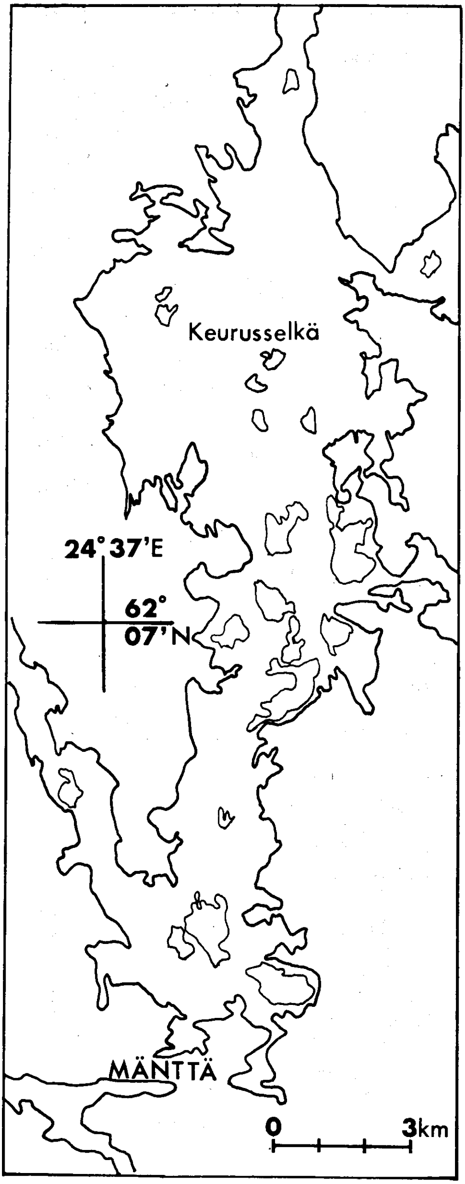

FIG. 1. Study area Keuruu water course area in central Finland.

about factors affecting the breeding in birds (e.g. LACK 1947, 1948, 1954, 1966, 1968; NICE 1957; MARSHALL 1959; KLOMP 1970; PERRINS 1970).

The White Wagtail *Motacilla alba* is one of these common birds, which has been little studied. DROST & SCHÜZ (1940, p. 160) waited for "eine ökologische Erforschung einer geschlossenen Gruppe mit Hilfe des Ringes und sorgfältiger Beobachtung" concerning this species. GLUTZ VON BLOTZHEIM (1962, p. 401) stressed that there are many open questions in the breeding biology of the Wagtail.

Since then the situation has not cleared. The aim of this paper is to report the main results of my studies on the breeding biology and behaviour of a Wagtail population living along a water course in Central Finland.

2. Study area and methods

The study area consists of the water course of Keuruu in Mänttä City and Keuruu Commune (62°02'N—62°12'N and 24°35'E—24°45'E) shown in Fig. 1. In both communes the areas with a dense human population were excluded. The area under consideration covers about 70 sq. km. ranging in east-west direction from 2 to 7 km. and in north-south direction about 21 km. The total length of shore lines, all islands included, is about 230 km.

In this paper the study area is called the Keuruu water course area. The northernmost part of it, covering about 5 sq. km. with a shore line of some 11 km., is called the northern part of Keurusselkä.

The Keuruu water course area is a typical example of a chain of dystrophic lakes in Central Finland. Aquatic vegetation is scarce. Most shores are characterized by cliffs and stones mainly with shrub in between and woods at the back. Only on about a tenth of the shore lines, eutrophic plants are growing. The number of isles and islets totals about 350. Only some little islets are not wooded.

Human settlement in the study area is characterized by solitary houses or small villages. In 1972, about 30 farms and 240 summer residences were situated along the lake shores, there being 1.2 buildings per 1 shoreline km. The numbers of summer-houses are increasing; at present they are least numerous in the central parts of the study area. Further details were given in earlier papers (LEINONEN 1964 a and b).

In 1967—1970, the breeding biology was studied mainly in the northern parts of Keurusselkä. The numbers of breeding Wagtails varied here year to year from 15 to 17 pairs.

In 1971—1972, investigations were carried out throughout the entire study area, where the breeding population consisted of about 165 pairs. The study is based on 309 nests found.

Breeding behaviour was studied mostly in the northern parts of Keurusselkä. The incubation of Wagtails was observed from a hiding hut at 8 nests totalling 210 hours, the nestling stage at 7 nests during 195 hours. During the incubation period in 94 % of the recordings, the observer saw the nest, during the nestling period the corresponding percentage was 72. The recording usually continued from 3 to 5 hours. For each day of the incubation and nestling periods, I have observations of at least 10 hours. My continuous observations concerned first clutches, and all nests were placed in artificial sites. Further data were obtained from visits to other nests.

Apparently, individual birds differ in their behaviour somewhat, although in my opinion the differences were not striking at the nests I studied. Hence, in the following no attention is paid to probable individual differences.

In the field work several schoolboys gave valuable assistance. The field work was made as follows (during some of the days, 2 or 3 groups were working simultaneously):

1967	16.5.—18.7.	60 days
1968	4.5.—29.7.	66 days
1969	3.5.—28.6.	46 days
1970	30.4.—10.7.	66 days
1971	7.5.—30.6.	
	12.7.—23.7.	61 days
1972	2.5.— 6.7.	
	21.7.—24.7.	49 days
	total	348 days

In addition, migration was recorded at Tampere 14—24.4.1967 and 16—25.4.1973.

3. Migration and occupation of territories

The first Wagtails arrived at Mänttä—Keuruu in the middle of April, the dates of first records ranging from April 8 to April 22 with a mean of April 14 ± 0.72 (29 years, 1932—1972). These data were gathered from the archives of A. O. Salonen (unpubl.) and local ornithologists.

According to v. HAARTMAN et al. (1971), the Wagtails arrive on the coast of southern Finland (Turku, Helsinki, about 250 km south of Keuruu), on an average, 8—9 days before the Keuruu area. On the other hand, they arrive at e.g. Lieksa (150 km north of Keuruu) and Oulu (300 km north) only 1—3 days later. Thus the species migrates rapidly through south and central Finland to the boundaries of Lapland, where the migration goes on more slowly according to MERIKALLIO (1954).

According to KIVIRIKKO (1947), BENT (1950), LEHTONEN (1955) and BLAEDEL (1959), males arrive earlier than females. This was confirmed at Tampere.

Among Wagtails observed on the shores of the lakes Näsijärvi and Pyhäjärvi during April 14 through 24, 1967, 58.9 % were males, 14.1 % females, and in the rest the sex was undetermined. The total number of birds recorded was 78. In Iidesjärvi area, on the other hand, during April 18—19, 1967, 38 Wagtails were seen, half of which were males, 5 % females and the rest undetermined as to their sex. Five of the males had already occupied a territory.

In Iidesjärvi area, during April 16—25 1973, the observations of migrating Wagtails were as follows:

	♂	♀	Unsexed	Total
16—19.4	41	5	12	58
20—23.4.	246	96	32	374
24—25.4.	26	14	16	56

(About 20.4. there began a big wave of migration, apparently coinciding with high temperatures. It stopped after some days, with the arrival of cooler air.)

The dates, at which territories were occupied in the Keuruu water course area, could not be determined exactly as the field work was usually not started before the beginning of May. However, some conclusions could be drawn from the following observations.

In 1969, 1970 and 1972, between May 1 and 5, 182 records of Wagtails were made. Of these records, 24.4 % concerned pairs, 31.3 % males and 7.2 % females in their territories. 22.4 % concerned individual Wagtails, who had not yet settled down in the territories, 9.3 % little flocks with two individuals and the rest, only 5.4 % flocks with at least three individuals. Thus, the occurrence of dispersed flocks, characteristic of the migration period (e.g. v. HAARTMAN et al. 1971), had already come to an end and the majority of the Wagtails had settled down in their territories already early in May.

In 1968, in the northern part of Keurusselkä the following was observed. On May 5 eight territories were occupied, on May 7 ten, on May 13 twelve, and on May 18 fifteen, which was the total number of pairs breeding in that area during the year in question.

Thus, a great part of the Wagtail population of the study area, had occupied territories about a fortnight after the first arrival, at a time when the lakes of Keuruu water course were still covered by ice. The mean date of ice melt in the area is 6. 5. according to the Hydrological Office. The rest of the territories were occupied within a few following days. These results are in good accord with those presented by e.g. PEUSSA (1965) and TAKATALO (1966), that in the whole country Wagtail flocks disperse rapidly after migration with the pairs settling down in their territories.

4. Nests and nest-sites

4.1. Choice of nest-site and nest building — Both sexes sought for a suitable nest-site (vgl. SCHWEINSTEIGER 1938, GEYR VON SCHWEPPENBURG 1942, 1943, NETHERSOLE-THOMPSON 1943). According to my observations, the female seemed to be more active. It is, however, difficult to say, whether the female or the male chose the nest-site. The nest-site seemed to be selected several days before the nest building began (also SCHWEINSTEIGER 1938), as birds were more alarmed close to the future nest than otherwhere in the territory, and they flew occasionally to the nest-site without beginning nest building. On the other hand, the pair could begin nest building in 2 or 3 places before finally choosing the nest-site.

According to my observations at 27 nests, the male took part in nest building roughly in every fourth case. At 6 nests, the male was seen to build alone. The male was seen to take part in nest building only in the beginning; at the end of nest building the female worked alone. Several authors have made corresponding observations (WRIGHT 1924, ELLIOTT 1932, 1933, SCHWEINSTEIGER 1938, GEYR VON SCHWEPPENBURG 1942, 1943, DORNBUSCH 1968). However, there seem to be great individual variations which apparently explain the great discrepancies in the opinions of handbooks about the share of sexes in nest building.

On May 15 and 16, 1972, I saw a female building a nest in an attic of a summer residence in the northern part of Keurusselkä. Simultaneously, the male was building another nest in the attic of a nearby bath-house. On May 21, the female laid her first egg in the nest built by herself. The nest built by the male was left uncompleted. But the second clutch of the pair was laid in the nest built by the male (laying started on about 4.7.). I have two other observations of the male building a nest of his own simultaneously with the female. In both cases these nests remained uncompleted. Corresponding records were made by ELLIOTT (1932, 1933) and NETHERSOLE-THOMPSON (1943).

In the study area the nest building took usually from 4 to 7 days. It was determined exactly in only 13 nests, the total range being from 3 to 13 days. Cold weather often interrupted the nest building completely or at least slowed it down.

