Empty nests in the great tit (Parus major) and the pied flycatcher (Ficedula hypoleuca) in a polluted area

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“Capsule”: Air pollution may be involved in the ’empty nest’ phenomenon for birds in the forest of Finland.

Abstract

Great tits (Parus major) are sometimes found to incubate in their nests even though the nests contain no eggs. This phenomenon has been observed in different parts of Europe (Sweden, Finland, UK, Netherlands, Germany) and it has become more common during the 1980s. We analysed the occurrence of empty nests in P. major and in pied flycatcher (Ficedula hypoleuca) in SW Finland from 6-year data collected in a polluted area around a copper smelter which emits large quantities of sulphuric oxides and heavy metals. Among first broods 3.3% of P. major females incubated in empty nests. Incubation on empty nests was not observed in F. hypoleuca, but in this species 2.4% of the nests remained without eggs. In both species empty nests were more common close to the pollution source than farther away. Histopathological analyses in P. major suggest that there are diverse reasons for the incapability of a female to lay. One out of five P. major females captured from incubating in an empty nest had dark cysts in her oviduct. Two P. major females had very scanty medullary bone tissue in their tibiotarsus and tarsometatarsus and one female showed exceptionally high concentrations of lead in her bone tissue. We conclude that air pollutants enhance the number of empty nests especially in F. hypoleuca, but cannot wholly explain the phenomenon in P. major. © 2000 Elsevier Science Ltd. All rights reserved.

Keywords: Air pollution; Acidification; Heavy metals; Egg shell; Passerines; Reproductive organs; Breeding failure; Calcium deficiency; Abnormal behaviour

1. Introduction

During the past 10–20 years several authors in different parts of Europe have reported cases where great tit (Parus major) females have incubated in nests where they have laid no eggs (e.g. Ojanen and Orell, 1981; Schmidt and Zitzmann, 1990; Winkel and Hudde, 1990; Carlsson et al., 1991; Hoffmann et al., 1992; Graveland and Drent, 1997; Zang, 1998). The reasons for this phenomenon are still unclear but according to existing long-term data it has become more common during the 1980s (Schmidt and Zitzmann, 1990; Winkel and Hudde, 1990). Suggested mechanisms include acidification of the environment (Zang, 1998) and consequent lack of calcium for laying females (Drent and Woldendorp, 1989), diseases (Ojanen et al., 1975), possible detrimental effects of winter feeding, insecticides and radioactivity (e.g. Winkel and Hudde, 1990), environmental oestrogens and air pollutants. In one reported case a cyst in the oviduct did obviously prevent a P. major female from laying (Ojanen et al., 1975). For the support of calcium shortage hypothesis there is also experimental evidence (Graveland and Drent, 1997). Other possible reasons mentioned above have not been studied.

Rarity makes this breeding failure difficult to study since relatively large data sets are needed to get any information of such cases. Furthermore, in many nest-box studies, empty nests have remained without attention. We present here the data about empty nests of P. major and the pied flycatcher Ficedula hypoleuca around an air pollution source, a copper smelter. Body size, mass and fat score are compared between females from empty and normal nests. Some of the P. major females which incubated in empty nests were captured for histopathological analyses to find out whether
tumours or other diseases could explain their inability to lay. Copper, cadmium and lead concentrations in these birds were measured in different tissues. *F. hypoleuca* female does not normally ‘incubate’ in an empty nest but since empty nests were frequently encountered in this species we present here the data for this species as a comparison.

2. Materials and methods

The breeding data were collected in the surroundings of the town Harjavalta (61°20′N, 22°10′E), SW Finland, during 1991–96. Twelve study sites, each with 30–50 nest-boxes, were established in 1991 along the air pollution gradient in three main directions (SW, SE, NW) from the copper smelter complex in the centre of town. Some new sites were added in 1992 and 1994 to increase the coverage of sites along the gradient. The total number of nest-boxes varied from 540 to 845 over years. The most distant sites were situated 64 and 74 km away from the factory. Since the pattern of occurrence of empty nests was similar each year, the data were analysed by pooling the years and splitting the whole data into three distance classes: zone I, <2 km; zone II, 2–8 km; and zone III, >8 km from the factory. These three zones were planned to represent heavy, moderate and minor pollution loads according to the information on heavy metal concentrations in birds (Eeva and Lehikoinen, 1996) and in forest floor vegetation (Jussila and Jormalainen, 1991).

