

# Annual and local reproductive variations of a Pied Flycatcher *Ficedula hypoleuca* population near a subalpine lake in Central Norway

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The breeding success of the Pied Flycatcher *Ficedula hypoleuca* was studied for 10 years (1986–1995) in a subalpine area of Central Norway. The data were collected from two nest-box transects, one along the exposed shore of a lake (Lauvsjøen) and the other in the more sheltered, innermost part of the same forest. The results showed: 1) significant annual variations in the breeding success and a decline in the breeding population during the study period, 2) the breeding success of pairs nesting near the shore varied more and was significantly poorer than that of those nesting higher up, 3) the difficulties near the shore were most pronounced when the weather was cold and wet in the early part of the breeding season.

## 1. Introduction

In the vicinity of the subalpine lake, Tjulträsk, in Swedish Lapland, breeding deficiencies were noticed in some insectivorous passerine bird species during 1965–76 (Nyholm & Myhrberg 1977). The decline was particularly significant in the local Pied Flycatcher *Ficedula hypoleuca* population. This local “lake effect” was believed to be caused by pollutants affecting limnic insects (mainly Plecoptera) hatching in the lake. More detailed analysis indicated that aluminium, lead and mercury might be the contaminants responsible (Nyholm 1981, 1994, Miles et al. 1993). Acidification from precipitation might also have reduced the amount of calcium available to the birds, causing a deficiency of this essential element during the egg-laying period (Scheuhammer 1991, Nyholm 1994) resulting in eggs with thin, porous shells, a high incidence of clutch desertion (Graveland et al. 1994) and reduced clutch sizes (Tyler 1992).

However, climatological and phenological investigations show that large lakes and reservoirs tend to lower the early summer ambient temperatures by up to several degrees, thereby retarding the phenological development during the spring (Barry et al. 1981, Skaar 1986, Utaaker 1992). Within relatively small areas this might cause some intraspecific, habitat-linked differences in the timing of breeding and thereby reduce the clutch sizes (Perrins 1965, Slagsvold 1976, Lundberg et al. 1981, Järvinen 1982, Thingstad 1992, Reitan & Sandvik 1995) and densities (Thingstad 1995) of passerine bird species breeding near large lakes.

As a “southern newcomer”, the Pied Flycatcher is more sensitive to harsh weather conditions than many other breeding passerine species in northern bird communities (Järvinen 1983, 1986, 1989ab). This makes it suitable to monitor the effects of environmental changes e.g. in climate and food access (cf. Thingstad 1992, 1993, Furness & Greenwood 1993).

The aim of this study was to verify the environmental variables that might be associated with annual and local variations in the breeding success of a Pied Flycatcher population located near a large, seemingly non-polluted, subalpine lake. The main questions were:

- 1) Can the unfavourable local climate in the surroundings of the lake directly and/or indirectly reduce the breeding success and density of the Pied Flycatcher population breeding close to the lake?
- 2) Is this local "lake effect" synergistic with the annual climatic variations during the breeding seasons in question?
- 3) Can variable local climatic conditions cause the same significant breeding deficiencies as have previously been reported to be caused by pollutants?

## 2. Material and methods

### 2.1. Study area

The study was undertaken in subalpine birch-spruce forest close to Lauvsjøen, a lake measuring 3.8 km<sup>2</sup> in Lierne, near the Swedish border in Central Norway (64°20'N, 13°45'E).

A lower transect consisting of 75 standard Great Tit *Parus major*/Pied Flycatcher nest-boxes

Table 1. The mean air temperature (in °C) and mean precipitation (in mm) in May and June at the Lierne observation station of the Norwegian Meteorological Institute during the study period.  $T_{cat}$  = The categorized values used for the mean temperatures of May and June combined.

