The White Wagtail *Motacilla alba* as a semi-hole-nester

MATTI LEINONEN

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In a White Wagtail population investigated by the author along a water course in Central Finland, 82.5 % of the Wagtails nested in artificial sites in more or less sheltered holes, usually at a height of 2 to 3 m above the ground. 17.5 % of the pairs studied bred in nest sites in holes or niches on the ground. Because the Wagtail cannot be placed among typical hole-nesters or open-nesters, either when breeding in man-made habitats or in natural ones, it may be called a semi-hole-nester. The nestling stage in the Wagtail was probably a little longer than in related open-nesters. The weight development curve of nestlings differed both from typical open-nesters and from hole-nesters, lying somewhere between the two. In other respects the breeding behaviour of the species resembled that of open-nesters, and, therefore, the species can be regarded as a secondary hole-nester. However, nesting success, which was not affected by the nest-site (natural sites/artificial sites), was 57.9 %, which lies very close to the mean for hole-nesters, as given by NICE (1957) viz. 60 %. Breeding in man-made habitats can hardly have been long enough to influence the breeding biology of the species through evolution. On the other hand, the non-specific habitat and nest site requirements of the species has led, in the Wagtail, to a preference for man-made habitats. Nesting success in such sites was rather good compared with related open-nesters.

1. Introduction

Most species in the Motacillidae family are open-nesters. However, some of the species, e.g. *Motacilla alba, M. cinerea and Anthus spinoletta most often breed* in a hole or niche. My own observations in Central Finland in the Keuruu area show that 82.5 % of the Wagtail nests were built in artificial sites, mostly in more or less sheltered holes at a height of 2 to 3 m above the ground. The remainder, 17.5 %, were placed in natural holes or niches on the ground (LEINONEN 1973a, Tables 1 and 2). This change in the Wagtail's nesting habits is matched by corresponding changes in other species, e.g. in *Phoenicurus phoenicurus* (SIIVONEN 1935, 1936, BUXTON 1950) from natural holes lying on the ground to artificial sites higher up, in *Delichon urbica* from natural nest-sites to almost exclusively artificial sites (LIND 1960) and in *Erithacus rubecula* from natural to man-made habitats (LACK 1965).

According to DAVIS (1955) the nest-site may reflect the evolution of a species. v. HAARTMAN (1957) grouped hole-nesters on the basis of their evolution into four groups: order, family, generic and specific ranks. As for the Wagtail, it apparently ought to be placed somewhere between the generic and specific ranks. In the former group most species of a genus breed in holes; in the latter most species of the genus breed in the open with a few species nesting in holes.

In this paper, the breeding biology and the breeding behaviour of the Wagtail is discussed. The *point de départ* is the fact that most Wagtail pairs

breeding on the shores of water courses similar to the Keuruu area nest in well-protected artificial sites above the ground, although in other respects the species seems to be a secondary hole-nester according to v. HAARTMAN's (1957) classification.

2. The Wagtail as a semi-hole-nester

Nest-site. — In natural habitats the Wagtail nest is usually placed in crevices in rocks or below stones, in holes in trees, stumps or roots, in niches on river banks, etc. In artificial sites nests are built in many kinds of places, similar to those of other bird species nesting in niches (HILDÉN & LINKOLA 1962, v. HAARTMAN et al. 1971). Different nest-sites have been treated earlier (LEINONEN 1973a, Table 1).

However, the Wagtail does not accept just any hole in artificial sites as its nesting-site. For example, the species has not, with a few more or less obscure exceptions, bred in nest-boxes built for small passerines which were in good condition according to several sources (in addition to my own observations, data gathered from ornithological literature, nest-cards of the Finnish Society of Sciences, and Palmen's and Merikallio's files). In the nest-card material there are more than 20 records of Wagtails breeding in nest-boxes, but about ten of these were open boxes placed on house walls, and the remainder mainly boxes that had been partly destroyed. Both HILDÉN & LINKOLA (1962 p. 195) and LIND & PEIPONEN (1963) mentioned that the species is able to breed in large nest-boxes. In the Keuruu area I have found a Wagtail in a nest-box intended for a Goldeneye (*Bucephala clangula*).