The nest was completed from 1 to 3 days before the first egg was laid (in 67 % of observations; n = 84). Relatively often, the nest was finished already 4 to 6 days before laying (26 %), rarely from 7 to 10 days before (7 %). The pairs studied by SCHWEINSTEIGER (1938) and LÖHRL (1957) had complete nests 2 days before the first eggs were laid in them. I have not observed any nest building by a Wagtail after the first egg has been laid.

Thus, in the Keuruu water course area, most Wagtails were building their nests at the end of the first third of May. The time lag between the arrival

TABLE 1. Nest-sites of the White Wagtail according to four Finnish studies. H & P = HYTÖNEN & PUTKONEN (1937), v.H = v. HAARTMAN (1969), A = ARO (1971), K = Keuruu water course area (1967—72).

Nest site	Percentage of nests			
	H & P	v.H	A	K
Number of nests	102	670	52	309
A. NATURAL SITES				
Crevices in rocks or below stones	9.8	23.1	34.6	13.6
Holes in trees, stumps or roots	3	4.3	—	2.6
Pits in the ground	3	1.9	—	—
In vegetation	4.9	3.0	1.9	1.3
In heaps of reed thrown up on the shore	—	0.3	—	—
In nests of other birds	+	+	—	+
Total	21.6	32.6	36.5	17.5
B. ARTIFICIAL SITES				
Buildings	14.7	24.0	15.4	57.2
Stone constructions	28.4	7.0	15.4	11.5
Wood constructions	13.7	2.2	9.6	5.6
Metal constructions	+	3.0	3.8	0.3
Heaps and piles	20.6	25.4	19.2	7.9
Ditches and other excavations	+	1.8	—	—
Total	78.4	63.4	63.4	82.5

in the spring and the onset of nest building and egg laying is rather long in the Wagtail.

4.2. *Nest-sites* — HYTÖNEN & PUTKONEN (1937) grouped nest-sites of the Wagtail. The same grouping has been thereafter used by v. HAARTMAN (1969) and ARO (1971), despite the fact that there are obvious difficulties in this grouping. In Table 1, my data are compared with the mentioned ones. (For the details of the grouping, see v. HAARTMAN 1969).

The preference of artificial sites as a nesting place is evident from Table 1. In the Keuruu water course area, 71 % of the nests found in artificial sites were placed in buildings. Apparently, at least the following facts have influenced the preference of man-made habitats as nesting ground of Wagtails in my study area. The human settlement is distributed fairly evenly, although sparsely along the water course. Buildings are surrounded by open terrain which is one of the habitat requirements of the species. In summer-houses and outbuildings, birds often have free access to attics. A house or a group of buildings on an open shore (waterside) apparently forms such a strong stimulus to a Wagtail searching for a nesting site as does the wall of a house to *Delichon urbica* (LIND 1960).

In such artificial places where similar structures repeat themselves, the Wagtails may build multiple nests, as do also, e.g. *Muscicapa striata, Turdus merula* and *T. iliacus.* So, in attics and on ridgepols several nests, finished or unfinished, were found side by side relatively often in places where birds have free entrance to their nest-sites from several directions and where the bird coming with nest material does not see the actual nest-sites when entering

Table 2. Height of nest-site in the Keuruu water course area.

Nest-site	Nest on the ground	Nest above the ground, cm				
		1—99	100—199	200—299	300	N
Buildings	6	19	37	91	23	176
Wood constructions, heaps and piles	12	17	9	2	1	41
Stone constructions	2	30	3	—	—	35
Natural sites	53	1	—	—	—	54
Total	73	67	49	93	24	306

the attic. At most, I have found from 4 to 6 nests. Tyler (1972) has made similar records concerning *Motacilla cinerea.*

In natural habitats Wagtails nest mostly on the ground or close to it. Simultaneously with the change to breed in artificial sites, the Wagtails have changed to breed higher above the ground. In Table 2 the heights of nests in different sites in the Keuruu water course area are given. The most common height, from 2 to 3 m, is the usual height of attics, as measured from the ground.

4.3. *Nest structure* — The Wagtail nest in a natural hole or niche was usually relatively small sized. The frame was built of small twigs, roots, mosses, leaves, dry grasses, bits of bark, etc. The frame was often uncomplete, as it did not totally surround the actual nest. The cup was lined with softer material, e.g. hairs and horsehairs, dry grasses, wool, etc., rarely with feathers (down). The cup was easily loosened from the frame, which was easily distinguished from material surrounding it on the ground.

In artificial sites, most typically in attics, the outer parts of the nest were built by the Wagtail of many, often several hundred, twigs among which there might also be relatively big ones. In addition, other material, e.g. leaves, mosses etc., were brought to this part of the nest. As a result, the framework was both large and high, surrounding the rest of the nest totally. Inside the framework the frame was usually easily loosened from the nest cup. The frame and the cup were, as to their structure in principal, similar as in nests built in natural holes, but often in the preceding more materials were used. In artificial sites Wagtails sometimes made a new nest on the one used a year before, and hence, the nest was still more enlarged.

Ten nests were taken from natural holes after breeding and dried. The dry weights of nest material ranged from 13 to 74 g, the mean weight being 44 g. Ten nests from artificial sites in attics (only nests used during one season were weighed) varied in their dry weights from 47 to 164 g, their mean being 108 g. The differences in nest sizes were essentially due to the great framework in nests situated in artificial sites.

Thus, the Wagtail in natural holes made a small nest consisting of two parts, and in artificial sites with wider space a larger one of three parts. Rosenius (1926), Lövenskiöld (1947) and Corti (1956) mentioned that Wagtail nests vary greatly as to their sizes. *Motacilla capensis* when breeding in shrubs, built a large level base and framework to support the nest (Skead 1954).

5. Egg laying

Wagtails lay one egg a day. Only once have I found an exception: in 1969, in the northern part of Keurusselkä, there was 1 egg in a nest on May 25 at 5.20 o'clock. On May 26 at 18.00, there was still 1 egg, on May 27 at 8.50 2 eggs, and thereafter egg laying took place normally, the sixth egg was laid on May 31. The weather at that time was not unusual, although before the onset of egg laying there were some cold days.

Egg laying took place during morning hours between 3.30 to 6.00. The earliest record was before 3.48 and the last at 5.50 o'clock (n = 33).

If a nest was found during the laying period, the date of the laying of the first egg could be estimated exactly, as Wagtails lay one egg a day. As to nests found within nestling period, the onset of breeding could also be estimated fairly accurately, as the age of nestlings could be calculated on the basis of their weight and plumage development, and the incubation usually takes 12.6 days, at mean (subsection 8.1.). Some single nestlings might be lost, and hence, the dates of the first eggs laid might be biased to a later date. The samples of 1971 and 1972 (n = 134) were tested by comparing direct observations concerning the exact dates of the laying of the first egg with those determined by the above method, and the results were in agreement.

TABLE 3. Start of egg laying. Data from central and south Finland according to v. HAARTMAN 1969.

Time of start	Keuruu water course area 1967—72	Central Finland	South Finland
1—5.5.	—	—	2
6—10.5.	1	1	10
11—15.5.	22	1	22
16—20.5.	70	4	50
21—25.5.	58	6	27
25—30.5.	37	7	11
31.5—4.6.	13	6	9
5—9.6.	8	2	10
10—14.6.	6	—	6
15—19.6.	6	—	9
20—24.6.	5	—	6
25—29.6.	8	1	12
30.6—4.7.	6	1	5
5—9.7.	1	1	1
Total	241	30	180

According to Table 3, the peak of egg laying in the Keuruu water course area was the same as in southern Finland, 16—20.5. (v. HAARTMAN 1969). However, the egg laying seems to begin in southern Finland earlier, the difference is statistically significant (($\chi^2 = 32.46$, f = 13, $P < 0.01$). In the Keuruu water course area, in clutches started between 1 May and 24 June (after the latter date second clutches were possible), 10.2 % of the Wagtail population started their egg laying during the first half of May, while the corresponding figure in southern Finland was 21.0 % (Table 3). The difference is statistically significant (binomial t-test, $P < 0.005$). Along the Keuruu water course area 83.2 % the Wagtails, and in southern Finland 87.7 % began laying in May. The difference is not statistically significant ($P > 0.05$). Positive conclusions about differences in the onset of laying cannot be drawn, as the data from south Finland are derived from a long period, in those of the Keuruu area a little more than half are from two years, 1971 and 1972.

The dates of the first eggs laid in May in the Keuruu area are summarized in the following tabulation:

	First observation	Mean date	n
1967	18	24±1.2	12
1968	10	22±1.4	20
1969	15	22±1.9	9
1970	16	23±1.1	13
1971	11	19±0.5	60
1972	11	21±0.5	74

The annual variations seen in the tabulation are statistically directive (analysis of variance, $P < 0.02$). The results of 1971 and 1972 (Figs. 2 and 3) differ significantly from one another ($\chi^2 = 5.86$, f = 1, $P < 0.01$). In May, 1971, 68.4 % of the clutches were commenced 11—20.5.; in 1972, the corresponding figure was 45.4 %.

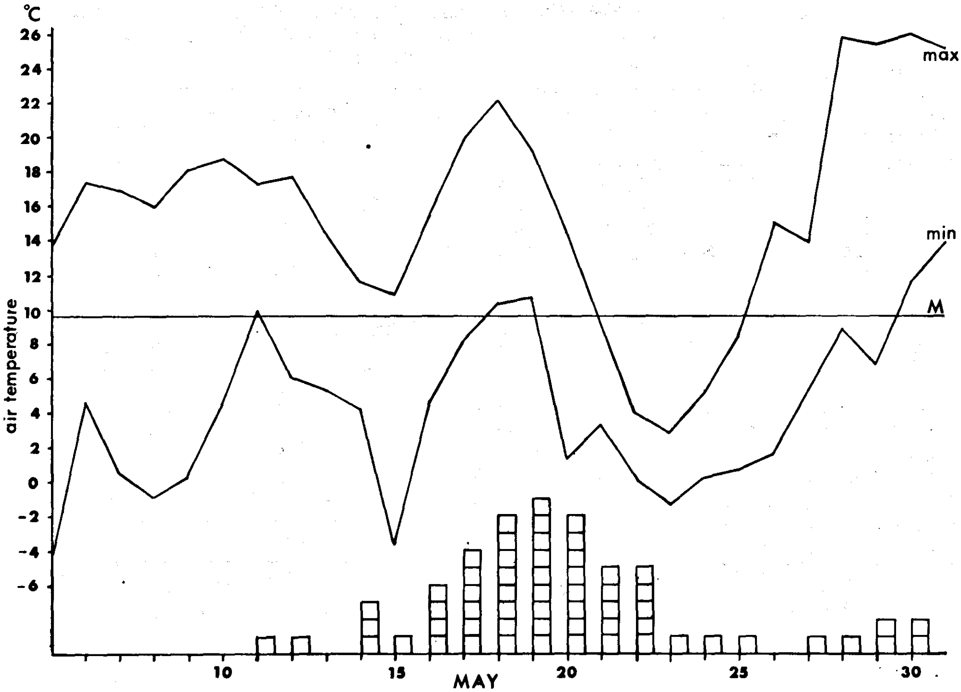

FIG. 2. Start of egg laying and maximum and minimum daily air temperatures in May 1971.