Year	May		June		$T_{cat}$
	Temp.	Prec.	Temp.	Prec.	
1986	6.8	62	12.3	9	5
1987	3.7	35	9.3	101	2
1988	6.4	38	10.6	12	4
1989	4.7	50	9.6	44	3
1990	5.0	32	10.6	26	3
1991	3.3	32	8.8	93	1
1992	6.5	42	11.9	56	5
1993	6.1	57	6.5	71	2
1994	4.0	18	7.2	103	1
1995	3.7	47	8.7	95	2
Normal	5.4	52	9.8	77	

was placed along the southwestern side of the lake at 538–545 m a.s.l. Another 75 boxes formed an upper transect at 600–680 m a.s.l. The boxes in both transects were spaced about 30 m apart, and the distance between the two transects was 400 to 1 500 m.

Apart from caesium fallout from the Chernobyl accident (Mould 1988), levels of airborne pollutants should be low in this area (Bernes 1993). There are no local contamination sources, and the lake water is almost neutral (pH = 6.4–6.7 according to Nøst 1982). The main types of bedrock in the area are mica schist and mica gneiss (Sigmond et al. 1984), which should be good acidification buffers.

The climatic data come from the Nordli meteorological station (433 m a.s.l.), 7–8 km away. However, as this was not operating in 1988, derived values based on "normal" differences between this station and a nearby one (Harran) had to be used (Aune 1993, Førland 1993) for 1988. The mean air temperature and precipitation in May and June during the study period are shown in Table 1.

A major caterpillar (Geometridae) outbreak began in 1986, lasted through 1987 and declined during the 1988 breeding season. No quantitative data on caterpillar numbers are available, but an index using the values 2 for 1986 and 1987, 1 for 1988 and 0 for the remaining years is used for some analyses.

Hardly any nests were raided by predators; only one brood was lost in 1989 and one in 1991, both in the lower transect.

### 2.2. Data collection

During the 10-year study period from 1986 to 1995, the nest-boxes were examined at least twice each breeding season. Clutches established during the "normal" egg-laying time for the year in question were visited once during the incubation period and once late in the nestling period, when the nestlings were at least 10 days old. All eggs and nestlings, including unhatched eggs and dead nestlings, were registered in each nest. Some eggs might have been lost before the first visit and some eggs/nestlings between the visits, without being noticed. However, possible losses must have been

very low and should not have been skewed towards any particular year or transect as the same registration method was used throughout the period. An additional visit took place after the breeding season, when any dead nestlings in the nests were registered and all the nest material was removed from the nest-boxes.

The data recorded from each nest-box were:

- 1) pair = nest containing at least one egg (Järvinen 1989b)
- 2) eggs = number of eggs in the clutch
- 3) nestlings = number of hatched eggs
- 4) successful pairs = at least one fledgling leaving the nest
- 5) fledglings = number of fledged young.

The BrS index, giving the percentage of eggs producing fledged young (Lundberg & Alatalo 1992: 240), was also calculated.

### 2.3. Statistics

The SPSS/PC Package (Norusis 1988) was used for most of the statistical analyses. Two-tailed probabilities are given. The Spearman rank,  $r_s$ , was used in the correlation analysis. The significance of the differences between the variances was analysed according to Sokal and Rohlf (1981: 190), giving  $F = s_1^2/s_2^2$ , where  $s_1$  is the greatest and  $s_2$  the smallest of the variances for the two samples compared. In the stepwise regression analyses, the adjusted  $R^2$  values were used as these should reflect the goodness of fit more closely than  $R^2$ , since the model usually does not fit the population as well as it fits the sample from which it is derived (Norusis 1988: B-202).

As the variances of the climatic parameters (T1–T10, P1–P10) in this paper are larger than the means, logarithmic transformations are used. For BrS, which is a proportion parameter, an arcsine transformation is used.

