Ann. Zool. Fennici 34: 61–71
Helsinki 28 February 1997

ISSN 0003-455X

The quality of pied flycatcher (*Ficedula hypoleuca*) and great tit (*Parus major*) females in an air pollution gradient

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Received 2 April 1996, accepted 26 August 1996

We studied whether pied flycatcher (*Ficedula hypoleuca*) and great tit (*Parus major*) females differed in quality between polluted and unpolluted habitats. Comparing female condition between incubation and nestling periods, we aimed at testing whether biometric differences in *F. hypoleuca* females were caused by assortative settlement (i.e. intraspecific competition) or as a consequence of breeding in environments exposed to different levels of pollution stress. Body mass, wing length, fat reserves, age distribution, timing of breeding and breeding density of females were measured along an air pollution gradient from a copper smelter in SW Finland in 1991–1994. We found few differences in female quality which could be explained by assortative settling. Females were of the same size in all areas. At nestling time *P. major* females were heaviest in a moderately polluted area. However, females in the most polluted area were not lighter than those in background areas. Female fat reserves in both species were smaller in the polluted area in one cold breeding season. This suggests that natural (weather) and human induced (pollution) stress factors affected female condition additively. The proportion of young *F. hypoleuca* females was slightly higher in the polluted area than elsewhere. *P. major* females started laying earlier near the factory complex than farther away. *F. hypoleuca* females laid later in the polluted area in early breeding seasons but in late seasons laying started simultaneously everywhere. Especially *F. hypoleuca* bred more sparsely in the polluted area. Observed differences in the condition of *F. hypoleuca* females along the pollution gradient emerged mainly in the course of breeding.

1. Introduction

Decreased breeding success of pied flycatchers (*Ficedula hypoleuca* Pallas) and great tits (*Parus major* L.) has been demonstrated around a polluting factory complex in SW Finland (Eeva & Lehikoinen 1995). The results suggested that *F. hypoleuca* nestlings were directly affected by increased amounts of heavy metals in the diet near the factory, whereas *P. major* suffered from a scarcity of suitable insect food for nestlings. The lowered breeding success may, however, also depend on the lower quality of parent birds in the polluted area. We find it necessary to evaluate the role of parent quality behind these reproductive effects.

The quality of breeding birds may vary between habitats for two reasons. First, birds may settle on territories according to their social dominance (e.g. Lundberg *et al.* 1981, Alatalo *et al.* 1985) forcing subdominant individuals to breed in areas of lower quality, such as areas affected by air pollution. Second, birds may be of the same quality at the beginning of breeding, but their condition decreases under pollution stress (either direct or indirect) during the course of breeding. In this case, the differences would become evident as breeding advances. In both cases, lower breeding success close to the pollution source would be expected. Biometric differences between habitats have been used as evidence for assortative settlement of birds on their territories, but whether they are a consequence of the stressful environment has seldom been studied.

Studies on habitat selection in *F. hypoleuca* and *P. major* have mainly been concerned with the differences between coniferous and deciduous habitats. We study whether female birds differ in quality between habitats where different degrees of anthropogenic changes have occurred due to aerial pollution. For *F. hypoleuca* females, which we have measured during the incubation and nestling periods, we also aim at separating whether possible biometric differences are caused by assortative settlement or are a consequence of breeding in a stressful environment. We examined the body size, fat reserves, age distribution, timing of breeding and breeding density of *F. hypoleuca* and *P. major* females around a copper smelter where raised concentrations of heavy metals and acidification occur due to current and the long-term effects of atmospheric deposition.

2. Study area

The study was carried out in the surroundings of the town Harjavalta (61°20´N, 22°10´E), SW Finland, during 1991–1994. Twelve study sites, each with 30–50 nest-boxes, were established in 1991 along the air pollution gradient in three main directions (SW, SE and NW) from the copper smelter complex in the center of town. Two more sites were established in spring 1992 at 64-km (60°44´N, 21°59´E) and 74-km (60°39´N, 22°1´E) distances south from the smelter. Nest-boxes were put on tree trunks two metres above ground level. The forests in the area are dominated by Scots pine (*Pinus sylvestris*), which forms mixed stands with spruce (*Picea abies*) and birch (*Betula* spp.). The proportion of spruce increases away from the centre of the town. In the field layer, the dwarf shrubs *Vaccinium vitis-idaea* and *V. myrtillus* dominate. In the three study sites closest to the factory complex, field layer vegetation is almost absent due to the long term effect of pollution (see Salemaa & Vanha-Majamaa 1993). The weather data derive from the Peipohja Meteorological Station (61°16´N, 22°15´E, Table 1).