In both years the first pairs laid their first eggs at a time which was preceded by relatively high temperatures about 5 days before. The temperatures had been measured at Kuorevesi Meteorological Station about 25 km south of the Keurusselkä area. In 1971, however, the main part of the population began laying, after a cold period lasting 2—3 days. As a releasing factor, there was apparently the warm period in the beginning of the second third of May, preceding the above mentioned cold days. Especially the minimum temperatures were high at that time. The onset of egg laying in 1972, at a later time than a year before, was likely due to the relatively low temperatures in the second third of May. Variations in the dates on which the first eggs were laid in different nests were greater in 1972, obviously as a result of the fact that temperatures raised slowly and more evenly than during the previous spring. In both years the first pairs started their laying about 10 days earlier than the main part of the population.

From the above, it can be seen that temperatures affected the onset of breeding of Wagtails as it does also that of many other passerines of the temperate zone (e.g. NICE 1937, KENDEIGH 1941, MARSHALL 1949, LACK 1950, 1954, KLUYVER 1951, 1952, DAVIS 1955, MYRES 1955, SNOW 1955, 1958, 1969, NEWTON 1964, SEEL 1969, PERRINS 1970).

6. Clutch size

Clutch size was regarded complete when: (1) it remained the same during two successive visits with a time lag of at least 24 hours in between, (2) it was determined at most 10 days before hatching (the shortest incubation ob-

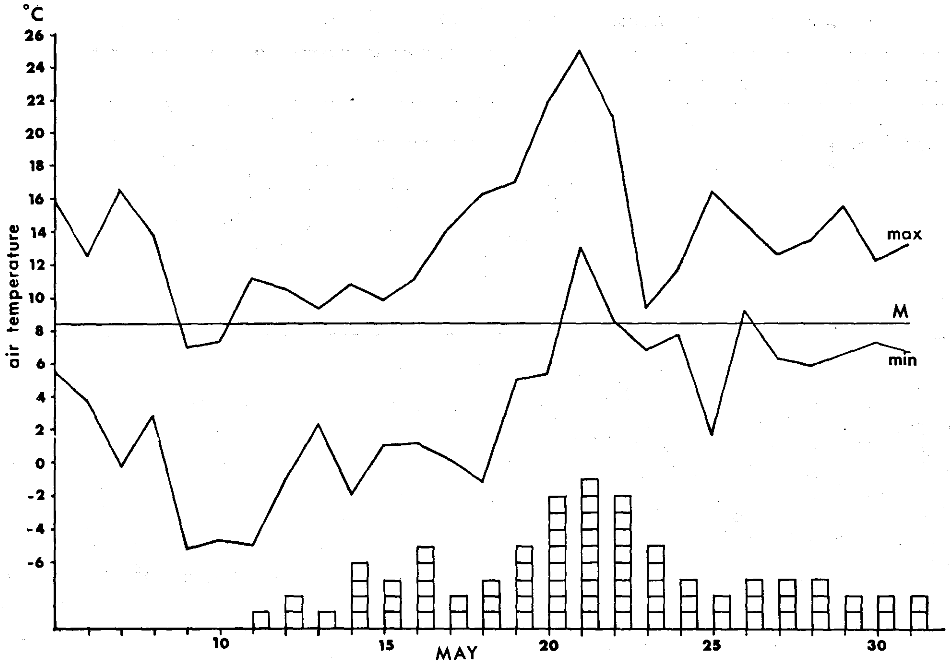

FIG. 3. Start of egg laying and maximum and minimum daily air temperatures in May 1972.

served lasted 11 days, see subsection 8.1.) or (3) when the nest was visited during hatching when hatched young and unhatched eggs were counted (cf. e.g. HILDÉN 1969, HAUKIOJA 1970). Single eggs were recorded to disappear from only two nests, so this did not cause any error in the determination of clutch size.

The size of 210 clutches was determined (Table 4), the mean being 5.7 ± 0.04. According to v. HAARTMAN (1969), the mean was 5.4 ± 0.05. The difference between these figures is statistically significant ($\chi^2 = 11.84$, $f = 5$, $P < 0.05$). Most records of v. HAARTMAN are likely from southern Finland, where the mean of clutches started in May was 5.6 ± 0.08 ($n = 76$). In the Keuruu area, the corresponding mean was 5.8 ± 0.06 ($n = 147$). The difference is statiscally directive ($\chi^2 = 6.93$, $f = 3$, $P < 0.1$). Although the data of my study and those of v. HAARTMAN are from different years, it seems possible that the clutch size of Wagtails increases with increasing latitude, as suggested also by v. HAARTMAN (1969).

TABLE 4. Clutch size. Whole Finland according to v. HAARTMAN 1969.

	Clutch size							
	2	3	4	5	6	7	$\bar{X} \pm S_{\bar{x}}$	N
Keuruu water course area	—	—	11	55	142	2	5.7±0.04	210
Whole Finland	1	5	21	60	119	3	5.4±0.05	209

TABLE 5. Clutch size in the Keuruu water course area 1967—72.

	Clutch size					
	4	5	6	7	$\bar{X}\pm S_{\bar{x}}$	N
1967	2	4	14	—	5.6±0.16	20
1968	—	4	12	1	5.8±0.13	17
1969	—	2	5	—	5.7±0.19	7
1970	—	1	12	—	5.9±0.10	13
1971	3	23	51	1	5.6±0.07	78
1972	6	21	48	—	5.6±0.08	75
Total	11	55	142	2	5.7±0.04	210

According to ARO (1971), the mean size of clutches, started at latest on June 6, was 5.9 ± 0.05 ($n = 36$) in the Helsinki archipelago and according to PUTKONEN (1942) that from Vyborg (Viipuri) area 5.6 (ranging from 4 to 7, $n = 26$). The results of these two samples will not be compared with those of the present investigation or of v. HAARTMAN (1969), as according to v. HAARTMAN (1967) many sources of error (e.g. small sample size, local, annual or seasonal variations) can be eliminated only by having a sample which is large enough.

Variations in the clutch size of the White Wagtail throughout Europe apparently are relatively small. According to GLUTZ v. BLOTZHEIM (1962), the mean of Swiss clutches from April through June is 5.6—5.7 (cf. also e.g. LØVENSKIOLD 1947, DEMENT'ev & GLADKOV 1954, CORTI 1956, WITHERBY et al. 1958).

Clutch sizes of Wagtails in the Keuruu area during the study period are given in Table 5. Data from 1967—70 are scarce, but it is quite obvious that annual variations were minute, differences in the data being not significant. The consistence of the clutch size from year to year likely agrees with the fact that the onset of breeding each spring took place on roughly the same dates (section 5).

Seasonal variation in clutch size is presented in Table 6. Clutch size decreased toward the end of the nesting period as is the rule in Finland in passerine birds (v. HAARTMAN 1971). A clear-cut decrease took place in the middle of June (10—14.6. clutch size 5.8; 15—19.6. 5.3). KLOMP (1970) mentioned about 30 passerines with a similar trend of decreasing clutch size by the season. Among these species there were no species of the genus *Motacilla.* LACK (1947), on the contrary included the whole family Motacillidae among this group.

In the Keuruu area 15 instances were recorded, when, probably, the same Wagtail pair nested in the same territory after losing the first clutch. The mean clutch size for these repeat clutches was 5.1 ± 0.17. The difference between these and clutches started in May is highly significant ($\chi^2 = 16.71$, $f = 3$, $P < 0.001$).

After successful first breeding 17 times the supposedly same pair was observed to renest. The mean size of these second clutches was 4.9 ± 0.05, which

TABLE 6. Clutch size in ten-day periods in the Keuruu water course area 1967—72.

Start of egg laying	Clutch size $\bar{X}\pm S_{\bar{x}}$	N
11—20.5.	5.8±0.06	71
21—30.5.	5.7±0.07	76
31.5.—9.6.	5.6±0.21	14
10—19.6.	5.6±0.18	10
20—29.6.	4.8±0.15	6
30.6.—9.7.	4.6±0.23	6

differs highly from that of the clutches started in May ($\chi^2 = 24.49$, $f = 3$, $P < 0.001$). In repeat broods, 60.0 % of the females laid a smaller clutch than in their first broods; in second broods the corresponding figure was 88.2 %. The rest of the females laid the same number of eggs in both clutches.

Clutch sizes of repeat and second clutches also demonstrate the significance of the date of laying in the formation of clutch size.

7. Hatching success

Losses of eggs are shown in Table 7. The words 'at least' on the second line point to the fact that in this connection, also such nests ($n = 10$) were taken into account, which failed before full clutch size was reached.

TABLE 7. Losses of eggs in the Keuruu water course area 1967—72.

Clutches	207
Eggs in clutches, at least	1147
Unhatched single eggs	45 = 3.9 %
Lost nests	35
Eggs in lost nests	173 = 15.2 %
Total losses of eggs	218 = 19.1 %
Losses of eggs/clutch	1.05

The total number of eggs hatched in the Keuruu area was 80.9 %. ARO (1971) found a similar result, 80.5 %, in the Helsinki archipelago.

The importance of the nesting site in breeding success has been demonstrated by, e.g. NICE (1937, 1957) and LACK (1954). The Wagtails of the Keuruu water course area had a better hatching success than have open nesters and it was not much lower than in true hole nesters.

In some passerines, the hatching success seems to depend on the date of laying. Significant factors may be, e.g. changes in temperature, food or shelter during the breeding season. Seasonal differences in hatching success have been recorded, e.g. in *Muscicapa striata* (SUMMERS-SMITH 1952), *Phylloscopus trochilus* (CRAMP 1955) and *Fringilla coelebs* (NEWTON 1964).

According to Table 8, the number of single unhatched eggs was higher in late clutches than in early ones. The difference between clutches commenced in May and those commenced later is highly significant ($\chi^2 = 10.84$, $f = 1$, $P < 0.001$). The factors causing this effect will be dealt with in a later paper. Also more of the whole clutches were lost during the summer months than in May. Differences are not significant, however.