## 3. Results

### 3.1. Annual variation

The numbers of breeding pairs, eggs laid and fledglings produced varied considerably during

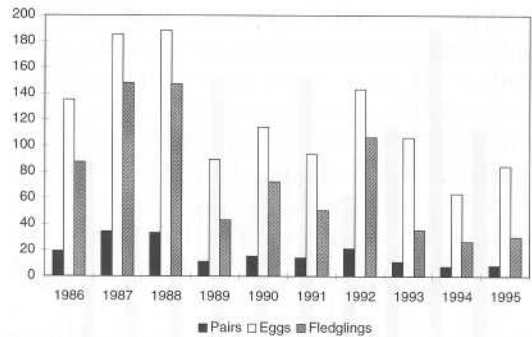


Fig. 1. Number of established pairs (pairs), eggs laid (eggs) and fledglings produced (fledglings) in both transects combined. The  $r_s$  and significance levels for their trends during the study period become  $-0.79$ ,  $p < 0.02$  (pairs),  $-0.69$ ,  $p < 0.05$  (eggs) and  $-0.76$ ,  $p < 0.02$  (fledglings).

the study period (Fig. 1), with 4 or 5 "good" years (1986, 1987, 1988, 1992 and, in particular in the upper transect, also 1990) and 5 "bad" ones (among them, the last three years). Most of the trends have been significantly negative during this 10-year period. The total number of breeding pairs has declined significantly, as have the numbers of eggs and fledglings (Fig. 1). In the upper transect, the numbers of breeding pairs and eggs did not show significant trends (Fig. 2a), but both declined. However, the numbers of successful pairs and fledglings produced declined significantly during the study period. In the lower transect (Fig. 2b), all declined significantly during the study period.

Clutch/brood sizes showed significant differences in egg and nestling numbers from one year to another (ONEWAY:  $F_{(9)} = 3.57$ ,  $p < 0.001$  and  $F_{(9)} = 5.23$ ,  $p < 0.001$  respectively), but according to the Scheffe range test no two years were significantly different at the 0.05 level. The number of fledglings (fledglings I in Table 2) varied significantly ( $F_{(9)} = 6.39$ ,  $p < 0.001$ ), and brood sizes were significantly greater in 1987 and 1988 than in 1993 according to the Scheffe range test. Using the significant level of 0.1 in the Scheffe test, in the last three years (1993, 1994 and 1995) there were significantly fewer fledglings than in 1987 and 1988. When only successful broods (fledglings II in Table 2) are considered, the differences between the years become less distinct ( $F_{(9)} = 1.92$ ,  $p = 0.05$ ).

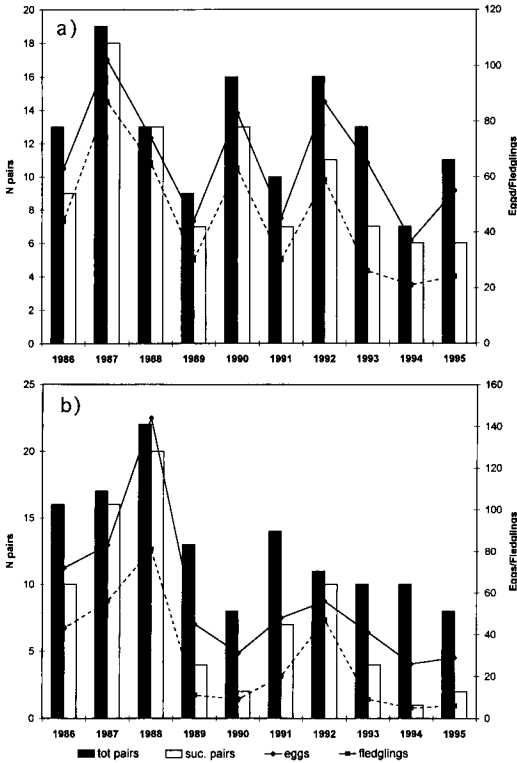


Fig. 2. a) Number of established pairs (tot pairs), successful pairs (suc. pairs), eggs laid (eggs) and fledglings produced (fledglings) within the upper transect during the study period. The  $r_s$  and significance levels for the trends become  $-0.41$ , n.s. (tot pairs),  $-0.73$ ,  $p < 0.05$  (suc. pairs),  $-0.37$ , n.s. (eggs) and  $-0.77$ ,  $p < 0.02$  (fledglings). b) Number of established pairs, successful pairs, eggs laid and fledglings produced within the lower transect during the same period. The  $r_s$  and significance level for the trends become  $-0.77$ ,  $p < 0.02$  (tot pairs),  $-0.71$ ,  $p < 0.05$  (suc. pairs),  $-0.79$ ,  $p < 0.01$  (eggs) and  $-0.74$ ,  $p < 0.02$  (fledglings).