The main source of air pollutants in this area is a factory complex producing copper, nickel and fertilizer. Especially copper, zinc, nickel and lead are common pollutants in the area (Kubin 1990, Jussila & Jormalainen 1991). Particulate atmospheric releases of these metals in 1993 were 50, 11, 7 and 6 t, respectively. During the early activity of the factory in the 1940s, sulphur dioxide produced in the process was not made use of, but was emitted in the surroundings. This led to the decline of forest in the surroundings of the factory. Later on, most SO_2 was utilized to produce sulphuric acid. During 1993 about 4 700 t SO_2 was emitted into the air. The pollution gradient around the factory has been confirmed by analyses of the SO_2 content of pine needles and observed reduction in the species number of bark lichen (Laaksovirta & Silvola 1975), by analyses of heavy metals with the moss bag method (Hynninen 1986), and by analyses of moss and rain water samples from the forest floor (Jussila & Jormalainen 1991). Also metal contents of *F. hypoleuca* and *P. major* nestling faeces decrease exponentially with increasing distance to the factory complex (Eeva & Lehikoinen 1996).

3. Material and methods

Nest-boxes were checked weekly to gather breeding data. *F. hypoleuca* females were caught in the nest-boxes when

Table 1. The mean temperatures (°C) at incubation (T_i) and in the nestling period (T_n) of *F. hypoleuca* and *P. major*. The incubation period was determined as 14 days before the median hatching date (HD) for both species. The nestling period was determined as 14 days after the median hatching day for *F. hypoleuca* and 18 days for *P. major*. Weather data from Peipohja Meteorological Station.

	P. major			*F. hypoleuca*		
Year	HD	T_i	T_n	HD	T_i	T_n
1991	5.6.	8.1	12.4	28.6.	13.4	16.3
1992	5.6.	16.2	15.9	15.6.	17.4	13.8
1993	26.5.	14.7	9.7	11.6.	10.2	11.0
1994	1.6.	7.0	11.6	19.6.	11.7	13.4

incubating or feeding nestlings. *P. major* females were caught when feeding nestlings or at night when they roosted with large nestlings. Females were weighed to the nearest 0.1 g with a 50 g Pesola spring balance. Visible subcutaneous fat was scored following Busse and Kania (1970). Wing length was taken to the nearest millimetre by the maximum method (Svensson 1992). Here we analyze only the data on breeding females. The females captured at second and replacement nests were omitted from all analyses.

The mass of *F. hypoleuca* females changes during the breeding cycle (Winkel & Winkel 1976, Silverin 1981). To make values comparable we fitted a polynomial regression for the combined data of four years: $M = 14.4 - 23.3E - 2A - 12.4E - 3A^2 + 14.7E - 4A^3 + 47.2E - 6A^4 - 41.5E - 7A^5$, where M = female mass at nestling age A (*d.f.* = 1 328, R^2 = 0.63). Nestling age was defined as –1 on the day before hatching, 0 on the actual hatching day and 1 on the day following, etc. Weights taken more than 12 days before hatching were omitted to exclude females which still had eggs in their oviduct. The mass of *P. major* females undergoes a similar change during the breeding (Rheinwald 1981), but for this species we had weight measurements only from the nestling period and a linear regression (*d.f.* = 185, $R^2 = 0.0051$) was used as a control for the slight mass change.

Female mass was analyzed using relative mass residuals which were calculated from the regression equations. Residuals were first transformed to percent values of the estimated mass. Because the same females were often weighed more than once, we used the mean of mass residuals (MMR) for each female to avoid pseudoreplication. For *F. hypoleuca* this was done separately for the incubation and nestling periods. The masses were compared among four distance zones around the factory complex (zone I: < 2 km, II: 2–7 km, III: 7–12 km, IV: > 12 km). This was done using analysis of covariance (ANCOVA), with MMR as the dependent and *year*, distance *zone* and female *age* as independent variables. Capture *time* and yearly standardized hatching *date* [$(x - \text{mean})/S.D.$] were used as covariates (day 1 = 1st January). Because the interaction effect between year and age was not significant for either species it was omitted from the final models. Wing length was analyzed with similar ANCOVA models as mass, except for time of measurement.

Visible fat was analyzed using logit-models where fat score (three levels in increasing order: 0, 1 or 2) was used as the dependent variable. There were few birds with fat score 3, and we combined scores 2 and 3. Scores higher than 3 were not encountered. Independent variables were *year* and distance *zone*. To get enough measurements for each zone in each year, the distance zones III and IV were combined for both species. Because there still were a few empty cells, a constant of 0.5 was added to each cell frequency before analyses. The fat scores from the incubation and nestling periods of *F. hypoleuca* were analyzed separately. The effect of female age on fat reserves was studied with similar models containing *age* instead of distance as a dependent variable.

Since there were five persons measuring the wing lengths we tested the reliability of the measurements by calculating the repeatability value R (Krebs 1989) for those 121 *F. hypoleuca* females which were measured by at least two persons during the same breeding period. Although the repeatability of the measurements was high ($R = 0.81$, $F_{120,127} = 9.76$, $P < 0.001$, see Harper 1994) there were significant differences in wing length values among the five persons. This was not caused by spatially biased distribution of measurements, because each person measured birds in every distance zone. Instead, this was probably due to a slightly different measuring routine among people despite the standardization of measurements. Therefore, we calculated for both bird species corrected wing lengths by standardizing the measurements of four other people (x_a) to those of the one whose average value ($\bar{x}_b$) was closest to the mean for the combined data: $x = x_a + (\bar{x}_b - \bar{x}_a)$.