The clutch size of the Wagtail varied so little that it hardly had any effect on the numbers of young hatching. In clutches with 6 to 7 eggs ($n = 835$ eggs), 4.2 % of the eggs dit not hatch, in clutches with 4 to 5 eggs ($n = 281$), it was correspondingly 3.9 %. This difference is not significant. Neither were there differences in respect to clutch size among nests which totally failed to hatch.

TABLE 8. Losses of eggs as related to date.

Start of egg laying	Unhatched single eggs	Eggs in lost nests	Total losses	Number of eggs
11—30.5.	3.5 %	9.6 %	13.1 %	854
31.5.—19.6.	10.7 %	16.1 %	26.8 %	123
20.6.—9.7.	8.8 %	14.3 %	23.1 %	72

8. Behaviour during incubation

8.1. *Duration of the incubation period* — During the study period, 101 inspections were made of clutches still lacking at least two eggs. During 93 % of the visits, neither of the parents was incubating, and the eggs were cold. Seven times the female was found in the nest in such connection that egg laying was excluded. The male was seen in the nest only once during this period. Three females of the seven were seen on May 21—22, 1971, when weather conditions were unusually bad (Fig. 2), three other observations were also made during rather cool periods, and only one during more or less normal temperature. Obviously, the female tried to shelter her eggs during the laying period, although it has been established (e.g. BALDWIN & KENDEIGH 1932) that low temperatures have no significant influence on unincubated eggs. Apparently there are also individual variations in the start of incubation. The female observed by SCHWEINSTEIGER (1938) was sitting in the nest during morning hours during the laying season. The White Wagtail female of the mixed pair *M. cinerea* x *M. alba* recorded by DORNBUSCH (1968) seemed to incubate two days before the clutch was completed.

The nests where one egg of the complete clutch was lacking were inspected 40 times. At 67.5 % of the inspections, the nest was empty and the eggs were cold. During this period the female was seen to incubate 12 times, the male only once. According to observations made from hiding huts, periods on the eggs at that time were short, and the rhythm of incubation irregular, the nest being empty for about 80 % of the day (Figs. 5, 6, 7). At that time, the eggs are rather brooded than incubated (RYVES 1943, SWANBERG 1950). According to KENDEIGH (1963), brooding only insignificantly contributes to the development of the embryo, as the temperature of the egg does not increase during brooding.

The duration of the incubation period in the Keuruu water course area from the laying of the last egg to the hatching of the last young is shown in the following tabulation.

Length of incubation in days	11	12	13	14	15	16	n	$\bar{X} \pm S_{\bar{x}}$
No. of clutches	14	23	17	11	3	1	69	12.6±0.15

The duration of the incubation period among the Wagtails of the Keuruu area was influenced by the date of laying (Table 9). The incubation period shor-

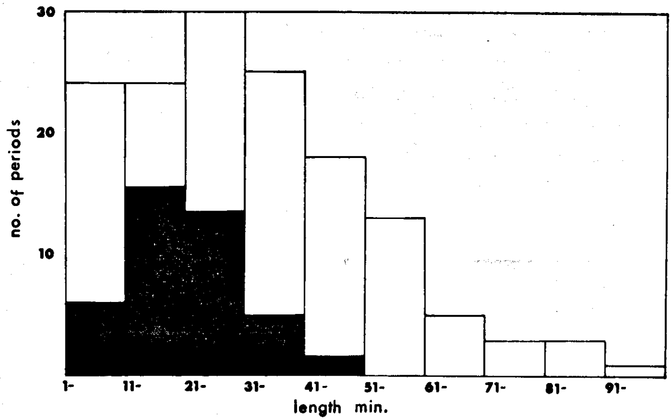

FIG. 4. Length of periods of incubation. White column = female, black column = male.

TABLE 9. Length of incubation as related to date.

Start of egg laying	Length of incubation in days								Mean air temperature
	11	12	13	14	15	16	$\bar{X} \pm S_{\bar{x}}$	N	
1—20.5.	2	7	9	4	2	—	13.3±0.24	24	11.6°C
21—30.5.	6	11	8	7	1	1	12.7±0.22	34	13.6°C.
31.5.—9.7.	6	5	—	—	—	—	11.5±0.16	11	14.6°C

tened 0.03 day per day of the breeding season. Possibly the temperature causes the shortening of the length of the incubation period, as temperatures rise with the advancing of the nest season. This was shown by v. HAARTMAN (1956) in the case of *Ficedula hypoleuca* (see also DAVIS 1955, KENDEIGH 1963, EL-WAILLY 1966).

Clutches with 6 eggs (n = 53) were incubated on an average 12.6 ± 0.14 days, those with 4 to 5 eggs (n = 16) 12.3 ± 0.28 days. This small material does not indicate that clutch size had an effect on the duration of incubation.

8.2. *Share of sexes in incubation* — The female Wagtail gets an incubation patch on her belly, when incubation begins. This physiological change does not take place in the male. BAILEY (1952), DAVIS (1955) and SKUTCH (1957) demonstrated that among some passerines, the male in spite of lacking the incubation patch takes part in incubation. His incubation has value at least in reducing heat losses during the absence of the female. According to handbooks, the males of the genus *Motacilla*, incubate, although less than the females. Among some bird species the male, when beginning to incubate, raises feathers on his belly in order to obtain better contact with the eggs. So behaved the male of *Motacilla flava* (SMITH 1950), and according to my observations, also the White Wagtail.

Records about the sharing by sexes in incubation during the day are summarized in the following tabulation. (The female spends the night on the nest.) Records were made at observation nests (210 hours) and during visits to other nests (n = 537 observations of complete clutches).

	Observation nests	Other nests
Female incubated	61.3 %	49.6 %
Male „	24.0 %	17.5 %
Sex undetermined	—	11.7 %
No incubation	14.7 %	21.2 %

The greater number of incubation pauses in the data gathered on visits may partly be due to the fact that the incubating bird may have left unnoticed.

About a fourth of all incubation taking place during the daytime was done by the male (cf. LÖHRL 1957). In this respect, the White Wagtail of the Keuruu area does not differ from related species (*M. flava,* SMITH 1950; *M. cinerea,* EGGEBRECHT 1939, BOASE 1952, TYLER 1972; *M. clara,* MOREAU 1949; *M. capensis,* SKEAD 1954).

8.3. *Length of attentive and inattentive periods* — In full clutches, periods on the nest before hatching lasted on an average 27.7 min. The attentive periods of other *Motacilla* species have been of approximately the same length, although individual variations and small samples in most studies restrict possibilities for further conclusions (*M. flava,* SMITH 1950; *M. cinerea,* EGGEBRECHT 1939, TYLER 1972; *M. clara,* MOREAU 1949).

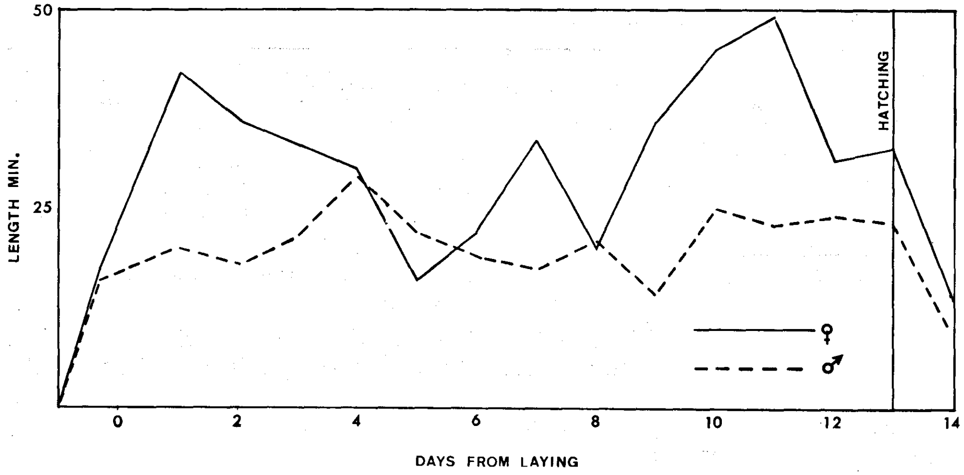

FIG. 5. Length of spells of incubation in female and male during incubation period.

The periods on the nest were, on average, 31.9 min. in the female Wagtail, 21.3 min. in the male. Further data are seen in Fig. 4.

According to LIND (1960) *Delichon urbica* has very short attentive periods. He assumed that insectivorous song birds usually have short attentive periods, because "sie ihre Nahrung schnell verdauen und infolgedessen bald wieder hungrig sind" (p. 77). Apparently this holds true in respect to such insectivores as e.g. Swallows which feed on 'light' insects. *Motacilla*-species feed on different, often large-sized insects which likely are not digested in a short time, as attentive periods in the whole genus are rather long and sometimes may last more than an hour (EGGEBRECHT 1939, MOREAU 1949, SMITH 1950, BUXTON 1954). According to NICE (1943), the average attentive periods of 10 passerines, was 29.8 min, which is almost the same as that of the Wagtail in the Keuruu area. The attentive periods of the Wagtail last longer than e.g. those of *Passer domesticus* (SUMMERS—SMITH 1963, DECKERT 1969) which feeds on miscellaneous items, and roughly as long as those of *Phoenicurus phoenicurus* (BUXTON 1950) and of *Melospiza melodia* (NICE 1943).

According to data given in Fig. 5, lengths of attentive periods of the Wagtail were typical from the very beginning of incubation, and did not clearly change, when incubation progressed. These results agree with those of MOREAU (1949) concerning *M. clara*. Attentive periods were at their shortest in the middle of incubation. No significant changes in the lengths of attentive periods took place from morning to evening during the whole incubation.

The mean for incubation pauses in complete clutches before hatching began, was 7.5 min. The pair observed by LÖHRL (1957) had pauses of 6.5 min, on an average. Most pauses were caused only by the change of the incubating bird. When pauses were grouped in periods of 5 minutes (1—5, 6—10 etc), it was established that the numbers of pauses decreased continuously with increase in time. Pauses of more than half an hour were recorded under undisturbed conditions only a few times. According to MOREAU (1949), *M. clara* does not usually have incubation pauses

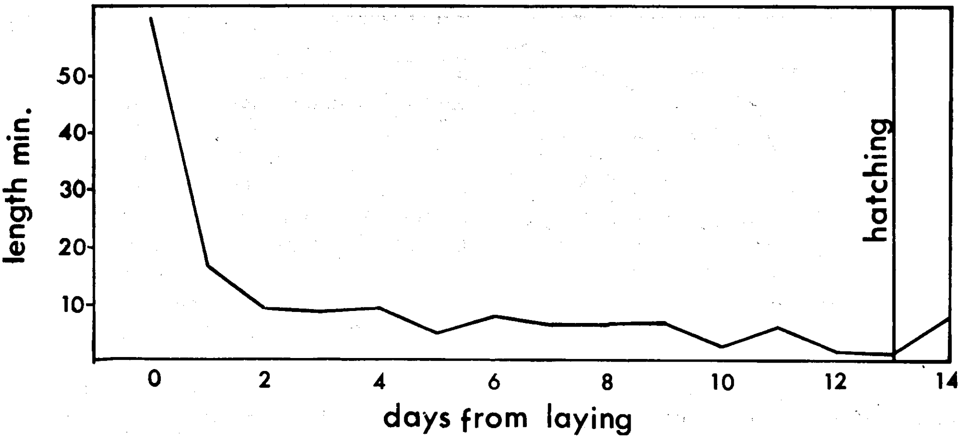

FIG. 6. Variation in length of incubation pauses during incubation period.

which exceed 15 min. NICE (1943) gave the average length of incubation pauses in ten passerines as 8.5 min.