Nest-boxes were visited at least once a week. All completely built nests with a well-developed nest cup were recorded as breeding attempts. When a nest was noticed to remain empty, special attention was paid to find out whether there were any signs of nest predation or, for example, intrusions by the Wryneck (*Jynx torquilla*). Since predated or otherwise destroyed nests were usually easy to recognise by remains of egg shells and mixed nest material, and subsequently omitted from the analyses, we do not consider nest predation to be a significant source of bias in our data. There is, of course, a possibility that some nests remained empty due to the death of the female at a time just before the start of laying. *P. major* female normally covers her eggs with lining hairs during the laying period and the cover material is usually brought to the nest already before laying. When the incubation starts, the eggs are no longer covered (Haftorn and Slagsvold, 1995). Thus, the existence of cover material in the nest could be used in empty nests as a cue for whether a female had started to incubate or not.

Altogether nine females from empty nests were captured, marked individually with aluminium rings and weighed to the nearest 0.1 g with a 50-g spring balance. Visible subcutaneous fat was scored following Busse and Kania (1970). Wing length was taken to the nearest 1 mm by the maximum method (Svensson, 1992). In 1994 we captured five incubating *P. major* females from empty nests for histopathological analyses to check whether tumours or other visible disturbances could explain the inability of females to lay. One of these females had laid one soft-shelled egg which was broken in the nest and, consequently, the female incubated an eggless nest. In the nests of four other females there were no signs of eggs. Females were captured at night when roosting in their nest-boxes, killed and kept frozen (−20°C) until dissected and analysed for visible aberrations in ovary, oviduct, kidney, liver, lung and tibiotarsus.

Light microscopic analyses were made for tissue samples from ovaries and oviducts. The samples were fixed in 10% phosphate-buffered formalin, embedded in paraffin and cut into 5-μm thick sections. The following stains were used: hematoxyline–eosine (HE) for all tissues, Alcian-Blue PAS (periodic acid Schiff), PAS, PASM (periodic acid Schiff metenamin silver), Berline Blue, Giemsa, Leder, Reticular stain, Herovici, Trichrome and Masson for a sample of tissues.

From five killed females we also took samples of liver, pectoral muscle, bone (tibiotarsus and tarsometatarsus), heart, lung, kidney, body- and flight-feathers (primaries and secondaries) for heavy metal (Cu, Pb, Cd) analyses. The feather samples were unwashed. Samples were dried at 60°C to constant weight (24 h) and were kept dry in a desiccator until processed. The samples were then redried at 60°C. Dry material was ground in an agate-mortar. Feathers and bone material were cut into small pieces with scissors. Thereafter, subsamples of 60 mg were weighed into 5-ml graded tubes, 100 μl concentrated H2SO4 and 200 μl concentrated HNO3 were added and boiled for 2 h in 95°C water bath. The tubes were allowed to cool, after which 0.3% HNO3 was added to get 5 ml. Determinations were duplicated and the mean of these is given. As a control for each series, we used a bovine-liver sample. The yield was 89.4% for copper, 100.8% for lead and 85.3% for cadmium.

3. Results

For the combined data of 6 years 3.3% of *P. major* females (5.2% in second broods) were observed to incubate in an empty nest (Table 1). In all, 6.3% of *P. major* nests remained empty without any sign of nest predation. Incubation of empty nests was not observed in *F. hypoleuca* but also in this species 2.4% of nests remained without eggs. In both species the amount of empty nests exceeded the frequency which could be expected on the basis of clutch-size distribution (Fig. 1). At least in one *P. major* female (H; Table 2) the brood patch was normally developed (this was not routinely checked). Duration of incubation periods are not
usually known for us but four females incubated at least 15 days and the longest observed period was 21 days. Males were present in at least 10 empty $P. major$ nests.