The females were aged as young (1 year old) or adult (≥ 2 years) following Karlsson *et al.* (1986) and Svensson (1992). We could not age 5.4% of the *F. hypoleuca* females; they were omitted from analyses involving age. The age distribution among distance zones was studied using logit-models, where age was a binary variable (0 = young, 1 = old). Independent variables were *year* and distance *zone*. The distance zones III and IV were combined for *P. major* to avoid empty cells in the contingency table.

In the analyses of laying date, ranked values were used due to non-normal distribution of dates and large yearly differences in variance. After ranking dates against years an ANOVA was performed, with distance *zone* as the explaining variable. Similarly, for the ANOVA among *year*s, dates were ranked against distance zones. A third model was used to study the interaction between distance and year, explaining factors being distance zone and the interaction term (the main effect of year was omitted because the values were ranked against study years). The effect of age on laying date was studied with similar models where female *age* was added as an explaining factor.

The relative occupation of nest-boxes was studied with logit-models where the occupation of the nest-box was used as a dependent variable. Independent variables were *year* and distance *zone*. Because part of the nest-boxes were already occupied by *P. major* at the time when *F. hypoleuca* started breeding, we regarded them to be unavailable for *F. hypoleuca*. To allow comparison with other studies, we also calculated the density of breeding birds (nests/ha) in each study site by the nearest-neighbour distance method (Krebs 1989). Nearest-neighbour distances were used to calculate an estimate of population density: $D = n/[\pi \times \sum(r^2)]$, where D = density, n = number of nests and r = distance to nearest neighbour.

4. Results

4.1. Body mass

The body mass of *F. hypoleuca* females did not differ significantly among distance zones either during the incubation period or at nestling time (Table 2). The *P. major* females were about 2% heavier in the intermediate zone II than in other areas (Table 2). There was, however, no indication that *P. major* females living in the most polluted area were lighter than females in unpolluted areas.

The body mass of incubating *F. hypoleuca* females differed among years, which was mainly due to different weather conditions: the average temperature during the incubation period was highest in 1992 (Table 1), when the birds were also heaviest. There were no significant body mass differences at nestling time (Table 2), which may be due to fewer measurements rather than to differences being smaller. Nor were there any significant among-year differences in body mass of *P. major* females at nestling time (Table 2).

During incubation, adult *F. hypoleuca* females were about 2% (0.3 g) heavier than young ones (Table 2). At nestling time the difference was not statistically significant (Table 2). Adult *P. major* females were about 1% (0.2 g) heavier than young ones (Table 2). In both species the body mass correlated positively with wing length (first covariate, Table 2). Body mass also correlated positively with time of day (second covariate, Table 2): for both species, females were about 4% heavier in the evening than in the morning. The body mass of *F. hypoleuca* females correlated negatively with hatching date (third covariate). This relationship was not significant for *P. major*, although in the same direction (Table 2).

4.2. Fat reserves

Female fat reserves varied significantly and in parallel with body mass among years in both species (Table 3), and reflected the weather conditions at breeding time. For example, fat scores of *F. hypoleuca* were highest in the warmest incubation period (in 1992), and were lowest in the coldest year (in 1993); they were intermediate in the two other years (c.f. Tables 1 and 3). Fat score correlated positively with body mass in both species (*F. hypoleuca*: incubation time, $r_s = 0.18$, $P = 0.0001$, $n = 674$; nestling time, $r_s = 0.14$, $P = 0.0041$, $n = 428$; *P. major*: nestling time, $r_s = 0.18$, $P = 0.015$, $n = 183$). However, fat score explained only about 3% of individual variation in body mass of *F. hypoleuca* and about 4% of that of *P. major*.

In a saturated logit-model the distance from the pollution source had no significant main effect on female fat score in either the incubation or nestling period of *F. hypoleuca* or in the nestling period of *P. major* (Table 3). However, there was a significant interaction effect of distance and year on fat score during the incubation period of *F. hypoleuca* and during the nestling period of *P. major* (Table 3). We fitted another model containing

Table 2. The mean mass residuals (%) of *Ficedula hypoleuca* and *Parus major* females in four distance zones (see Methods). In ANCOVA models, *wing* length, *time* of weighing and yearly standardized hatching *date* [$(x - \bar{x})$/*S.D.*] were used as covariates.

	F. hypoleuca Incubation time[1]			*F. hypoleuca* Nestling time[2]			*P. major* Nestling time[3]		
Zone	*n*	$\bar{x}$	*S.E.*	*n*	$\bar{x}$	*S.E.*	*n*	$\bar{x}$	*S.E.*
I	92	0.11	0.58	39	– 0.84	0.66	25	– 1.06	0.67
II	269	0.41	0.32	143	– 0.32	0.43	73	1.17	0.55
III	190	– 0.65	0.37	104	0.68	0.47	54	– 0.71	0.79
IV	83	0.67	0.55	73	0.84	0.60	21	– 1.44	1.19
Source:	*d.f.*	*F*	*P*		*F*	*P*		*F*	*P*
Year	3	7.18	0.0001		0.97	0.4089		1.94	0.1247
Zone	3	1.09	0.3523		0.64	0.5871		2.92	0.0356
Age	1	8.87	0.0030		0.32	0.5723		4.51	0.0353
Wing	1	18.51	0.0001		14.20	0.0002		23.22	0.0001
Time	1	19.51	0.0001		3.76	0.0533		11.36	0.0009
Date	1	9.30	0.0024		23.88	0.0001		1.25	0.2653