The lengths of incubation pauses changed, however, when incubation advanced (Fig. 6). During the first days of incubation, pauses were long, but thereafter they shortened close to the mean, and towards the end of incubation to below the mean.

8.4. *The time used daily for incubation* — The Wagtails of the Keuruu area incubated 85.3 % of the day time, on an average, according to records made at nests under direct observation, and 78.8 % according to records made during visits to nests. The mean of ten passerine species studied by NICE (1943) was 75 %. The Wagtail, thus, is rather intensive in incubation as compared with many song birds (see also SKUTCH, 1962). The pair recorded by LÖHRL (1957) incubated 70 % of the observation period. *M. clara,* according to MOREAU (1949), incubated during the first clutch from 66 to 90 %, during the second clutch from 54 to 77 % of the day time.

The time spent in incubation changed, however, when incubation progressed (Fig. 7). The behaviour during incubation developes as a rule gradually (e.g. KENDEIGH 1963, WEEDEN 1966). A distinct change in the drive takes place in the beginning of incubation. This probably explains the great increase in the time used for incubation during the first days of incubation. After the 10th day of incubation, adults mostly changed their incubation turn without any pauses. MOREAU (1949) observed rather similar development in the incubation of *M. clara,* in which adult birds changed their incubation turns without pauses during the two last days before hatching.

Summarizing, the increase in the time used for incubation was not due to changes in the lengths of periods on the nest (Fig. 5), but in the shortening of the incubation pauses (Fig. 6).

8.5. *Other aspects of the behaviour during incubation* — When nesting above the ground, the White Wagtail of the Keuruu area arriving at the nest, first flew close to it. If not disturbed, it often then jumped down on the ground, there running a couple of metres and thereafter flying up to the nest almost vertically. LÖHRL (1957) also

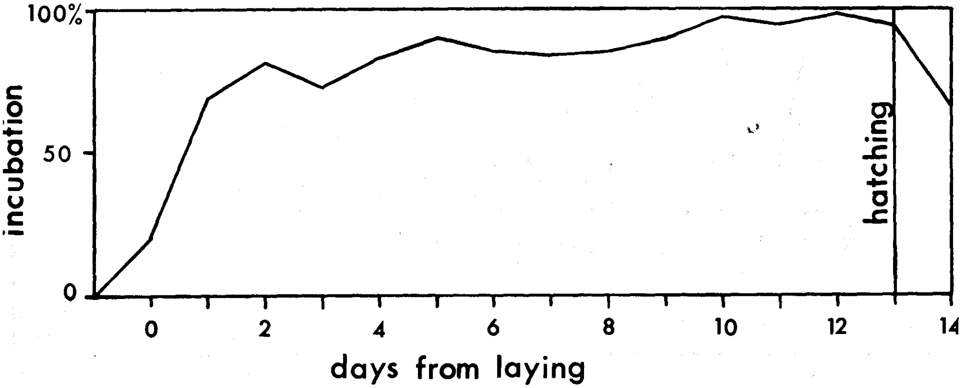

FIG. 7. Percentage of time of incubation in day time during incubation period.

observed that the adults ran to the nest. According to SCHÜCKING (1963), *M. cinerea* behaves similarly. In this behaviour the White Wagtail resembles related species that nest exclusively on the ground as, e.g. *M. flava* (SMITH 1950), and also other passerines nesting on the ground as e.g. *Emberiza citrinella* (WALLGREN 1956).

In artificial sites, the Wagtail has changed to nest above the ground, but the original habit of running to the nest has so far remained unchanged.

On the contrary, when White Wagtails nesting above the ground left the nest, they usually flew directly from it. The same was recorded by LÖHRL (1957). The Yellow Wagtail runs some metres when leaving its nest (SMITH 1950). This is the habit of the White Wagtail, too, when it nests on the ground.

When disturbed during incubation, the White Wagtail usually left the nest by jumping down, and then moving just above the ground or running on the ground for a short distance. Then the bird flew higher up and disappeared. Also this behaviour seems to refer to the nesting habits in original nesting sites.

Six times I have seen a disturbed female during incubation behave as follows. She flew up from the nest silently and arose with shivering wings high up. Then she dropped down on the ground and toddled there in stiff position with wings raised obliquely upward and shivering. Then her stiffness decreased and the bird slowly let the wings fall down. Thereafter she twittered once and flew away. Apparently the bird showed distraction display (NICE 1943, ARMSTRONG 1956, LACK 1965).

When the Wagtail incubated, it — especially the female — slept fairly often. The sleeping was interrupted, however, every now and then, and the bird was startled. During the day sleeping lasted on an average 3.9 min. at a time. Mostly the awakening was not caused by any stimulus recognizable to the observer. Probably the species has a typical habit of controlling the environment with short intervals during incubation which apparently has survival value.

When the nest was situated in a place from where the incubating bird did not see out, the bird coming to incubate usually twittered once or twice before entering the nest, usually at a fixed place. If, on the other hand, the nest was so placed that the incubating bird was able to see the relieving one, the latter was in most cases silent when arriving at the nest. Probably the sound is a signal to the incubating bird to leave the nest. In *M. cinerea* similar behaviour has been observed (TYLER 1972). The pair observed by LÖHRL (1957) behaved correspondingly; when one bird called outside the nest, the other left it. The bird leaving the nest usually moved out silently.

The bird, which did not incubate, rarely visited the nest. Three times when such a visit was recorded, the incubating bird left the nest, but it returned, as the other left the nest. During the incubation period, I have never seen anything in the way of display or copulation. This was also the case with White Wagtails observed by SCHWEINSTEIGER (1938) and LÖHRL (1957), and in *M. clara* by MOREAU (1949), in *M. flava* by SMITH (1950), and in *M. capensis* by SKEAD (1954). As a matter of fact, during incubation the Wagtail mates have rather little contact with one another.

After the tenth day of incubation (in one case earlier) there are records of the incubating bird being unwilling to go away when the relieving bird arrived at the nest. LÖHRL (1957) mentions that the male once threatened the female coming to the nest, and drove her away. I have once observed how both adults came to the nest simultaneously and began to fight, whereby the female drove the male away from the nest.

9. **Fledging success**

Table 10 shows the numbers of young that have survived from hatching to fledging. A young has been regarded as fledged when it reached an age of at least 11 days, which is the shortest nestling period observed. At this age, at least part of young birds apparently survive e.g. predatory attacks by escaping from the nest.

TABLE 10. Losses of nestlings in the Keuruu water course area 1967—72.

Broods	153
Nestlings in broods	832
Lost single nestlings	72= 8.6 %
Lost nests	24
Nestlings in lost nests	120=14.4 %
Total losses	192=23.0 %
Losses of nestlings/brood	1.26

Of the young hatched, 77 % reached the fledging stage. The fledging success is of the same magnitude in *M. cinerea* (TYLER 1972). The proportion of young fledged was higher than among open nesters as a rule, but slightly lower than among true hole nesters and swallows nesting in buildings (NICE 1937, 1957, v. HAARTMAN 1951, LACK 1954).

In passerines, losses of young may change during the breeding season. Factors affecting this may be e.g. changes in climate, food or shelter conditions, or in numbers of predators. Seasonal differences in fledging success have been established, e.g. in *Erithacus rubecula* (LACK 1948), *Parus major* and *P. caeruleus* (GIBB 1950, KLUYVER 1951), *Carduelis chloris* (MONK 1954), *Phylloscopus trochilus* (CRAMP 1955), some species of *Turdus* (SNOW 1955, 1958), *Fringilla coelebs* (NEWTON 1964).

The losses of young Wagtails during different times of the breeding season are presented in Table 11. There were no seasonal differences as to losses of

TABLE 11. Losses of nestlings as related to date.

Start of egg laying	Lost single nestlings	Nestlings in lost nests	Total losses	Number of nestlings
11—30.5.	6.7 %	16.3 %	23.0 %	714
31.5.—9.7.	12.3 %	12.3 %	24.6 %	114

total broods, but the losses of single nestlings increased towards the end of the breeding season. The difference is statistically directive ($\chi^2 = 3.61$, $f = 1$, $P < 0.1$). The affecting factors will be dealt with in a further paper.

Brood size varied so little that it hardly had any effect on the fledging success. From broods with 6 to 7 young (510 pull.) losses of single young amounted to 7.5 %, from broods with 3 to 5 young (322 pull.) also 7.5 %. Nor were there any differences, if only clutches commenced in May were considered.

The hatching success in different-sized broods is seen from the following tabulation.

No. of eggs	Young hatched	No. of nests	% hatched
6	4.91	138	81.8
5	4.20	49	84.8
4	3.18	9	79.5

Young fledged are seen from the next tabulation

No. of hatched young	Fledged young	Nests	% fledged
6	4.70	85	78.3
5	3.67	53	75.4
4	3.08	12	77.0

Thus, in the Wagtail of the Keuruu area, the largest brood size produced the largest number of hatched and fledged young. The brood size did not have any significant effect on the breeding success, roughly the same percentage fledged from different-sized broods.

According to Table 12, human beings caused more losses during the egg period than during nestling time. Egg clutches were destroyed rather easily in early summer, when human activities at summer-houses became more lively. Nests with young were more easily detected, and after detection were usually actively protected. Among animal predators in the Keuruu area the most important was the Crow. This species did not, however, enter buildings. The second in importance was the Squirrel which often is seen searching in buildings. The snakes are rare in the study area. Twice nestlings were ill probably due to too high temperatures and once due to some kind of poisoning. Adult birds disappeared relatively often, most probably due to attacks of birds of prey.

TABLE 12. Causes of nest failure in different phases of breeding cycle.