We were not able to capture all the females each year but the recapture data show that many females stayed in the same area in succeeding years, despite unsuccessful breeding (Table 2). We could observe only one case where a female (F) first laid normal clutches and then lost her ability to lay (Table 2). Four females (B, D, E, I) incubated in an empty nest already in their first breeding season (Table 2). We observed no cases where an eggless breeding female would later have started to lay again (Table 2).

In both bird species empty nests were more common near the air pollution source (Zone I) than farther away (Table 3). There was no di$c$ference in the frequency of empty nests between two distant zones. In two distant zones the frequency of empty nests in $F. hypoleuca$ was low (total 16 nests, 1.3%) and at least in some of these cases a female may have died or deserted her nest. It thus remains unclear whether such empty nests, where $F. hypoleuca$ female was not able to lay, exist in background zones at all.

Wing length, body mass and fat score of five $P. major$ females captured from empty nests were compared with those captured from normal nests during the same 2-week period (1–14 June). There was no significant di$c$erence in wing length (size) between groups but the body mass and fat score were significantly higher in females from empty nests than in other females (Table 4).

For both species we checked the clutch-sizes of other females breeding in different years in the same territories as those with empty nests to see whether the quality of individual territories could account for the difficulties of females to lay. As a measure of territory quality we used the mean clutch-size over 6 years for each territory (only first broods were included here and empty nests omitted). Before taking the mean, clutch-sizes were standardised within years $[(x–\bar{x})/SD]$. In a logistic regression model standardised clutch-size means were used as an independent variable to explain the occurrence of an empty nest in a territory (binary variable: 0, at least one egg in a nest; 1, empty nest). Neither in $P. major$ nor in $F. hypoleuca$ could the occurrence of empty nests be explained by the mean clutch-size in a territory ($P. major$: df = 1, $\chi^2 = 0.49$, $p = 0.483$; $F. hypoleuca$: df = 1, $\chi^2 = 1.05$, $p = 0.307$). Instead, the correlation between the mean clutch-size and the proportion of empty nests over the 15 study sites was negative and highly significant for $F. hypoleuca$ ($n = 15$, $r = -0.80$, $p = 0.0003$) and non-significant, although into the same direction, for $P. major$ ($n = 15$, $r = -0.43$, $p = 0.11$). These results suggest that, in either species, empty nests are not tied to certain territories but, especially in $F. hypoleuca$, they occur in greater numbers in areas of generally small clutches.

<table>
<thead>
<tr>
<th>Year</th>
<th>$P. major$</th>
<th>$F. hypoleuca$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>All nests</td>
<td>All empty</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Incubated</td>
</tr>
<tr>
<td></td>
<td></td>
<td>empty nests$^c$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Incubated</td>
</tr>
<tr>
<td></td>
<td></td>
<td>empty nests (%)</td>
</tr>
<tr>
<td>1991</td>
<td>98 (51)</td>
<td>1 (4)</td>
</tr>
<tr>
<td>1992</td>
<td>148 (37)</td>
<td>13 (8)</td>
</tr>
<tr>
<td>1993</td>
<td>137 (71)</td>
<td>13 (4)</td>
</tr>
<tr>
<td>1994</td>
<td>116 (30)</td>
<td>14 (3)</td>
</tr>
<tr>
<td>1995</td>
<td>93 (23)</td>
<td>4 (2)</td>
</tr>
<tr>
<td>1996</td>
<td>109 (40)</td>
<td>11 (3)</td>
</tr>
<tr>
<td>Total</td>
<td>701 (252)</td>
<td>56 (24)</td>
</tr>
<tr>
<td></td>
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</tbody>
</table>

$^a$ The combined second and replacement nests of $P. major$ in parentheses.