[1] Error MS = 24.93, *d.f.* = 623; [2] Error MS = 22.76, *d.f.* = 348; [3] Error MS = 19.69, *d.f.* = 162

only the main effect of year with the interaction term. In this model the interaction was still significant for *F. hypoleuca* (*d.f.* = 12, x^2 = 29.8, *P* = 0.003) but only marginally significant for *P. major* (*d.f.* = 12, x^2 = 18.8, *P* = 0.092). The fit of this model was good for both species (deviance for *F. hypoleuca*: *d.f.* = 4, x^2 = 2.2, *P* = 0.699; for *P. major*: *d.f.* = 4, x^2 = 6.27, *P* = 0.180).

The interaction effects were interpreted visually from the graphs (Fig. 1a and b). In the warmest incubation period of *F. hypoleuca*, in 1992, the highest fat score was the commonest one in every distance zone (Fig. 1a). By contrast, in the cold incubation period of 1993 high scores were more common in the distant sites. For *P. major* females, fat score tended to increase towards the pollution source, but during the coldest nestling period (cf. Table 1) this trend was reversed (Fig. 1b).

Female age had no significant effect on fatness in either bird species, nor were there any interaction effects between year and age (the main effects in a saturated logit-model: incubation period, *F. hypoleuca*, *d.f.* = 2, x^2 = 3.09, *P* = 0.213; nestling period, *F. hypoleuca*, *d.f.* = 2, x^2 = 0.30, *P* = 0.859; *P. major*, *d.f.* = 2, x^2 = 0.40, *P* = 0.819). This means that the age distribution did not bias the observed pattern of fat scores along the pollution gradient.

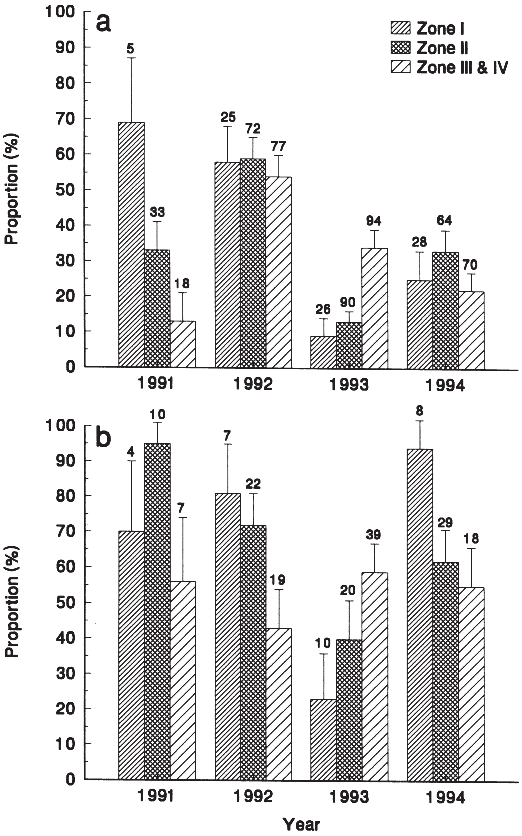

Fig. 1. The proportions of (a) *Ficedula hypoleuca* females having the fat score 2 (see Methods) during the incubation period and (b) *Parus major* females having a fat score greater than 0 during the nestling period. The two most distant zones are combined.

4.3. Wing length

No significant differences were found in wing length among distance zones in either species (Table 4). The mean wing length of *F. hypoleuca* increased during the first three study years, but there

Table 3. The proportions (%) of three fat scores (in increasing order: 0, 1 or 2, see Methods) in four years for incubation and nestling periods of *Ficedula hypoleuca* and for the nestling period of *Parus major*. In logit-models fat score was used as dependent variable.

	F. hypoleuca Incubation time				*F. hypoleuca* Nestling time				*P. major* Nestling time			
Year	*n*	0	1	2	*n*	0	1	2	*n*	0	1	2
1991	56	16	54	30	19	32	63	5	21	19	81	0
1992	174	1	41	58	97	24	53	23	48	38	54	8
1993	210	43	35	21	139	61	34	5	69	52	48	0
1994	162	27	46	27	124	70	24	6	55	35	52	13
Source:	*d.f.*	x^2	*P*		*d.f.*	x^2	*P*		*d.f.*	x^2	*P*	
Year	6	57.5	0.000		6	36.0	0.000		6	13.8	0.032	
Zone	4	1.9	0.753		4	5.9	0.206		4	5.5	0.238	
Year × Zone	12	31.2	0.002		12	13.0	0.370		12	20.9	0.051	

was no longer any difference between the last two years (Table 4). The trend was the same in *P. major*. In both species adult females had longer wings than young ones (Table 4). In the combined data the difference between age classes was 0.72 mm for *F. hypoleuca* and 1.88 mm for *P. major*. For *F. hypoleuca* there was also a significant interaction effect between year and age. This interaction was studied visually drawing the yearly means separately for young and adult birds. The reason for the interaction was that the wing length of adult birds increased more strongly. This may happen when 'adults' include several age classes and if wing length still increases after the age of two years. Consequently, the average age of 'adult' birds increased over years in the study populations, which were founded in 1991. The changes in age distribution, however, cannot wholly explain the yearly increase in wing length since this was observed also among young birds. Hatching date (a covariate) was not related to variation in wing length in either species (Table 4).