BRANDER (1959) gave instructions for an open nest-box suitable also for the Wagtail. In the spring of 1966 I set up 50 such open boxes along the shores of my study area. The boxes were of five different types with 10 boxes of each type. The boxes differed from each other in respect to their inner dimensions and in the sizes of the entrances. The boxes were placed in terrain close to the shoreline near the ground in stumps or roots, at the base of a tree, or among stones. In none of the boxes did breeding occur in 1966—1972.

The most distinct difference between a nest-box and a natural hole used by Wagtails as a nest-site is that the former clearly projects from its background; the latter, on the other hand, is inset. Additional factors contributing to the avoidance of nest-boxes may be that the entrances are too narrow, and the nest-boxes too small and restricted with the result that nest-boxes are darker than natural holes. In natural circumstances box-nesting species usually use holes made by Woodpeckers or make them themselves in decaying trees. In habitats originally occupied by Wagtails such natural nest-sites are rare, and competition for them is strong. It is therefore likely that they do not satisfy the demands of the nest-site stimuli of the species. Apparently undamaged nest-boxes used by small passerines as well as open-boxes distinctly projecting from their artificial backgrounds do not agree with the innate nest-site requirements of the Wagtail, although among nest-sites otherwise used by the species there is great variation. The avoidance of nest-boxes as nesting sites probably also shows that suitable nest-sites are found in abundance in such areas as the Keuruu area.

As to the opposite breeding habit, nesting in the open, it seems that there exist no clear-cut limits. A lot of records of Wagtails breeding among vegetation in the open can be found from the literature. There are especially many observations concerning Wagtails breeding under junipers in the archipelago. In Finnish nest-card material there are some fifty such records. Also from the

TABLE 1. Clutch sizes of some Motacillidae species in Finland according to V. HAARTMAN et al. 1971.

	Range	Mean	N
Anthus cervinus	4—7	5.5	35
A. pratensis	4—6	5.2	61
A. trivialis	2—6	4.7	103
A. spinoletta	3—6	4.8	10
Motacilla alba	2—7	5.4	209
M. flava	3—9	5.7	87

Keuruu area there are observations of nesting among vegetation. The nest may be totally without shelter (RÄSÄNEN 1957; among nest-card material there are three records). According to GARLING (1941) a Wagtail nest found on the ground resembled closely a nest of a Pipit or a Lark. WÖRNER (1933) said that a nest found under a grass hummock resembled a Lark nest. On the other hand, the nests of the ground-breeding species in Motacillidae are often very well hidden among vegetation or under some projecting features (see e.g. DEMENT'EV, GLADKOV et al. 1954, WITHERBY et al. 1958, BLAEDEL 1959, GLUTZ VON BLOTZHEIM 1962, HILDÉN & LINKOLA 1962, V. HAARTMAN et al. 1971).

Clutch size. — The clutch size of hole-nesters is on average larger than that of open-nesters. Semi-hole-nesters form an intermediate group in regard to their clutch size (LACK 1948, 1954, 1968, V. HAARTMAN 1957). However, among Motacillidae, this general trend in clutch sizes does not seem to hold true, as seen from Table 1. However, in the data given by LACK (1948) clutch size in the genus *Motacilla* (5.5) is somewhat larger than in the genus *Anthus* (4.5—5.3).

Incubation. — V. HAARTMAN (1957) and LACK (1968) stated that the incubation and nestling stages take longer among hole-nesters than among open-nesters. Species nesting in niches or roofed nests (LACK 1968, p. 172) form an intermediate group. In the Keuruu area incubation of the Wagtail usually took 12 days, the mean being 12.6 days and range of variation was from 11 to 16 days (n = 69 clutches; LEINONEN 1973a). These observations agree well with those obtained in other parts of Finland. The nest-site did not influence the duration of the incubation period (LEINONEN 1973c). In Table 2 the length of the incubation period of the Wagtail is compared with some other species belonging to the same family. As can be seen, the incubation of the Wagtail does not last longer than in other species. On the contrary, *Anthus spinoletta* probably incubates longer than other species, a fact that can also be seen from the table presented by LACK (1948) for the same bird family.