The BrS also showed a negative trend during the study period, although not significant for the lower transect (Fig. 3).

**3.2. Local variation**

In spite of considerable annual variations in reproductive success, there was a prevailing tendency for poorer breeding success in the lower transect compared with the upper one (Table 2). The numbers of eggs, nestlings and fledglings were significantly lower in the lower transect (ac-

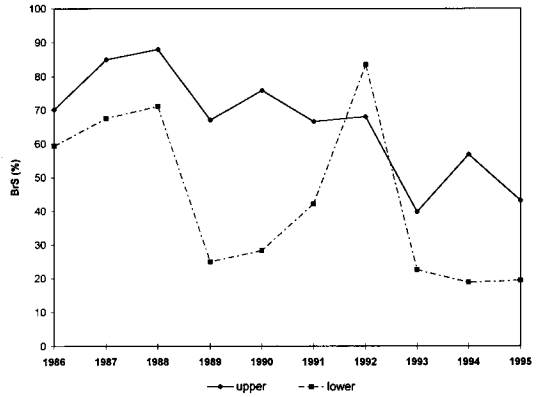


Fig. 3. The breeding success, BrS, given as the percentage of eggs producing fledged young in the upper and lower nest-box transects. The  $r_s$  and significance level for the trend in the upper transect become  $-0.81$ ,  $p < 0.01$  and that for the lower  $-0.64$ , n.s.

ording to the ONEWAY analysis of the 256 clutches, the F values became 22.28, 28.14 and 19.27 respectively, all with  $p < 0.001$ ), and so were the numbers of fledglings for the 173 successful pairs ( $F = 10.74$ ,  $p = 0.001$ ). As many as 41% (53 of 129) of the established pairs (at least one egg laid) deserted their nest in the lower transect, while the corresponding figure for the upper transect was 24% (30 of 127). This difference is significant according to a Chi-square test with Yates' correction ( $X^2 = 5.32$ ,  $p < 0.05$ ).

The coefficient of variations for the clutch sizes ( $CV\% = 100 \text{ S.D./mean}$ ) for the 10 years in question was greatest in the lower transect (cf. Table 2). In the upper transect, the CV% for the egg, nestling, fledgling I and fledgling II numbers were 6.8, 21.8, 27.9 and 13.5, whereas corresponding values for the lower transect were 20.7, 58.8, 73.0 and 24.7. The difference in the CV for the egg numbers was significant ( $F = 5.92$ ,  $p < 0.01$ ), but not for the rest ( $F = 2.48$ , 2.30 and 2.30, respectively).

The annual variation in the breeding success, given as BrS (Fig. 3), also showed the same tendency towards lower values in the transect close to the lake. Only in 1992 did proportionately fewer eggs produce fledged young in the upper transect compared with the lower one. The differences between the BrS index values in the two transects were significant (Wilcoxon matched pairs signed-ranks test,  $Z = -2.60$ ,  $p = 0.01$ ).

### 3.3. Annual versus local variation

Two-way repeated measures, ANOVA, showed that both the year and the transect had significant importance for the breeding success of the Pied Flycatcher, whereas two-way interaction between them gave no significance (year:  $F = 3.74$ ,  $df = 9$ ,  $p < 0.001$ , transect:  $F = 24.01$ ,  $df = 1$ ,  $p < 0.001$ , year  $\times$  transect interaction:  $F = 1.22$ ,  $p = 0.29$ ).

The situation was the same for the number of nestlings and fledglings in all nest-boxes containing established pairs (year:  $F = 5.73$ ,  $p < 0.001$ , transect:  $F = 31.31$ ,  $p < 0.001$ , two-way interaction:  $F = 1.36$ ,  $p = 0.21$  and year:  $F = 7.21$ ,  $p < 0.001$ , transect:  $F = 24.79$ ,  $p < 0.001$ , two-way interaction:  $F = 1.38$ ,  $p = 0.20$ , respectively). When only successful broods were used, the transect variable became the most significant factor (year:  $F = 2.31$ ,

Table 2. Average breeding data (mean  $\pm$  1 S.D.) expressed as number of eggs, nestlings and fledglings (fledglings I) in all clutches (N) and number of fledglings (fledglings II) for the successful pairs only ( $N_1$ ). T = combined values for both transects, U = upper transect, L = lower transect.

