

Habitat-related differences in clutch size of the Pied Flycatcher *Ficedula hypoleuca*

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The mean clutch size of the Pied Flycatcher in South Sweden was invariably, but not significantly, smaller in coniferous than in deciduous forest, which agrees with previously published information. Egg laying usually started a few days later in coniferous than in deciduous forest. Furthermore, females averaged slightly smaller and the age composition was biased in favour of one year old females in a coniferous compared with a deciduous study plot. The latter results are consistent with the view that the birds' habitat distribution is partly determined by dominance interactions. Since both the size and the age of the female, as well as the timing of laying, have been shown to influence clutch size in the Pied Flycatcher, all three factors may exert a direct influence on clutch size, but habitat productivity is likely to add to the differences observed.

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1. Introduction

Several authors have reported differences in mean clutch size of Pied Flycatchers *Ficedula hypoleuca* breeding in different habitats. Perhaps the difference most commonly observed is that between deciduous and coniferous forest, clutches in the former habitat averaging larger than those in the latter (for exceptions, see below). In this paper we present some additional data on clutch size in the Pied Flycatcher with an emphasis on the difference between these two main habitat categories and discuss possible explanations for this difference. The material derives from a more detailed analysis of Källander's (1975) data and from two studies carried out in spring 1983 (L. Gezelius & M. Grahn unpubl., G. Högstäd unpubl.), supplemented with information from a long-term study by Sten Svensson (Källander, Karlsson, Rosenlund & Svensson unpubl.).

All studies were carried out in the province of Skåne, southernmost Sweden, the maximum distance between any two areas being about 50 km (Table 1). The two coniferous habitats were Vombs Fure, a ca. 10 km² large pine *Pinus sylvestris* dominated wood, and Revinge, a

military training area containing small plantations of pine as well as deciduous woods and copses. Among the deciduous woods, oak *Quercus robur* strongly dominates in Linnebjerg, Bjärsjölagård and Rynke, while Frueråften and Dalby Norreskog also contain areas of beech *Fagus sylvatica* and sycamore *Acer pseudoplatanus* as well as other species of deciduous trees. The deciduous woods at Revinge have a varied composition; in 1971 and 1973 the boxes were situated in small woods dominated by elm *Ulmus glabra*, beech, and oak, but in 1983 they were scattered over a larger area, most of them in beech, birch *Betula*, and alder *Alnus glutinosa*.

2. Results and discussion

Table 1 presents the mean clutch sizes observed in the various study areas in different years, together with median dates for clutch commencement. Within each year, mean clutch size is larger in the deciduous habitat in all comparisons, although this difference only reaches conventional statistical significance in one case (between Linnebjerg and Vombs Fure in

Table 1. Clutch size in the Pied Flycatcher *Ficedula hypoleuca* in deciduous and coniferous habitats in Skåne, southernmost Sweden. For each locality and year, the mean clutch size, standard deviation (SD), number of clutches (*n*) and the median date (in May) for the start of egg laying (Md) are given.

	1971				1972				1973				1983			
	Mean	SD	<i>n</i>	Md	Mean	SD	<i>n</i>	Md	Mean	SD	<i>n</i>	Md	Mean	SD	<i>n</i>	Md
Deciduous																
Linnebjerg	6.93	0.80	28	21	7.15	0.59	20	21	6.61	0.69	28	21				
Frueråften	6.57	0.79	23	20					6.75	0.75	12	26				
Dalby Norreskog	6.85	0.67	20	19	6.61	0.85	18	26								
Bjarsjölagård	6.46	1.05	13	18					6.71	0.76	7	23	6.53	0.70	19	22
Rynke	6.39	0.92	28	24	6.79	1.05	14	?	6.87	0.83	15	21				
Revinge	7.00	0.71	9	18					6.43	0.53	7	24	6.59	0.73	29	20
Coniferous																
Vombs Fure	6.13	1.63	8	21	6.59	0.53	8	25	6.07	1.43	14	26	6.19	0.54	16	24
Revinge													6.31	1.11	13	20

1972). Median laying dates were rather similar, but in most cases the start of laying in deciduous wood preceded that in coniferous wood by a couple of days (the largest difference was 5 days, in 1973).