Nestling stage. — The nestling period in the Keuruu area lasted from 11 to 16 days, being most often 14 days and averaging 13.7 days (n = 44; LEINONEN 1973a). This record also agrees well with observations from other places in Finland. The nest-site had no influence upon the length of the nestling stage (LEINONEN 1973c). According to Table 2 the nestling stages of *Anthus pratensis* and *A. trivialis* are short (e.g. according to the data of GLUTZ VON BLOTZHEIM 1962) compared with other species. In both species the young leave their nest when still unable to fly. On the other hand, the nestling stage lasted longer in the Wagtail and *A. spinoletta,* both of which breed most often in some kind of hole. (The nestling stage is fairly long also in *M. capensis,* which often breeds rather high up e.g. in shrubs, lasting from 14 to 18 days according to SKEAD 1954). The nestling stages of *M. flava* and *M. cinerea* are longer than those of most *Anthus*-species, but shorter than the nestling stages of the Wagtail and *A. spinoletta.* According to TYLER (1972) *M. cinerea* seems to breed among vegetation or in very low holes more often than the Wagtail, resembling in this respect *M. flava.*

TABLE 2. Duration of incubation and nestling period in some Motacillidae species according to some handbooks. v.H = v. HAARTMÅN et al. 1971; D & G = DEMENT'EV & GLADKOV 1954; W = WITHERBY et al. 1958; G = GLUTZ VON BLOTZHEIM 1962.

	Incubation, days				Nestling, days			
	v.H	D & G	W	G	v.H	D & G	W	G
A. pratensis	12—15	13	13—14	13	12—14	—	13—14	12—14
$\bar{x}$	13.9							
A. trivialis	—	10—11	13—14	12—14	—	9—10	12—13	10—14
A. spinoletta	—	14—15	14	13—16	—	—	—	15
M. alba	10—14.5	12	12	12—14	11—16	11	14	13—16
$\bar{x}$				13.1				14.4
M. flava	12—14	13	13—14	12—13	—	—	11	12—13
M. cinerea	—	11—14	13—14	11—13	—	12—14	12	12—13

From the above it may be concluded that among Motacillidae species nesting in the open have shorter nestling stages than species nesting in holes. *M. flava* and *M. cinerea,* which are intermediate as to their nesting sites, are also intermediate as to the lengths of their nestling stages. However, there is some controversy in the data of Table 2 but the data given in handbooks are often relatively general. v. HAARTMAN (1957) stated that within the genus *Motacilla* such differences apparently do not exist, but "the nestling period is somewhat prolonged in *M. alba*" (p. 346). Also, according to LACK (1948), the Wagtail has a longer nestling period than two other *Motacilla* species. Due to lack of data concerning the nesting habits of other Finnish *Motacilla* species, it is impossible to make further comparisons with Finnish investigations.

Nesting success. — Generally hole nesters have better nesting success than species nesting in the open (NICE 1937, 1957, v. HAARTMAN 1951, LACK 1954). In the Keuruu area hatching success in the Wagtail was 80.9 %, fledging success on the other hand 77 % (LEINONEN 1973a). According to these figures the Wagtail resembles true hole nesters and species nesting in buildings more than species nesting in the open.

Nesting success as a whole was 57.9 % (LEINONEN 1973a) in the Keuruu area. NICE (1957) estimated that altricial birds of the northern temperate zone had, on average, a nesting success of some 60 %, those birds with partially enclosed nests about 50 % and those nesting in the open some 40 %. For the middle group figures ranged from 44 to 63 %. LACK (1954) concluded that the nesting success of open-nesting passerines averaged 45 % while that of hole-nesting passerines was 67 %. The nesting success of the Wagtails breeding in the Keuruu area was therefore fairly high and close to the nesting success of true hole-nesters or species breeding in buildings. The difference was great, when comparison was made with related *Motacilla cinerea,* 42 % (TYLER 1972) or *Anthus pratensis,* 43 % (COULSON 1956).