Table 4. The mean wing length (mm) of *Ficedula hypoleuca* and *Parus major* females in four distance zones. In ANCOVA models, yearly standardized hatching *date* [$(x - \bar{x})/S.D.$] was used as covariate.

	F. hypoleuca[1]			*P. major*[2]		
Zone	*n*	$\bar{x}$	*S.E.*	*n*	$\bar{x}$	*S.E.*
I	106	78.3	0.14	30	75.1	0.34
II	340	78.2	0.09	86	75.1	0.19
III	227	78.4	0.10	66	75.1	0.21
IV	144	78.3	0.12	22	74.9	0.38
Source:	*d.f.*	*F*	*P*	*d.f.*	*F*	*P*
Year	3	42.6	0.000	3	1.2	0.311
Zone	3	1.2	0.297	3	0.4	0.741
Age	1	22.7	0.000	1	61.7	0.000
Year × Age	3	7.0	0.000	3	1.1	0.340
Date	1	1.0	0.310	1	2.0	0.161

[1] Error MS = 1.960, *d.f.* = 805; [2] Error MS = 2.187, *d.f.* = 192

4.4. Age distribution

The proportion of young *F. hypoleuca* females was slightly higher in the first study year, but in the saturated logit-model there was no significant difference in age distributions among years (Table 5). However, the distance to the pollution source affected the age distribution (Table 5, Fig. 2a). Because the interaction between year and distance was not significant, we fitted the main effect model in which the effect of year was still non-significant (deviance: $d.f. = 9, x^2 = 4.79, P = 0.852$). The third model only contained the effect of distance and showed that the proportion of young birds was in general higher near the factory (zone I) than in other areas (deviance: $d.f. = 12, x^2 = 7.91, P = 0.792$).

Unlike in *F. hypoleuca*, the proportion of young *P. major* females clearly varied among years, being highest in the warm spring of 1992 (Table 5, Fig. 2b). There was a tendency for females to be younger in distant sites than in sites near the pollution source, but neither the effect of distance nor the interaction of year and distance was significant in the saturated logit-model. For this species, the number of females, especially in zone I, was too small to reliably estimate the population's yearly age distribution (Table 5). Leaving the interaction term out of the model, however, reduces the fit of the model. The age distribution of *P. major* varies yearly more than that of *F. hypoleuca*, but a possible relationship between year and distance to the pollution source cannot be confirmed here.

4.5. Laying date

The mean laying date of *F. hypoleuca* varied among years ($F_{3,1056} = 208.4$, $P < 0.001$) but not among distance zones (Table 6). However, there was a significant interaction between distance and year (Table 6). During the early breeding seasons (1992 and 1993), *F. hypoleuca* females started laying

Table 5. The proportion (%) of young (see Methods) *Ficedula hypoleuca* and *Parus major* females in four study years. In logit-models age was used as dependent variable. *n* = number of all females.

		F. hypoleuca			*P. major*	
Year		%	*n*		%	*n*
1991		52.3	111		56.3	32
1992		41.4	263		68.5	54
1993		38.9	262		42.5	87
1994		41.7	216		38.5	65
Source:	*d.f.*	*F*	*P*	*d.f.*	*F*	*P*
Year	3	4.9	0.180	3	12.3	0.007
Zone	3	9.2	0.026	3	1.9	0.383
Year × Zone	9	4.3	0.890	9	9.0	0.176

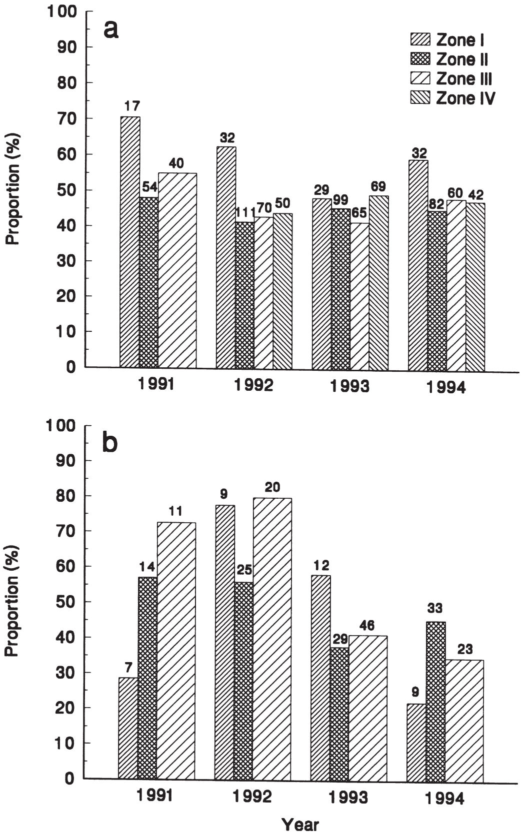

Fig. 2. The proportion of young (1-yr) *Ficedula hypoleuca* (a) and *Parus major* (b) females at different distances from the pollution source during 1991–1994. The two most distant zones are combined for *F. hypoleuca* in 1991 and for *P. major* in all years. Numbers denote the total number of individuals in each zone.

somewhat later in the polluted than unpolluted areas, whereas in the late season (1991) this difference was absent or even the opposite trend occurred (Fig. 3a). Median laying dates were more equal than means among distance zones in every year. Young females started laying one day later than adult ones ($F_{1,798} = 19.0, P < 0.001$), but adding age into the model did not remove the interaction effect of year and distance.