Similar differences in mean clutch size between deciduous and coniferous forest have also been found in other studies (Creutz 1955, Löhrl 1965, Berndt & Winkel 1967, Lundberg et al. 1981), while Mikhelson (1964) found clutch size to be positively related to a measure of forest productivity within the latter habitat. In two studies the situation was the reverse, i.e. a higher mean clutch size was found in the coniferous habitat (Hanson et al. 1967, Järvinen & Lindén 1980), while Askenmo (in litt.) found no difference in clutch size between the Botanical Garden in Gothenburg (predominantly deciduous) and Svartedalen some 40 km further north (mainly coniferous). In the first two studies, the deciduous habitat was subalpine birch forest which was compared with coniferous forest at a lower elevation and, in Järvinen's and Lindén's study, also at considerably lower latitudes. As a matter of fact, the latter authors explained the trend in clutch size that they observed as an effect of the progressively later laying period at higher latitudes. However, laying dates were very similar in the study of Hanson et al. and their study areas were only some 15 km apart.

Although some of the differences in mean clutch size between the deciduous woods themselves were as large as those between the deciduous and coniferous habitats, the latter

invariably had the lowest mean clutch size (Table 1). Together with the similar results quoted above we regard this as evidence that the mean clutch size of the Pied Flycatcher is in fact smaller in coniferous than in deciduous wood. If this is true, the difference calls for an explanation. Here we will discuss five factors that, either singly or in combination, might affect clutch size in the Pied Flycatcher.

(1) *Breeding density.* Clutch size has been found by some authors to correlate negatively with breeding density (e.g., Curio 1959, Lundberg et al. 1981), but not by others (e.g., Berndt & Winkel 1967, Järvinen & Tast 1980). However, breeding density is usually higher in deciduous than in coniferous woods, so any effect of density would rather be to increase clutch size in coniferous relative to that in deciduous habitats.

(2) *Laying date.* As seen from Table 1, median laying dates were slightly later in the coniferous woods and similar results have been obtained elsewhere (e.g., Berndt & Winkel 1967, Lundberg et al. 1981). In the Pied Flycatcher, mean clutch size has been found to decrease with the progress of the season, the decrease being in the order of 0.06–0.08 eggs per day with a remarkable agreement between studies (Creutz 1955, Lack 1966, von Haartman 1967, 1969, Berndt & Winkel 1967, Källander 1975, Järvinen & Lindén 1980, Lundberg et al. 1981). The decrease does not always begin from the very start of the laying period, however, and in some years and in some places mean clutch size remains stable, or even increases, before

beginning to drop (von Haartman 1969, Järvinen & Lindén 1980, Källander, Karlsson, Rosenlund & Svensson unpubl.). Linear regressions of clutch size on laying date therefore may not adequately describe the relation between clutch size and laying time. Nevertheless, there is reason to expect laying date to have an effect on clutch size in the Pied Flycatcher. Since median laying date was usually a few days later in the coniferous woods, this could potentially explain the smaller mean clutch size in this habitat. However, although it is possible that some of the difference in clutch size between the deciduous and coniferous habitats could be explained by differences in laying dates, a decrease of 0.07 eggs/d is inadequate to account for all of it. Furthermore, in some cases the difference is present despite identical laying dates (and similar distribution of laying dates), so obviously at least part of the difference must have some other cause(s).