Year	Transect	N	Eggs		Nestlings		Fledglings I		Fledglings II		
			Mean	S.D.	Mean	S.D.	Mean	S.D.	$N_1$	Mean	S.D.
All years	T	256	4.7	1.6	3.2	2.3	2.9	2.4	173	4.3	1.7
	U	127	5.2	1.4	3.9	2.2	3.6	2.4	97	4.6	1.6
	L	129	4.2	1.7	2.5	2.3	2.3	2.3	76	3.8	1.7
1986	T	29	4.7	1.9	3.0	2.6	3.0	2.6	19	4.5	1.7
	U	13	4.8	2.0	3.4	2.8	3.4	2.8	9	4.9	1.8
	L	16	4.5	1.8	2.8	2.6	2.6	2.5	10	4.2	1.8
1987	T	36	5.1	1.2	4.1	1.8	4.1	1.8	34	4.4	1.6
	U	19	5.4	1.0	4.6	1.7	4.6	1.7	18	4.8	1.4
	L	17	4.9	1.4	3.6	1.9	3.6	1.9	16	3.8	1.7
1988	T	35	5.4	1.1	4.3	1.9	4.2	2.0	33	4.5	1.7
	U	13	5.7	0.8	5.0	1.6	5.0	1.6	13	5.0	1.6
	L	22	5.2	1.2	3.8	2.0	3.7	2.0	20	4.1	1.7
1989	T	22	4.0	1.7	2.0	2.3	2.0	2.3	11	3.9	1.8
	U	9	4.9	1.8	3.6	2.3	3.6	2.3	7	4.6	1.3
	L	13	3.5	1.5	0.8	1.7	0.8	1.7	4	2.8	2.1
1990	T	24	4.8	1.7	3.3	2.4	3.0	2.5	15	4.8	1.1
	U	16	5.2	1.5	4.3	1.8	3.9	2.2	13	4.8	1.1
	L	8	3.9	1.9	1.1	2.1	1.1	2.1	2	4.5	0.7
1991	T	24	3.9	1.8	2.3	2.2	2.1	2.1	14	3.6	1.6
	U	10	4.5	1.8	3.0	2.4	3.0	2.4	7	4.3	1.5
	L	14	3.4	1.7	1.9	2.1	1.4	1.7	7	2.9	1.3
1992	T	27	5.3	1.4	4.4	2.1	3.9	2.5	21	5.0	1.6
	U	16	5.4	1.3	4.5	2.2	3.7	2.8	11	5.4	1.5
	L	11	5.1	1.5	4.3	2.1	4.3	2.1	10	4.7	1.6
1993	T	23	4.6	1.7	2.1	2.2	1.5	1.9	11	3.2	1.4
	U	13	5.0	1.7	2.5	2.4	2.0	2.2	7	3.7	1.5
	L	10	4.1	1.6	1.5	2.0	0.9	1.2	4	2.3	0.5
1994	T	17	3.7	1.9	1.7	2.3	1.5	2.3	7	3.7	2.3
	U	7	5.3	1.0	3.0	2.6	3.0	2.6	6	3.5	2.4
	L	10	2.6	1.5	0.8	1.8	0.5	1.6	1	5.0	–
1995	T	19	4.4	1.2	3.2	1.9	1.6	2.1	8	3.8	1.5
	U	11	5.0	0.6	4.3	1.1	2.2	2.4	6	4.0	1.7
	L	8	3.6	1.3	1.6	1.6	0.8	1.4	2	3.0	–

$p < 0.02$ , transect:  $F = 34.85$ ,  $p < 0.001$ , two-way interaction:  $F = 0.45$ ,  $p = 0.91$ ).