The laying date of *P. major* varied among years ($F_{3,444} = 77.7, P < 0.001$) and among distance zones (Table 6). In general, *P. major* females started to lay earlier near the pollution source than farther away, but also in this species the effect of distance depended on year (Table 6). The difference between distance zones did not exist in the latest breeding season of 1992 (Fig. 3b). *P. major* females of different age did not differ significantly in their laying date ($F_{1,189} = 0.52$, $P = 0.473$), although the difference was in the same direction as in *F. hypoleuca*.

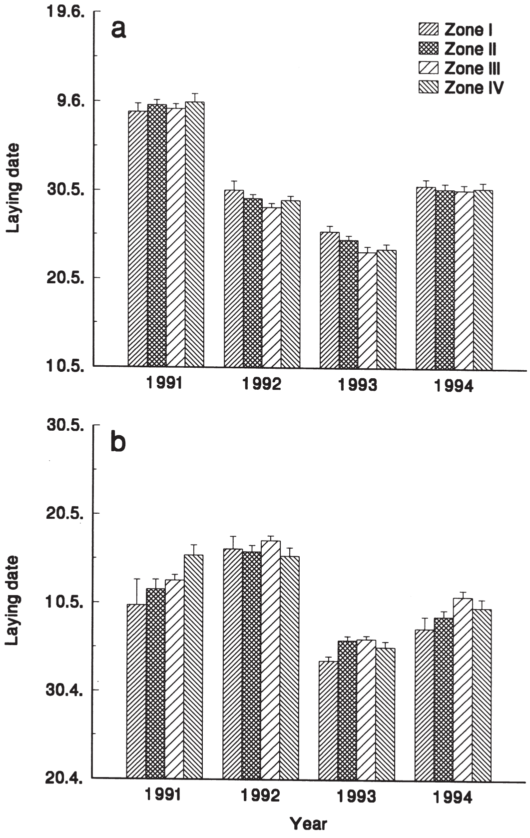

Fig. 3. The mean (± *S.E.*) laying date of *Ficedula hypoleuca* (a) and *Parus major* (b) at four distance zones during 1991–1994.

Table 6. The mean (± *S.E.*) laying dates of *Ficedula hypoleuca* and *Parus major* in four study years. ANOVA for yearly ranked values.

	F. hypoleuca[1]			*P. major*[2]		
Year	*n*	Mean	*S.E.*	*n*	Mean	*S.E.*
1991	221	8.6.	0.35	93	12.5.	0.72
1992	314	29.5.	0.28	132	16.5.	0.43
1993	285	24.5.	0.30	123	5.5.	0.26
1994	240	30.5.	0.34	100	9.5.	0.51
Source:	*d.f.*	*F*	*P*	*d.f.*	*F*	*P*
Zone	3	2.2	0.0919	3	7.5	0.0001
Year × *Zone*	12	5.9	0.0001	12	3.6	0.0001

[1] Error MS = 6105.0, *d.f.* = 1044; [2] Error MS = 1041.5, *d.f.* = 432

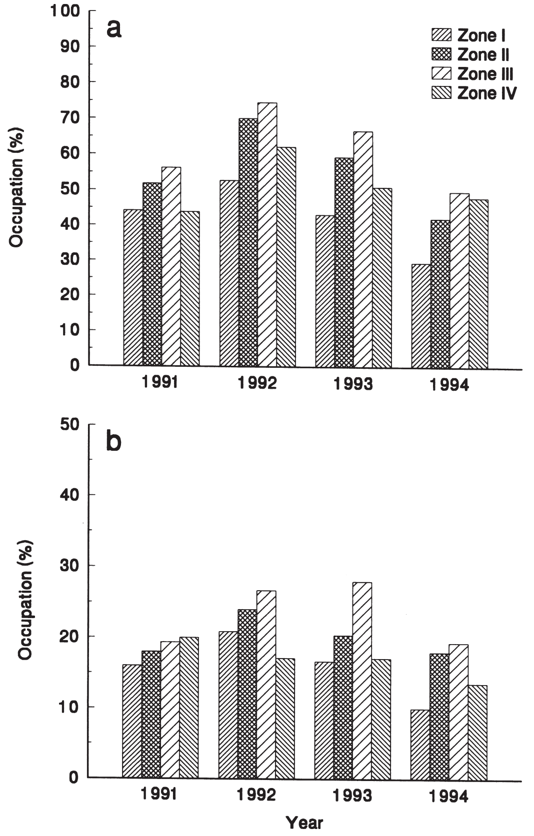

Fig. 4. The occupation (%) of nest-boxes by *Ficedula hypoleuca* (a) and *Parus major* (b) at four distance zones during 1991–1994. Nests occupied by *P. major* were omitted when calculating the values for *F. hypoleuca*.