	Building period	Incubation period	Nestling period
Nest abandoned by parents	2	7	3
Animal predator	—	11	9
Destroyed by man	3	10	3
Disturbed by man	—	7	3
Disease	—	—	5
Cause unknown	—	—	1
Total	5	35	24

10. **Nestling stage**

10.1. *Length of nestling period* — The length of the nestling period as delimited from the hatching of the last young to the fledging of the last young is seen from the following tabulation:

Length in days	11	12	13	14	15	16	n	$\bar{X} \pm S_{\bar{x}}$
No. of broods	1	4	12	21	5	1	44	13.7±0.47

According to v. HAARTMAN (1969), the most common length of nestling period was 14 days, which also was the mean given by him and ARO (1971).

In order to test whether the length of the nestling period is influenced by brood size, the following method was applied. All clutches commenced within May were considered. The mean duration of the period was in the b/6 ($n = 27$) 13.7 ± 0.20 days, in the b/5 and b/4 (n = 12) 13.8 ± 0.20 days. Thus, the period was evidently not influenced by brood size.

10.2. *Hatching* — In addition to the nests under direct observation, hatching was recorded also in 11 other nests. Occasional visits to nests were made 21 times during hatching.

Hatching usually took about 12 hours; hatching which began in the morning, was finished by the evening. The longest time required for hatching was almost 40 hours. Great differences between the weights of young of the same brood at an age of some days (Fig. 12) indicate that incubation had started before the last egg was laid, and hence, that hatching had taken a longer time than usual.

Already about two days before hatching started, the adult birds, in nests under direct observation, began to peck the nest bottom, apparently searching for eggshells. As these were still lacking, the reaction was released by substitute objects, viz. light-coloured leaves and bits of bark.

During hatching, especially in its beginning, the female usually took care of the brood alone. The female incubated at this time, brooded the hatching young, took away bits of eggshell and brought food to the young. Only once the male was seen to brood the hatching young. Also in *M. cinerea* (EGGEBRECHT 1939) and *M. boarula* (ROSHARDT 1927) the female was in the nest during hatching. The behaviour of the Wagtail female at that time is shown in Figs. 6, 7, 8, 9, and 11.

The female behaved similarly for relatively long periods after hatching, i.e. when brooding the nestlings. The male's behaviour changed distinctly on the day of hatching. In most cases he did not incubate after hatching had begun. Neither did he brood the young nor feed them or the female, at least, during the first hours after hatching. He could visit the nest, but usually he flew away immediately. He remained within the territory and twittered eagerly. ROSHARDT (1927) described the behaviour of the male of *M. boarula* which resembled greatly that of the White Wagtail.

10.3. *Brooding* — During the hatching and the first days of nestling life, the female spent much time in the nest brooding. Also the females of *M. flava* and *M. boarula,* according to SMITH (1950) and to ROSHARDT (1927) respectively, brood their young at that time.

The time spent in brooding changed by the development of the young as shown in Fig. 8. During the day of hatching, the female has been off the nest 37 % of the day time, on average. This time of being off the nest is rather high, due to the fact that at that time the female alone usually took care of the brood. During the second day, when the male took part in feeding, the female was absent from the nest 21 %, on average, of the day time. After the 6th day, the female was observed to brood the young only during the night.

The shortening of the time spent by the female in brooding the young is due to attentive periods getting shorter as the young grow up (Fig. 9). On the day of hatching, the female brooded, on average, 9.2 min. at a time. This figure is rather low, as the male at that time did not take care of the brood. On the second day brooding periods were at their longest, the average being 16.7 min. at a time. Thereafter they became shorter. MOREAU (1949) made corresponding observation on *M. clara.*

As brooding periods shortened, their numbers also decreased. During the two first days, the female brooded 3.5 times an hour, and 12.6 minutes at a time. On the other hand, during the 5th and

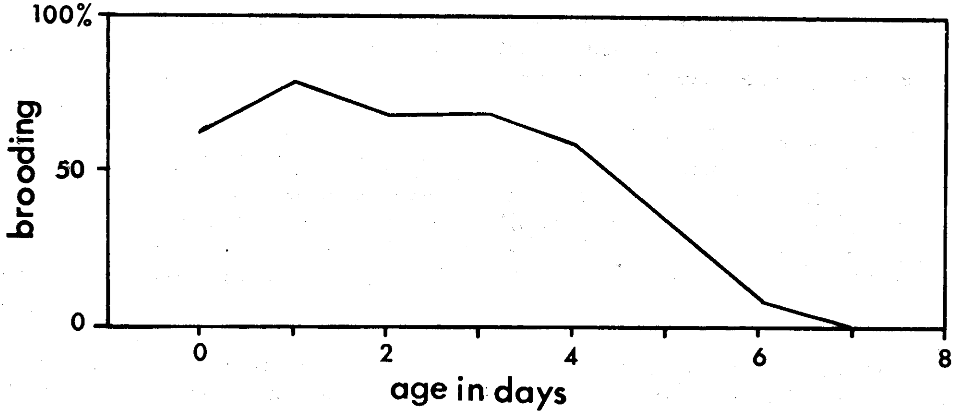

FIG. 8. Percentage of time of brooding in day time during nestling period.

6th days, she brooded 1.6 times an hour, on an average, 5.0 minutes at a time.

10.4. *Feeding* — Both parents feed the young. Feeding began on the day of hatching (although the male did not usually feed yet at that time), as it did in *M. cinerea* (EGGEBRECHT 1939).

Feedings grew more numerous with the growing of the young (Fig. 11). Despite the fact that individual differences exist, the figure gives a general view of the amount of feeding in the Wagtail. Observations made about the feeding of other species of the genus *Motacilla* do not significantly differ from those made in the Keuruu area; although some of these species have been observed during short periods only (*M. boarula,* ROSHARDT 1927; *M. clara,* MOREAU 1949; *M. flava,* SMITH 1950; *M. cinerea,* SCHIFFERLI 1961; SCHÜCKING 1963; *M. cinerea* x *M. alba,* DORNBUSCH 1968).

As shown earlier, (p. 66) the Wagtail spent longer times on the nest than many other insectivorous song birds. It also fed the young at longer intervals than, e.g. *Phylloscopus trochilus* (KUUSISTO 1941), *Phoenicurus phoenicurus* (RUITER 1941, BUXTON 1950), *Ficedula hypoleuca* (v. HAARTMAN 1954), *Parus major, Parus caeruleus* and *Erithacus rubecula* (PFEIFER & KEIL 1962) and *Delichon urbica* (LIND 1960).

The share of both sexes varied depending on the age of the young. At the age of 3 days, the brood was fed almost exclusively by the male (Fig. 10). At the nest shown in Fig. 10 the male fed 6.8 times an hour, the female only 0.8 times an hour at that time. When the brood was aged 8 days, the male fed on an average 5.9 times an hour, the female 6.3 times.

The above mentioned results apply to a single pair, only. The share of the sexes in the feeding of the young during the total nestling period is shown in Fig. 11. The peculiarities in the feeding in the beginning of the nestling stage are due to the fact that the female spent so long a time in brooding, and therefore the male fed more. It is not so easy to say why the feeding intensity of the male decreased at the end of the nestling stage. Considering the nestling period as a whole, both sexes fed roughly equally.

The rhythm of feeding in the White Wagtails (Fig. 10) was similar to that found in other song birds, e.g. in *Phylloscopus trochilus,* (KUUSISTO 1941),

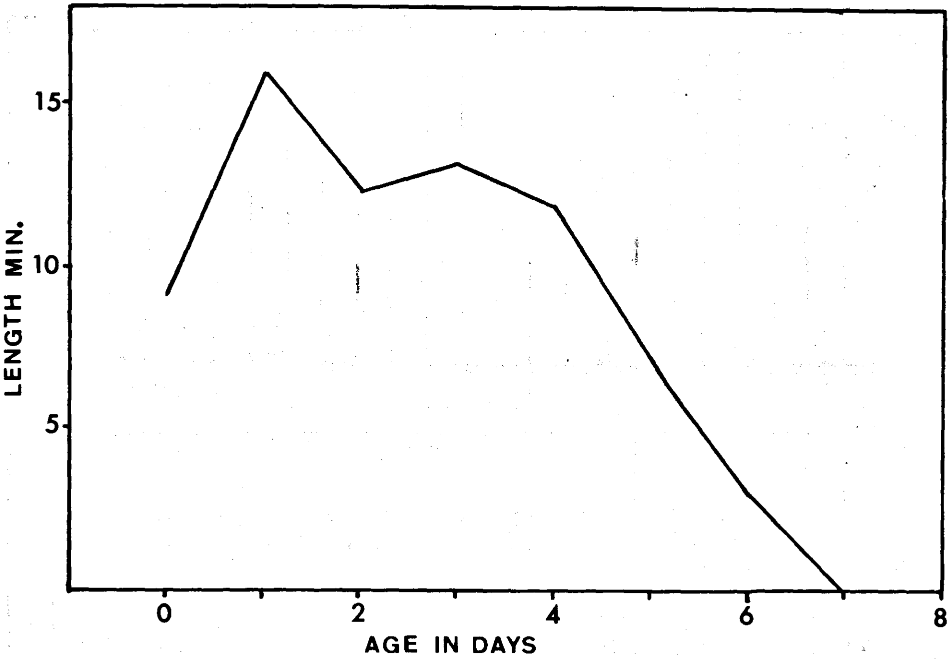

FIG. 9. Length of spells of brooding during nestling season.

in *Phoenicurus phoenicurus* (BOËTIUS 1949) and in *Delichon urbica* (LIND 1960). Probably the rhythm is caused by variations in the hunger and satiety of the young (v. HAARTMAN 1953, LIND 1960). When the young Wagtail called anxiously, the female either remained in the nest brooding or increased her feeding intensity. The following may serve as an example of the effect of begging young on the behaviour of the female:

At a nest in the northern part of Keurusselkä with young aged 6 days, the female fed at 20.54 a'clock. Thereafter she began to prepare herself to spend the night in the nest. The last feeding by the male took place at 20.40. As the young continued to whimper, the female rose up, looked at the young for a while, then aimed to fly away, but returned to the nest. As the calling of the young still continued, she began to feed them at 21.05. After six feedings the brood quieted down, and at 22.30 began to spend the night.

When the female brooded, the male fed her; the younger the nestlings, the more often he fed. During the first two days he usually gave all the food to the female, who herself ate part of it, and then fed the young with the rest. Gradually, the male began to feed the young directly. After the sixth day, when the female ceased to brood the young, both adult birds fed the young independently.