$^b$ Includes predated or otherwise accidentally destroyed nests where eggs may have been laid but were not observed.

$^c$ Includes those empty nests where $P. major$ female was observed to incubate.

$^d$ Includes the empty nests where no signs of predation was observed. This figure may include nests where female died just before the start of laying.

Fig. 1. The distribution of clutch-sizes in $F. hypoleuca$ ($n = 1395$) and in $P. major$ ($n = 625$). Clutch-size 0 denotes the completely built nests where no eggs were laid. Destroyed nests were omitted. Data from years 1991–96.
Four out of five dissected females had healthy looking ovary, oviduct, liver, lung and kidney tissues, containing no visible aberrations. Instead, one female (C) from Zone III showed dark cysts at the distal end of her oviduct and had a relatively small and pale liver. Females C and D had very scanty medullary bone tissue, while the three other females showed normal medullary bone. Two females (A, E) had developing egg cells in their ovary (largest egg diameter ca. 9 mm) while in three others (B, C, D) no development could be observed.

Histopathological survey showed that in the ovaries and oviducts of two females (A, E) there were degenerative areas, which we judged to be caused by normal degenerative processes during the ceasing of physiological activities related to breeding (Fig. 2a and c). Vasculitis around blood vessels and areas of chronic round-cell inflammation were seen in the oviduct of female E (Fig. 2b and c). In the oviduct and ovary tissue of three females (B, C, D) there were dark pigment granules, which did not appear to be connected to cells (Fig. 2d). Differential staining showed that the dark bodies were not iron, but we were not able to discriminate more details from these granules. The three females with pigment granules were those that had no developed egg cells in their ovary (see above).

The number of sampled females was too low to confirm any statistically significant trends in tissue heavy metal concentrations. Among the five females the heavy metal concentrations in pectoral muscle, heart, kidney, liver and lung were not elevated in the vicinity of the pollution source (Fig. 3). Instead, the heavy metal concentrations in feathers tended to increase towards the factory complex (Fig. 3). Since the feather samples were not washed this increase is probably due to heavy metal.

### Table 3
The proportions of empty nests in three distance zones (I < 2 km, II 2-8 km, III > 8 km) around the factory complex

<table>
<thead>
<tr>
<th>Species</th>
<th>Zone I</th>
<th>Zone II</th>
<th>Zone III</th>
<th>df</th>
<th>( \chi^2 )</th>
<th>( p )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Parus major</td>
<td>11.2</td>
<td>5.2</td>
<td>4.9</td>
<td>2</td>
<td>6.46</td>
<td>0.0396</td>
</tr>
<tr>
<td>Ficedula hypoleuca</td>
<td>6.0</td>
<td>1.4</td>
<td>1.2</td>
<td>2</td>
<td>23.27</td>
<td>0.0000</td>
</tr>
</tbody>
</table>

* Logit-model for the occurrence of empty nests with distance zone as a dependent variable. For P. major \( n = 701 \) and for F. hypoleuca \( n = 1503 \).

### Table 4
Comparison of wing length, body mass and fat score between Parus major females captured from empty and normal nests

<table>
<thead>
<tr>
<th></th>
<th>Females from empty nests</th>
<th>Females from normal nests</th>
<th>df</th>
<th>( \chi^2 )</th>
<th>( p )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wing length</td>
<td>5 76.4 0.748</td>
<td>32 76.0 0.233</td>
<td>1</td>
<td>0.019</td>
<td>0.889</td>
</tr>
<tr>
<td>Body mass</td>
<td>5 21.5 0.362</td>
<td>31 18.8 0.208</td>
<td>1</td>
<td>10.420</td>
<td>0.001</td>
</tr>
<tr>
<td>Fat score</td>
<td>5 2.40 0.678</td>
<td>32 0.88 0.126</td>
<td>1</td>
<td>5.870</td>
<td>0.015</td>
</tr>
</tbody>
</table>

* Only adult birds from first breeding attempt were included (Wilcoxon rank sum test).
dust on the surface of the feathers in the polluted area. Also, bones have probably accumulated heavy metals, especially lead, near the pollution source (Fig. 3). Female E which laid one soft-shelled egg had exceptionally high lead concentration (88.2 ppm) in her bone tissue (Fig. 3). In general, lead concentrations were highest in bone tissue whereas cadmium accumulated in kidney and copper in liver.