4.6. Breeding density

The occupation of nest-boxes varied among years and among distance zones for both species (*F. hypoleuca*: $df_{\text{year}} = 3, x^2 = 51.9, P < 0.0001$; $df_{\text{zone}} = 3, x^2 = 39.8, P < 0.0001$; *P. major*: $df_{\text{year}} = 3, x^2 = 9.28, P = 0.026$; $df_{\text{zone}} = 3, x^2 = 11.3, P = 0.010$). In a saturated logit-model there was no interaction effect between year and distance for either species. *F. hypoleuca* occupied proportionally fewest nest-boxes near the pollution source, in zone I, and proportionally most boxes in zone III (Fig. 4a). The difference between zones II and IV was not statistically significant. The same applies to *P. major* (Fig. 4b), but zone I only differed marginally from zone IV ($x^2 = 3.18, P = 0.075$). Both species occupied more nest-boxes in 1992 than in the three other years. The slightly lower number of nests in 1994 may partly be due to ageing of the nest-boxes.

The mean density of nests by the nearest-neighbour method was 0.8/ha for *F. hypoleuca* and 0.3/ha for *P. major*. The highest densities were found in zone III (*F. hypoleuca*: 1.2 nests/ha; *P. major*: 0.5 nests/ha) and lowest density in zone I (*F. hypoleuca*: 0.5 nests/ha; *P. major*: 0.2 nests/ha). Also, the density of available nest-boxes tended to be highest in zone III, but even relating the density of nests to the density of nest-boxes gives essentially the same result as the relative occupation.

5. Discussion

5.1. Body mass, size and fat reserves

We found few differences in female quality (body mass, size, fatness) which could have been caused by an assortment of birds along the pollution gradient. Here it must be remembered that age effects were removed in biometric analyses. Our data on *F. hypoleuca* suggest that the differences emerged mainly during the breeding. This is supported by the existence of a year-distance interaction effect on fat reserves, which is not likely to arise as a side effect of competition. Wing length, which for an individual bird remains more or less unchanged during breeding, and thus reflects the situation at the actual time of settlement, was not related to the distance from the pollution source.

Neither *F. hypoleuca* nor *P. major* females differed in size among the zones. The yearly variation in body mass and fat score clearly exceeded any variation caused by the pollution gradient. *F. hypoleuca* females showed a slight decrease in body mass towards the factory complex, but the total variation explained by distance was small. Similarly, *F. hypoleuca* females' fat reserves during the incubation period were smaller close to the pollution source, but this effect was found only in a year when the weather was bad during incubation. This result suggests that the extra stress caused by air pollution may lower the female's condition only together with other simultaneous stress factors, such as bad weather.

P. major females did not show reduced body mass in the polluted area. However, also in this species, the fat reserves decreased towards the pollution source in the year with a cold nestling period. *P. major* females were heaviest in the moderately polluted zone. The reason for this is probably more abundant food in the area. In another study of the same area, we observed that caterpillars, which are an important food source for *P. major*, were abundant and formed a larger proportion of the nestling diet in this moderately polluted area than elsewhere (unpubl. data). Tinbergen and Dietz (1994) found that daily energy expenditure of *P. major* females was negatively associated with caterpillar abundance. We think that the observed interaction effects of year and degree of pollution indicates the dependence of female condition on available food.

In conclusion, we found differences in female condition along the pollution gradient only in connection with unfavourable weather conditions, and this does not support the idea that females were assortatively settled along the pollution gradient. However, the observed patterns in age distribution, timing of breeding and breeding density can well be an outcome of assortative settlement.

5.2. Age distribution

The proportion of young *F. hypoleuca* females was higher near the factory than farther away (Fig. 2a). The higher number of young birds and later mean laying date near the factory suggest that later-breeding young individuals had to select lower quality habitats. This kind of assortment has been noticed for this species also between coniferous and deciduous habitats (e.g. Gezelius *et al.* 1984). The slightly higher proportion of young birds during the first study year can be expected after putting up a new nest-box area, because site fidelity causes an increasing number of breeding females to return to their home site in subsequent years. Nyholm and Myhrberg (1983) found the average return rate for *F. hypoleuca* females to be 8% after the first breeding and about 50% after the second breeding.

Hõrak and Lebreton (1995) found that the proportion of adult *P. major* females was higher in urban than rural populations. Also, in our study area, there was a tendency for a higher proportion of young females farther away from the pollution source, but this trend was not statistically significant (Fig. 2b). This kind of pattern may, however, be expected because the species is to some extent associated with human settlements (e.g. Eeva *et al.* 1989), which tend to be sparser in our distant study sites. Association with human settlements in general means good wintering conditions (see Hõrak 1993). The observed differences in female age distributions, however, can only explain a marginal amount of variation in breeding success when compared with variation caused by the pollution gradient.