When the female was sitting on the nest, and the male came to feed the brood, the young started to beg as soon as the female arose. In other cases, the bird coming to feed called a few times either while running towards the nest or while at the nest. The young reacted to this calling. Sometimes the adult bird had to call several times. If a young let its head sink down while feeding still continued, the calling of the feeding bird usually immediately stimulated it to

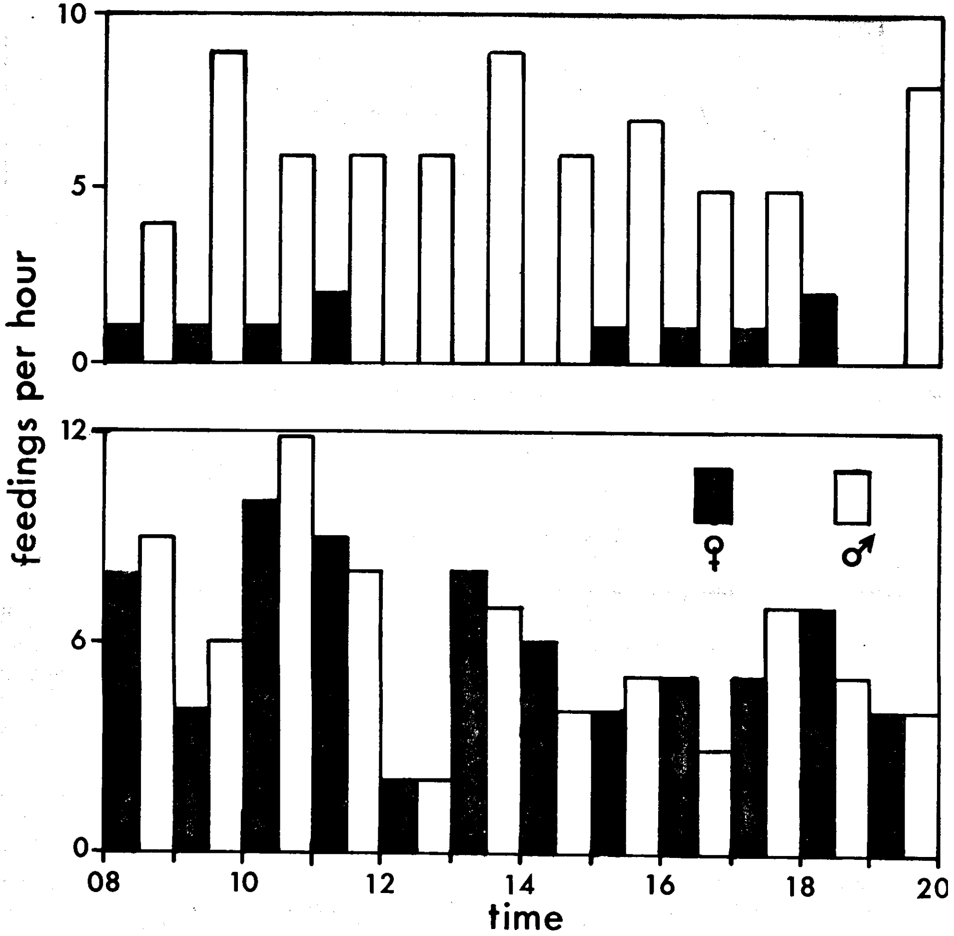

FIG. 10. Share of female and male in feeding. Upper figure: age of nestlings 3 days. Lower figure: age of nestlings 8 days.

straighten up. Older young reacted either to the sight of the approaching bird or to the darkening of the nest hole or nest opening. LÖHRL (1957) described the behaviour of the young in similar manner.

10.5. *Nest sanitation, dead nestlings* — Egg shells were carried away immediately after hatching. During the first days faeces were eaten by the parents. During the first two days they all were swallowed, during the third day about half of them were carried away, and from the fourth day they were almost regularly carried away from the nest. Sporadic eating of faeces was recorded even on the fifth day. At the nest of *M. cinerea* faeces were eaten only during the first day after hatching (SCHIFFERLI 1961).

Often the parents remained waiting for defecation by the young, especially when the previous carrying of faeces had taken place a rather long time ago. If no excrements were voided, the adult

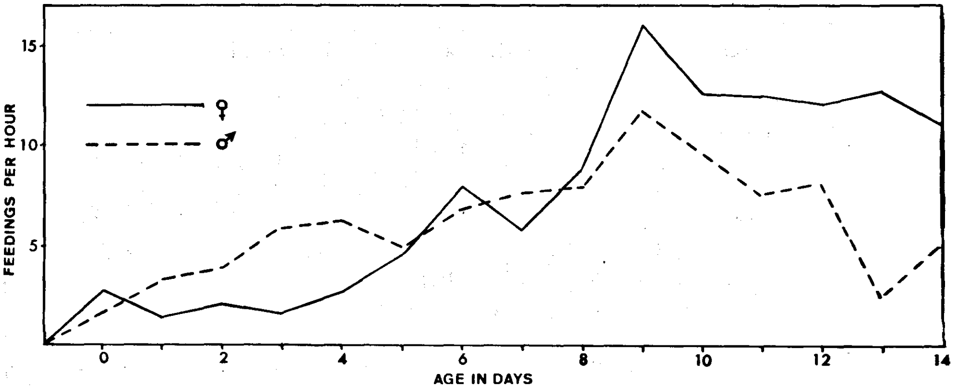

FIG. 11. Feeding rhythm of female and male during nestling period.

pecked the cloacal parts of the young in order to get it to defecate, and it often managed in this. If no voiding took place, the carrying reaction was sometimes released by a substitute object as some light-coloured objects from the nest or from its close vicinity.

At the age of 6 to 7 days, defecating young rised their hind parts towards the edge of the nest, where the adult bird picked faeces in its bill immediately when these appeared. At the age of 10 days, the young defecated over the nest edge, when this was possible in respect to space. Many times the nest was, however, soiled with faeces during the last part of the nestling period.

If a young did not gape, the adult kept pushing it with the bill. If the young was continuously quiet, the adult carried it out by holding it from the neck. At least till the age of 5 to 6 days, dead young would be carried away from the nest. Young which were older were too heavy (Fig. 12) to be carried away. At least twice a dead decaying young which was left in the nest, caused the sickness and the death of the whole brood.

10.6. *Growth of nestlings* — In Fig. 12 the growth of Wagtail nestlings is shown. The data consists of 710 weighings on a letter scale (Swiss scale of Pesola type). The degree of accuracy in weighing was 0.5 gram. Although the weight development of young birds may vary rather markedly both individually and in respect to different broods (e.g. RICKLEFS 1968), the main features of the weight development of the nestling Wagtail are shown in Fig. 12.

The weight loss seen after the tenth day is likely due to the fact that the development of the young at that time culminates. The young begin to move outside the nest, if there is space for this, the plumage has developed all over the body and thermoregulation is in operation (BALDWIN & KENDEIGH 1932, ROYAMA 1966, SEEL 1970). They call in similar manner as fledged young Wagtails do and they defecate over the nest edge. Thus, weight losses can be caused by increasing moving activities.

10.7. *Post-fledging season* — According to observations made in the Keuruu area, the young did not leave their nest while unable to fly, although they might move in the close vicinity of the nest, if space enables this. But if disturbed, the young were prone to leave the nest prematurely, at the age of 12 to 13

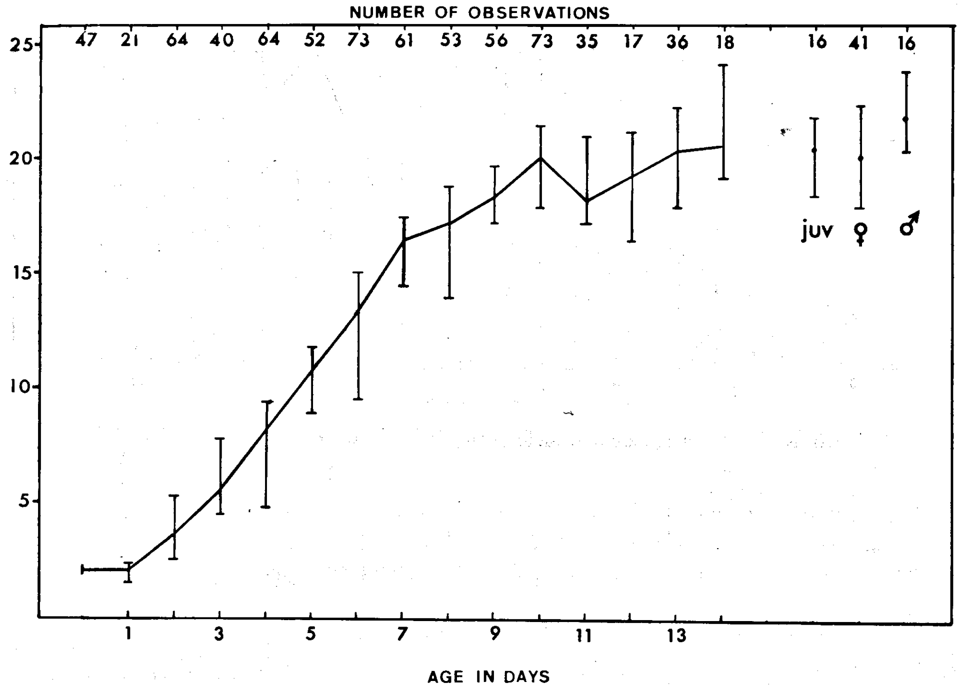

FIG. 12. Weight of nestlings during nestling period.

days, sometimes even at the age of 11 days. The immediate cause of leaving the nest when disturbed was that one or a few of the young gave the alarm call with strong voice. The brood remained in the nest so long as all the young were quiet. Similar observations were reported e.g. by GIBB (1950) and LÖHRL (1950).

When the young left their nest undisturbed, both parents were present. When the first young flew from the nest, they both followed it eagerly twittering to the place where it landed, whereafter one of them returned to the nest. Now one adult might twitter outside the nest apparently tempting other young to leave the nest. According to SMITH (1950), adult birds of *M. flava* in the corresponding situation behaved more passively.

Usually the young left the nest at short intervals. LACK (1948) stated that the fledged young stimulate the other members of the brood. However, there might be a time lag af a day between the departures of the first and the last young. Longer intervals than two days have not been recorded.

Usually the brood remained in the proximity of the nest for the first day after fledging. Thereafter it dispersed farther away from the nest, forming, in the Keuruu area, typical moving chains along shorelines. Parents fly to and fro between the ends of the chain feeding the young. In the evening the brood assembled together for roosting. TYLER (1972) assumed that the young of *M. cinerea* do not leave the vicinity of their nest until a fortnight after fledging.