4. Discussion

Although the data gathered from *P. major* females incubating in empty nests are still sparse and somewhat anecdotal, some common features arise from different studies. One important observation is that the inability of a female to lay is not always (but may sometimes be) an innate character but may develop after one or more successful breeding attempts. In our data there was one known case where the female first laid normal clutches and then lost her ability to lay. On the other hand, we had no cases where once eggless breeding female started to lay again. This is consistent with the observation of Winkel and Hudde (1990) who noted that, once developed, the change is irreversible. It is also known that *P. major* females incubating on empty nests can incubate and raise the nestlings normally, once artificially provided with eggs (Hoffmann et al., 1992; Winkel, 1993).

*P. major* females incubating empty nests were of similar size but tended to be heavier and have greater fat reserves than other females. A similar trend was observed by Winkel and Hudde (1990). These observations indicate that such females were not in particularly poor condition. This may partly be due to energy saved when eggs are not produced (Ojanen et al., 1975). Furthermore, eggless females probably do not show the decrease in body mass shown by normal females at the time of hatching (c.f. Schmidt and Zub, 1993, p. 691). It is known that *F. hypoleuca* females who brood non-viable eggs far beyond the normal incubation period retain their body mass whereas it normally drops at hatching (Winkel and Winkel, 1976).

Graveland and Drent (1997) showed that the provision of extra calcium significantly reduced the percentage of empty nests in an area with otherwise low availability of calcium. This may well be the case also in our study area since in addition to heavy metals the smelter also emits large quantities of acidifying compounds. Acidification of the environment manifest, for example, in the decreased number of bark lichens near the factory complex (Jussila et al., 1991). In the vicinity of the factory *F. hypoleuca* females have laid smaller
clutches and thin-shelled eggs and nestlings have suffered from defective leg bone development (Eeva and Lehikoinen, 1995). In *F. hypoleuca*, empty nests seem to occur essentially in the same areas as nests with small clutch-size and poor quality egg shells. However, we consider it unlikely that the lack of calcium would explain the phenomenon in *P. major*, in which empty nests were more frequently encountered also in uncontaminated areas. Egg-shell thinning has been insignificant in this species in our study area and, furthermore, the clutch-size of *P. major* does not vary with distance from the smelter (Eeva and Lehikoinen, 1995). Also, in many cases, *P. major* females bred successfully in the territory where another female incubated an
empty nest in the previous and/or following season. Thus, the empty nests of *P. major* are not at one end in a continuum of a series of diminishing clutch-sizes, which would be the case if the phenomenon were caused by resource (e.g. Ca) limitation.

Histopathological analysis gave only suggestive information for the reasons leading to the inability to produce eggs. Medullary bone is the key element for the proper development of egg shell (e.g. Simkiss, 1967). In two *P. major* females the medullary bone was poorly developed, indicating problems in their calcium-physiology. Unfortunately we had no ‘normal’ birds in our histopathological study and we do not know if they also had poorly developed medullary bone in our study area. One female had dark cysts in her oviduct suggesting some kind of a disease preventing laying. The third female showed a chronic inflammation in her oviduct and had a very high concentration of lead in her bone tissue.

Although many possibilities still remain unstudied it seems that there is no single reason to explain the empty nests. We suggest that diverse reasons are involved and these include the effects of anthropogenically induced calcium deficiency and heavy metal exposure, which may trigger the inability of females to lay. Also the physiological mechanisms leading to inability to lay are probably diverse and affect different sites in the reproductive organs. The increased number of empty nests during the past 20 years and the wide geographic area where they occur indicate that the phenomenon needs further attention.

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**References**