### 3.4. Possible causes of variation

A superficial comparison between the weather conditions during the breeding seasons (Table 1) and the reproductive output of the local breeding population of Pied Flycatchers showed that, apart from 1987, there seemed to be a close connection between warm weather and good breeding success (Fig. 1). By categorizing the mean temperatures for May and June combined (from 1 for the worst conditions to 5 for the best, cf. Table 1) and the amount of caterpillars (given the values 0–2 cf. 2.1), it is possible to make another analysis of two-way repeated measures for the 256 clutches. The mean temperatures were found to have some significant importance for the number of eggs laid ( $F = 3.18$ ,  $p = 0.01$ ) and the number of nestlings ( $F = 2.62$ ,  $p < 0.04$ ), but the amount of caterpillars did not give any further contribution ( $F = 0.06$

and 0.37). However, the two-way interactions were significant (temp  $\times$  caterpillar:  $F_{\text{egg}} = 6.27$ ,  $p = 0.01$  and  $F_{\text{nestl}} = 15.68$ ,  $p < 0.001$ ). When the production of fledglings was considered, the amount of caterpillars gave a significant contribution ( $F = 4.19$ ,  $p < 0.02$ ), but not the temperature ( $F = 1.60$ ). The two-way interactions (temp  $\times$  caterpillar) were again significant ( $F = 7.00$ ,  $p < 0.01$ ).

Additional analysis using the mean temperature and precipitation during 5-day periods (pentads) in the breeding season was done to confirm the connections between the breeding success and the climatic conditions. The first pentad began on 22 May and the last one ended on 10 July, putting the third and fourth pentads within the "normal" egg-laying period (1–11 June) and resulting in T1–T10 and P1–P10 for temperature and precipitation.

When the mean clutch and brood sizes for the two transects were examined separately (U = upper, L = lower) and combined (T) (cf. Table 3), stepwise regression analyses confirmed that a significant proportion of clutch size variations can

Table 3. Results of stepwise regression analysis of the climatic parameters used to explain the annual variations in clutch and brood sizes. The parameters used in the equations are given to the left. P1–P10 refer to the precipitation and T1–T10 to the mean temperature during the pentads 1–10 (1 = 22–26 May, 2 = 27–31 May, 3 = 1–5 June and so on). The variable applied to the model at each step is shown. Up = upper transect, Low = lower transect, Tot = both transects combined, the multiple R (R), adjusted R square (R<sup>2</sup>), F value for testing the overall regression (F) and its significant level (p) are also given.

Parameters	Dependent variable	Step	Variable	R	R <sup>2</sup>	F	p
	Eggs Up	1	Log P2	0.740	0.491	9.696	0.014
P1–P4	Eggs Low	1	Log T2	0.733	0.479	9.262	0.016
T1–T4	Eggs Tot	1	Log T2	0.897	0.781	33.115	0.000
P1–P7	Nestlings Up	1	Log T2	0.846	0.461	20.162	0.002
T1–T7	Nestlings Low	1	Log P2	0.758	0.521	10.772	0.011
		2	Log T4	0.922	0.808	19.958	0.001
	Nestlings Tot	1	Log T2	0.897	0.781	33.115	0.000
P1–P10	Fledglings I Up	1	Log T7	0.680	0.395	6.877	0.031
T1–T10	Fledglings I Low	1	Log P2	0.729	0.473	9.082	0.017
		2	Log T4	0.936	0.840	24.552	0.001
	Fledglings I Tot	1	Log T2	0.690	0.410	7.254	0.027
	Fledglings II Up	1	Log T4	0.865	0.716	23.664	0.001
		2	Log P1	0.941	0.853	27.134	0.001
		3	Log T1	0.974	0.924	37.518	0.000
	Fledglings II Low	1	Log T3	0.736	0.484	9.447	0.015
		2	Log T9	0.867	0.681	10.626	0.008
		3	Log P10	0.961	0.884	23.930	0.001
		4	Log P2	0.994	0.977	97.837	0.000
	Fledglings II Tot	1	Log T4	0.900	0.787	34.291	0.000

be explained by climatic conditions alone. In fact, the mean temperature during the period 27–31 May (T2) explained 78% of the mode of the variation in the mean clutch size for the two transects combined (Egg Tot in Table 3), and as much as 98% of the mean brood size variation in the lower transect (Fledglings II Low in Table 3) could be explained by the T3, T9, T10 and P2 pentad values during this 10-year study. In the analyses using the number of eggs as dependent variables, only the pentads for the periods prior to the nestling phase are used, and for the analyses using the number of nestlings as dependent variables only the seven periods prior to the normal hatching time for the eggs are used.