5.3. Timing of breeding

In early breeding seasons, *F. hypoleuca* females bred later in polluted than unpolluted areas. We think that in early seasons the start of laying happens much in the same order as females (and males) arrive in our study area. Birds first occupy the distant and richer habitats which are known to be preferred by this species (e.g. Lundberg & Alatalo 1992). In favourable conditions females start laying as soon as possible after their arrival, and this results in later average laying dates in polluted or otherwise poorer areas. In contrast, when laying is delayed by cold weather the order of arrival no longer determines the order of laying, and females start laying simultaneously everywhere, or even earlier in polluted areas.

P. major started laying earlier near the pollution source, but also in this species the pattern was absent in the latest breeding season. Dhondt *et al.* (1984) noted that urban *P. major* females started breeding earlier than rural ones, and suggested that it was probably caused by differences in food availability. In addition to more intense winter feeding by humans, the sites near the pollution source are phenologically more advanced than those farther away (Julia Koricheva, pers. comm.). These two factors might well explain the earlier start of laying in *P. major* in the polluted area.

The start of laying also depends on female age. Järvinen (1991) reviewed studies on the effect of age on the timing of breeding in *F. hypoleuca* and *P. major*: young females of both species started laying later than adults. In our study, *F. hypoleuca* laid later in the polluted area in early breeding seasons. Although young *F. hypoleuca* females laid later than adult ones, the age effect did not explain the observed pattern along the pollution gradient. Similarly, tended to lay earlier in the polluted area, where the proportion of young females was somewhat lower than in the more distant areas (Figs. 2 and 3), but in this species, young and adult *P. major* females did not significantly differ in their laying dates. We conclude that age effect cannot explain the observed patterns in laying dates along the pollution gradient. In all, differences were small and probably have a minor significance for breeding success.

5.4. Breeding density

The density of *F. hypoleuca* nests in our study area (0.8 nests/ha) corresponds well with other estimates from nest-box areas in coniferous forests. For example, Lundberg and Alatalo (1992) found a mean density of 0.6 pairs/ha, with a somewhat lower nest-box density than in our area. The lower breeding density near the pollution source indicates that these habitats are not favoured by *F. hypoleuca*. This is further supported by the observation that the proportion of adult *F. hypoleuca* females was highest in the area where the density of breeders was highest. The difference was less clear for *P. major*, which may be due to the greater value of inhabited areas as a wintering habitat for this species.

The density of nest-boxes affects the density of breeding *F. hypoleuca* females (e.g. von Haartman 1971, Virolainen 1984, Hågvar *et al.* 1990). Virolainen (1984) suggested that this may be because a high nest-box density promotes polygyny in this species. In our study area, the mean distance of available nest-boxes for *F. hypoleuca* varied between 42 and 44 m ($\bar{x} = 42.6$, *S.D.* = 0.74) among zones. This small variation in nest-box density can not wholly explain the variation in breeding density among zones.

5.5. The use of body mass in biomonitoring

The often-observed reduction in body mass during reproduction, has been interpreted to indicate either a cost of reproduction or an adaptive mass adjustment for lowering the flight cost (Freed 1981, Hillström 1992). Hillström (1992) provided *F. hypoleuca* pairs with an extra food supply and found that females exhibited the same body mass change as those without extra food. Furthermore, if breeding advances normally, the decline in body mass starts about four days before hatching (own observation). These observations support the idea that the drop in female weight at time of hatching is an active process rather than a proximate consequence of stress. That the "decision" to lose weight is made by the female, is further supported by the observation of Winkel and Winkel (1976), who noted that *F. hypoleuca* females who had brooded non-viable eggs for several days beyond the normal incubation period were almost the same weight as during the first 14 days of incubation. However, clutch and brood manipulation experiments have shown that females lose weight in relation to the size of their clutch or brood (e.g. Askenmo 1977, Moreno & Carlson 1989, Johnston 1993). Thus, both causes are probably involved. These two simultaneous phenomena make it difficult to use body mass for biomonitoring purposes. A minimum prerequisite for such use is that the exact stage of breeding is known. Mass loss from incubation to the nestling period is probably a poor measure of stress, because better parents may in fact show greater mass loss (Martin 1987).

A compensatory effect of smaller brood size in a polluted area may also make female body mass an insensitive indicator of pollution stress. In our study area, the hatching success of *F. hypoleuca* is very poor close to the factory complex due to low quality eggshells (Eeva & Lehikoinen 1995). Thus, birds breeding close to the pollution source generally have fewer nestlings to feed. This means that adult birds are less strained by the feeding duties than those breeding farther from the factory complex and rearing larger broods. This may partly compensate effects of a poor breeding environment on female condition. If females had been rearing broods of similar size in each study site, the differences in female condition may have been greater.

Acknowledgements. We thank Simo Veistola, Vesa Koivunen, Juha Tiainen, Jan-Åke Nilsson and Markku Orell for reading and for their comments on the earlier versions of this paper. We are also grateful to Jorma Nurmi, Tapio Aalto, Petteri Ilmonen and Jari Valkama who assisted us with the field work. The language was kindly checked by Hans Källander. This study was supported by the Academy of Finland.

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