Fledging. — Wagtail young did not usually leave their nest before being able to fly (LEINONEN 1973a). Apparently the young have better shelter and survive better in their nests both in artificial and natural sites than when moving, flightless, outside them. In this respect the Wagtail resembles hole-nesters (NICE 1943, LACK 1954, v. HAARTMAN 1957, ROYAMA 1966). However, when disturbed, the brood may leave the nest prematurely, even when almost unable to fly (LEINONEN 1973a). According to my observations the young did not always leave their nest immediately when disturbed, but did so after a while. For example, sometimes when a brood

already able to fly was touched, it first remained quite quietly in the nest, but if the observer soon returned to the nest, it was observed that the whole brood or some of the young had left the nest. A few times I recorded that even only looking at the young at close quarters resulted in the young leaving their nest soon afterwards. This kind of behaviour indicates affinity with open-nesters.

A similar indication is also provided by the behaviour of females when young which had fledged but still remained near the nest were disturbed. In this situation the adults were very anxious, running low with their legs bent and with wings and tail dragging along the ground immediately in front of the observer, as if hurt; the related pipits behave in a very similar manner.

Growth of nestlings. — The weight development of nestlings has been described earlier (LEINONEN 1973a, Fig. 12). In true hole-nesters there is a decrease in weight development before fledging, while in open-nesters weight increases until fledging (v. HAARTMAN 1954, 1957, RICKLEFS 1968). In the Wagtail a decrease in weight development after the tenth day was recorded, but thereafter weight again increased to the earlier level, wich was close to the adult weight.

ROYAMA (1966) found that semi-hole-nesters are intermediate between the hole-nesters and open-nesters also in the weight development of their young. RICKLEFS (1968) suggested that weight development is genetically determined and is adapted to environmental conditions, especially to predators. The weight development of the Wagtail seems to be between the weight development of open and hole-nesting species.

Observations concerning breeding behaviour. — It has already been stated that when leaving and approaching its nest a Wagtail behaved, especially if disturbed, in a similar manner to related species nesting in the open on the ground (see also LEINONEN 1973a, pp. 67—68).

According to v. HAARTMAN (1957) it is keen competition for nest-sites that has led to several behavioural adaptations among hole-nesters. In the following some records concerning the Wagtail are given.

When the male in the spring arrived at the breeding ground, he occupied a territory. The nest-site was not chosen until pairing had taken place, and usually the choice was made by both mates together or the female did it alone selecting the actual nest-site from among several alternative sites (LEINONEN 1973a). True hole-nesters, however, first occupy a nest-site. For them territory is primarily a matter of a suitable nesting-site; habitat as such is less important. Unlike true hole-nesting species, the Wagtail did not concentrate its territory defence or its display to the immediate vicinity of its nest-site, nor did the display activities of the male contain any ritualized ceremonies of showing the nest-site to the female. When a territory was abandoned, it was not usually re-occupied as is the case with true hole-nesters. Even what seemed to be a good territory could remain empty for the rest of breeding season in the Keuruu area, although the pair originally occupying it had already abandoned it in May. In the Keuruu area I never observed any competition for nesting-sites between Wagtails and other bird species; interspecific competition between hole-nesters is rather common. (In the data of Finnish bird files there are some records concerning this kind of competition, however.)

3. Discussion

From the above it may be concluded that in the Wagtail the nestling stage is probably somewhat prolonged compared with related species nesting in the open. The weight development of nestlings is apparently intermediate between

typical hole-nesters and open-nesters. In other respects the breeding biology and breeding behaviour of the species resembles related open-nesters. The transition on the part of the Wagtail to breeding in artificial sites above the ground has taken place so recently that it has not yet had enough time to influence the breeding biology of the species through evolution. In natural nest-sites, however, differences between the Wagtail and related species nesting among vegetation in the open are rather indistinct. Apparently the Wagtail is a secondary hole-nester (v. HAARTMAN 1957), in which there have probably not taken place any profound adaptations for holenesting. Nest-site (artificial/natural) or habitat (natural/man-made) has no effect upon this (LEINONEN 1973c).