The brood kept together after fledging usually from 4 to 7 days. I have, however, seen adult birds feeding their young still on the ninth day after fledging. Zidbäck (in a letter in Palmén's Archives) mentioned that Wagtails may feed their young 10—11 days after fledging. According to Boase (1952), *M. cinerea* fed the young at least during 4 days after fledging.

The male has been seen to feed fledged young more often than the female. Most observations concern, however, first broods. This difference between the sexes probably depends on the fact that at least some of the females become ready for laying their second clutches. Armstrong (1965) placed the Wagtail among those bird species whose males take care of fledged young while the females get ready to lay a new clutch.

11. Length of the nesting; repeat and second clutches

The length of the nesting as delimited from the laying of the first egg to the fledging of the last young was 30.9±0.94 days, ranging from 27 to 35 days (n = 38). The total length of the nesting is summarized in the following tabulation:

(1) nest building usually	from	4	to	7	days
(2) time lag before egg laying	»	1	»	3	»
(3) time from the first egg to the fledging of the last young	„	27	„	35	„
(4) feeding of fledged young usually	„	4	„	7	„
	„	36	„	52	„

Most pairs of the Wagtail population living in the Keuruu area began their egg laying after 10th May (Table 3). Thus, the onset of laying the second clutch could take place at the end of June or in the beginning of July. In 16 instances, the interval between the laying of the first egg of the first brood and that of the second brood could be determined. It averaged 40.1±1.04 days, the range of variation being from 35 to 50 days. v. Haartman (1969) gives three records: 36, 37, and 44 days. Thus, there is a mean time lag of 9.2 days (40.1—30.9) between the fledging of the first brood and the laying of the first egg in the second one. This figure corresponds well to data given earlier (Palmén 1912, Rosenius 1926, Schweinsteiger 1938, Mester 1957).

In Central Europe the Wagtail, as a rule, has a second clutch (e.g. Corti 1956, Glutz von Blotzheim 1962). In Finland some of the pairs lay a second clutch, more often so in southern than in northern Finland (e.g. v. Haartman 1969). In 1971 and 1972, I checked all territories of the total study area twice at the time when the second clutches could be expected to be laid. In 1971, four pairs, and in 1972, 12 pairs laid a second clutch in the same territory as the first one. Thus, only few pairs in the Keuruu area laid a second clutch. Similar observations were made in the northern parts of Keurusselkä, where I spent my summers also during other days than those mentioned on p. 55 as working days.

The total number of records of second broods laid in the same territory as the first one was 20 in the Keuruu area. Among these clutches, four were found in the same nest as the first one, and eight nests were in the same building or construction at a distance varying from 0.3 to 2.0 m from the first nest. The rest of the second nests were placed in a new site within the same territory. In placing the second nests, *M. cinerea* behaved rather similarly (Tyler 1972).

Either during nest building, egg, or nestling stage 64 nests were lost. Of these pairs, 49 abandoned their territories. According to Drost (1948), *M. flava* behaved similarly. In 15 cases only, the White Wagtail pair built a repeat nest in the same territory as the first one. One of these was built upon the destroyed nest, four nests were close to the previous ones in the same building or construction, and the rest, ten nests, in a new place in the same territory. Once a pair built three successive nests in the same territory; breeding succeeded in the last one. When the first clutch was lost during the nestling period, it was repeated only in two cases in the same territory. The shortest building of a repeat nest was observed in a case when the first nest was deserted during egg laying. Thus, the new nest was ready and the first egg laid only two days after the destruction of the first nest. The longest intervals were found when the nests were lost during the nestling period, viz. from 7 to 10 days. The earliest date of commencement of a repeat clutch was May 22, and the latest one June 27.

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Selostus: **Västäräkin pesimisbiologia Keski-Suomessa.**

Tutkimuksessa selvitetään Keski-Suomessa sijaitsevan Keuruun reitin (kuva 1) västäräkkipopulaation pesimisbiologiaa ja pesimiskäyttäytymistä vv. 1967—72. Keuruun reitti on tyypillinen sisäsuomalainen dystrofinen reittijärvi. Rannoilla on 1.2 asumusta rantakilometriä kohden. Tutkimusalueen ala on noin 70 km², rantaviivan pituus noin 230 km. Pesimisbiologisen aineiston muodostaa 309 pesälöytöä. Pesimiskäyttäytymistä on seurattu haudontavaiheessa kahdeksalla pesällä yhteensä 210 tunnin ajan, poikasvaiheessa seitsemällä pesällä yhteensä 195 tunnin ajan. Lisämateriaalia on saatu muiden pesällä käyntien yhteydessä.

Ensimmäiset västäräkit ovat saapuneet tutkimusalueelle vv. 1932—72 keskimäärin 14.4. Koiraat saapuvat naaraita aikaisemmin. Suuri osa populaatiosta on asettunut reviireille toukokuun ensimmäisellä kolmanneksella.

Koiras on osallistunut pesän rakentamiseen noin neljänneksessä kaikista havainnoista. Naaras näyttää viimeistelevän pesän. Rakentaminen kestää tavallisesti 4—7 vrk ja se loppuu useimmiten 1—3 vrk ennen ensimmäistä munaa. 82.5 % Keuruun reitin pesistä sijaitsee tekoaineksessa (taulukko 1). Asiaan vaikuttanee rannassa olevien rakennusten ja rakennelmien ja niihin liittyvien avointen habitaattien toimiminen voimakkaana ärsykkeenä pesäpaikkaa etsivälle västäräkille. Pesän sijoittaminen tekoainekseen on johtanut myös pesän nousuun alkuperäisistä maakoloista huomattavasti ylemmäksi, Keuruun reitillä useimmiten 2—3 m:n korkeuteen (taulukko 2). Luonnonkoloissa pesä on pieni kaksiosainen, tekoaineksessa väljissä tiloissa huomattavasti suurempi, kolmiosainen.

Muninta alkaa Keuruun reitillä hieman myöhemmin kuin Etelä-Suomessa (v. HAARTMAN 1969), vaikka muninnan huippu sattuukin samalle ajanjaksolle, 16—20.5. Asiaan vaikuttanevat erityisesti toukokuun lämpötilat, toisen kolmanneksen ajalle sattuvat korkeat lämpötilat laukaisevat helposti munimisen (kuvat 2 ja 3).

Keuruun reitin västäräkkien keskimääräinen munaluku, 5.7, on suurempi kuin Etelä-Suomen (5.4) (v. HAARTMAN 1969). Ilmeisesti munaluku nousee pohjoiseen päin. Toisaalta Sveitsissä on munaluku kuitenkin huhti—kesäkuussa 5.6—5.7 (GLUTZ VON BLOTZHEIM 1962). Munaluku ei ole vaihdellut merkittävästi vuosittain (taulukko 5). Munaluku vähenee pesimiskauden loppua kohden (taulukko 6). Uusintapesyeissä munaluku on ollut 5.1, toisissa pesyeissä 4.9, mitkä kumpikin ovat merkitsevästi pienempiä kuin munaluku toukokussa aloitetuissa pesyeissä.

80.9 % munituista västäräkin munista kuoriutuu (taulukko 7). Tulos on suurempi kuin avopesijöillä eikä jää paljon jälkeen tyypillisistä kolopesijöistä. Kuoriutumattomien munien määrä lisääntyy pesimiskauden loppua kohden (taulukko 8). Kuoriutuneiden munien osuus ei riipu pesyekoosta.

Haudonta alkaa tavallisesti viimeisen munan munimisesta. Keskimääräinen haudonta-aika on ollut 12.6 vrk. Haudonta-aika lyhenee pesimiskauden loppua kohden (taulukko 9). Syynä on mahdollisesti lisääntyvä lämpö. Pesyekoko ei vaikuta haudonta-ajan pituuteen.

Koiras hautoo noin neljänneksen päiväajan haudontamäärästä. Naaras hautoo keskimäärin 31.9 min, koiras 21.3 min kerrallaan (kuva 4). Haudontajaksojen pituus ei vaihtele päivän aikana eikä muutu yhdensuuntaisesti haudontavaiheen aikana (kuva 5). Haudontataukojen pituus on keskimäärin ollut 7.5 min. Haudontaan kuluu tarkkailupesien mukaan 85.3 %, muun aineiston mukaan 78.8 % päiväajasta. Laji hautoo siis hyvin tiiviisti. Haudontaan käytetty aika lisääntyy haudonnan edistyessä (kuva 7), mikä johtuu haudontataukojen lyhenemisestä (kuva 6).

77 % kuoriutuneista västäräkin poikasista selviää lentokykyisiksi (taulukko 10). Tulos on parempi kuin avopesijöillä ja huonompi kuin kolopesijöillä. Yksittäisiä poikasia tuhoutuu enemmän myöhemmin kesällä (taulukko 11). Pesyekoko ei vaikuta lentokykyisten poikasten määrään. Pesätuhojen syitä selvitellään taulukossa 12.

Pesäpoikasvaiheen pituus on ollut keskimäärin 13.7 vrk. Asiaan ei vaikuta munimisaika eikä pesyekoko. Kuoriutuminen kestää tavallisesti noin 0.5 vrk. Kuoriutumisen aikana, varsinkin sen alkupuolella, naaras huolehtii yksin poikueesta: lämmittää, ruokkii ja vie munankuoret. Naaras lämmittää poikasia kuudenteen päivään asti. Lämmittämiseen käytetty aika lyhenee ja naaraan lämmittämisjaksojen pituus pienenee toisen päivän jälkeen (kuvat 8 ja 9). Poikasten ruokkimistiheys nousee kymmenenteen päivään asti, väheten sen jälkeen (kuva 11). Koiraan ja naaraan osuus ruokinnasta on erilainen poikueen iästä riippuen (kuva 10). Emot syövät poikasten ulosteet kahden ensimmäisen päivän aikana, neljännestä päivästä alkaen ne miltei aina viedään pesästä pois. Poikasten painonkehitystä selvitetään kuvassa 12. Poikaset eivät lähde lentokyvyttöminä pesästä. Pesästä lähdön jälkeen ei ole havaittu poikueen palaamista pesään. Poikue pysyttelee yhdessä pesästä lähdön jälkeen tavallisesti 4—7 vrk.

Västäräkin pesimiseen ensimmäisestä munasta viimeisen poikasen lähtöön kuluu keskimäärin 30.9 vrk. Aikaväli ensimmäisen pesyeen ensimmäisen munan ja toisen pesyeen ensimmäisen munan välillä on ollut keskimäärin 40.1 vrk. Vain harvoilla pareilla on toinen pesye. Niistä 64 parista, joiden pesä tuhoutui 49 hylkäsi reviirin.

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