(3) *Size of the birds.* Askenmo (1982) found a positive correlation between clutch size and female body weight in the Pied Flycatcher. Since female body weight was highly correlated with wing length (an index of size), this would imply that large females tend to lay large clutches and small females small clutches. Therefore, habitat-linked differences in clutch size could occur if the habitat distribution of females was non-random, i.e., in this case, if small females tended to predominate in the coniferous habitat. Although Lundberg et al. (1981) were able to establish such a size difference in male Pied Flycatchers, they found none among the females. However, we found a statistically significant difference in mean wing length between females in deciduous (Bjärsjölagård) and coniferous (Vombs Fure) woods in 1983 (78.77 vs. 77.56 mm, $P < 0.05$, t -test); this difference, however, may be age-related (see below) and it is difficult to separate the influence of each of these two factors.

(4) *Female weight.* Askenmo (1982) also found that an effect of weight on clutch size still remained after the influence of female size had been accounted for in a partial correlation. He interpreted this result as indicating that flycatcher females adjust their clutch size to prevailing feeding conditions (see also Järvinen 1983).

Some support for this idea was obtained from a positive (but not statistically significant) correlation between mean clutch size and mean

Table 2. Age of Pied Flycatchers at Bjärsjölagård (deciduous) and Vombs Fure (coniferous forest) in the breeding season 1983. 2Y = second calendar year; 3Y+ = third calendar year or older.

	Females		Males	
	Deciduous	Coniferous	Deciduous	Coniferous
2Y	3	11	8	11
3Y+	5	2	5	1
Not aged	3	2	1	1

female weight in different years. Deciduous woods seem to produce more insects, especially lepidopteran caterpillars, than do coniferous woods (e.g., van Balen 1973). So, if female weight reflects feeding conditions, one would expect higher weights in deciduous than in coniferous woods; however, weights taken in these two habitats in spring 1983 failed to reveal any difference of this kind, but weighing time was not standardized and the number of females weighed was small. Lundberg et al. (1981) found a tendency towards higher mean weight in deciduous wood but the difference was not statistically significant. Therefore, a possible habitat-related difference in female weight, perhaps indicative of differing feeding conditions, should be looked for in future studies.

(5) *Age.* In many birds, females breeding for the first time lay smaller clutches than those who have bred before and this has also been found to be the case in the Pied Flycatcher (Creutz 1955, Berndt & Winkel 1967, von Haartman 1969) with the difference being in the order of 0.5–0.8 eggs. Thus, if there was a difference in the age composition of the flycatcher populations inhabiting deciduous and coniferous wood, respectively, this could affect the mean clutch sizes recorded. In 1983, we captured a total of 53 Pied Flycatchers in Vombs Fure (coniferous) and at Bjärsjölagård (deciduous) and aged them on the basis of the method used at Ottenby Bird Observatory to age spring-caught flycatchers (Staffan Bensch, Dennis Hasselquist & Jan Pettersson pers. comm.); the results are presented in Table 2. For females, the distribution is significantly different between the deciduous and the coniferous habitat ($P = 0.04$, Fisher exact probability test), whereas there is only a tendency in the same direction for males ($P = 0.10$). It

should be observed, however, that five females and two males could not be aged and were not included in these calculations. The results should therefore be treated cautiously.

Clearly all factors discussed above are more or less inter-related but, more importantly, they constitute only proximate explanations and therefore immediately give rise to new and more penetrating questions. In our opinion, the results are consistent with the idea that the birds' habitat distribution is the result of competitive interactions (Lundberg et al. 1981), i.e. larger and older birds being able to settle in the most productive habitats. This idea presupposes that some re-distribution takes place between years; that Pied Flycatchers to some extent do change breeding place between years has in fact been shown (e.g., Creutz 1955, Berndt & Sternberg 1965), but whether this movement goes predomi-

nantly from less productive towards more productive habitats, as required by this hypothesis, remains to be demonstrated.

Since both age (von Haartman 1969) and size (Askenmo 1982) has been shown to affect clutch size in the Pied Flycatcher independently of habitat, part of the difference in clutch size between deciduous and coniferous forest could have these direct (proximate) causes. However, an effect of habitat quality on clutch size is likely to remain; otherwise the bias in habitat distribution indicated by our data would have to be explained by fitness gains other than a larger clutch size in the deciduous habitat.

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