As to nesting success, however, the species seems to resemble hole-nesting rather than open-nesting species. Abundant breeding in artificial sites has not influenced this result, because nesting in natural sites and habitats is at least as successful as nesting in artificial sites and habitats (LEINONEN 1973c).

The habitat requirements of the Wagtail include open terrain with areas devoid of vegetation and with suitable nest-sites (v. HAARTMAN et al. 1971, LEINONEN 1973a). Apparently these requirements are rather non-specific and, therefore, the species has been able to nest not only in its original breeding grounds, open shores, but also in a great variety of different, mostly man-made environments (LEINONEN 1973c). Since the requirements for the actual nesting site are not very strict, either, it is easy for the Wagtail to find a nest-site within a territory which is otherwise suitable.

The Wagtail is therefore a species which finds it easy to occupy a territory in such areas as the present water course area of Keuruu (the situation was probably different along the shores in their original, natural state, LEINONEN 1973b). From its nesting success it may be concluded that there are good nesting-sites available. Moreover, as man is benevolent towards the species, "the Wagtail is among the few bird species with a future", as stated by HILDÉN & LINKOLA 1962, p. 195).

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S e l o s t u s : **Västäräkki puolikolopesijänä.**

Kirjoittajan havaintojen mukaan 82.5 % Keski-Suomessa sijaitsevan Keuruun reitin västäräkeistä pesi tekoaineksessa; siinä taas enemmän tai vähemmän suojaisessa kolossa ja useimmiten 2—3 m:n korkeudella maasta. Vain 17.5 % pesistä sijaitsi lajin alkuperäisillä pesimispaikoilla, luonnonkoloissa maanrajassa (LEINONEN 1973a).

Västäräkki ei kuitenkaan aivan harvinaisia poikkeuksia mahdollisesti lukuunottamatta pesi pikkulinnuille tarkoitetuissa pöntöissä. Keuruun reitillä se ei myöskään pesinyt ns. avopöntöissä, joita sijoitettiin lähelle rantaa maanrajaan. Ilmeisesti kumpikaan pönttömalli ei sovi lajin synnynnäisiin pesäpaikkavaatimuksiin. Raja avopesinnän suuntaan sen sijaan on hyvin liukuva, västäräkki pesii melko usein pelkästään kasvillisuuden suojaan (erityisesti saaristoalueella), joskus aivan avoimesti maahan.

Kirjoittaja tarkastelee kolopesinnän vaikutuksia västäräkin pesimisbiologiaan ja -käyttäytymiseen. Pesyekoossa ei Motacillidae-heimossa ole eroa avo- ja kolopesijöillä (taulukko 1). Haudonta-aika ei kolopesijöillä ole sen pitempi kuin avopesijöillä (taulukko 2). Pesäpoikasvaihe sen sijaan on västäräkillä mahdollisesti hieman pitempi kuin tyypillisillä avopesijöillä (taulukko 2). Västäräkin pesimistulos Keuruun reitillä, 57.9 %, on lähempänä kolo- kuin avopesijöiden pesimistulosta. Tähän ei kuitenkaan vaikuta pesän sijainti tekoaineksessa, sillä pesi-

mistulos on luonnonkoloissa yhtä hyvä (LEINONEN 1973c). Poikasten kasvukäyrä (LEINONEN 1973a) edustaa kolo- ja avopesijöiden välimuotoa. Västäräkin pesimisaikaisessa käyttäytymisessä (esim. pesälle ja pesältä kulku, reviirin valinta ja sen puolustaminen, soidin, lajienvälinen kilpailu pesäpaikoista, hylättyjen reviirien vapaana pysyminen) on tyypillisiä avopesijöiden piirteitä.

Ilmeisesti västäräkki on ns. sekundaarinen kolopesijä (v. HAARTMAN 1957), jonka pesimisbiologiassa ja -käyttäytymisessä ei paljonkaan ole tapahtunut kehitystä kolopesijöiden suuntaan, vaikka laji valtaosaltaan pesii tekoaineksen suojaisissa koloissa. Pesimistulos kyllläkin on selvästi avopesijöiden pesimistulosta parempi.

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