The number of young fledged the previous year may also have influenced the number of established pairs the following year, as was the case for the lower transect during this study (the stepwise regression analyses in Table 4 showed that this parameter gave a significant contribution to explain the number of pairs in this transect, but not for the total number of pairs nor for those in the upper transect).

## 4. Discussion

### 4.1. Trends and dynamics in the breeding population

Although considerable variation in the breeding parameters of the local Pied Flycatcher population was recorded during this 10-year survey

(1986–95), the overall trend was a significant decline (Fig. 1). A similar trend has been found in several recent Fennoscandian studies of the Pied Flycatcher (Enemar et al. 1984, Virolainen 1984, Solonen 1986, Petersen & Brøgger-Jensen 1992), although Järvinen (1989b) found no long-term trend.

However, caterpillar outbreaks in northern subalpine birch forest are highly irruptive within an approximately 10-year cycle (Tenow 1972, Haukioja 1991). The importance of a superabundance of *Epirrita* caterpillars for insectivorous bird species is not fully understood (Lennerstedt 1983, Enemar et al. 1984), but Brambling *Fringilla montifringilla* densities in subalpine birch forest are known to be highest in years with high caterpillar density (Lindström 1987). A long-term study of insectivorous bird species in this particular habitat must therefore cover at least two such peak periods for caterpillars before the real trend in the breeding population can be revealed and the factors causing the dynamics understood. The caterpillar outbreak here occurred during the first two to three years of the survey, which could well account for some of the declining trend observed.

### 4.2. Some factors which may influence breeding success

Some habitat-related differences in clutch size are known to occur in the Pied Flycatcher and other passerines (Lundberg et al. 1981, Gezelius et al. 1984, Telleria et al. 1992, Thingstad 1992, Sjöberg et al. 1993, Sanz 1995, Siikamäki 1995). How-

Table 4. Results of stepwise regression analyses when the number of young produced the previous year are added to the climatic parameters and used to explain the annual variations in the numbers of established pairs during the 9-year period of data. Young Up = Number of young produced in the upper transect the previous year. Young Low = Number of young produced in the lower transect the previous year. Young Tot = Total number of young produced in the two transects combined the previous year. – = no variable entered. For further explanations, see the text of Table 3.

Parameters analysed for	Dependent variable	Step	Variable entered	R	R <sup>2</sup>	F	p
P1–P10 T1–T10 Young Up Young Low Young Tot	Pairs Up	–	–				
		1	Young Up	0.779	0.550	10.777	0.013
	Pairs Tot	1	Log P2	0.737	0.479	8.341	0.023
		2	Log T7	0.956	0.884	31.476	0.001
		3	Log P9	0.987	0.959	63.452	0.000

ever, since the habitat type and the vegetation structure and mosaic were considered to be identical in the two transects studied here, habitat should be of little importance for explaining the variations. The mating status of the female may be an important factor (Lundberg & Alatalo 1992: 106) as some polygyny is known to occur in the Pied Flycatcher (Alatalo et al. 1981). However, polygyny is reported to be infrequent among northerly breeding populations (Nyholm 1984) and its possible impact on the local and annual variations in breeding success is probably rather low at Lauvsjøen.

The daily intake of nutrient has to be sufficient to form eggs during the pre-breeding period (Krementz & Ankney 1995). Insufficient calcium is known to reduce clutch sizes, and eggs laid may also be lighter and their shells thinner (Tyler 1992). However, birds can only afford to spend a limited amount of energy on reproduction when conditions are very unfavourable (Järvinen 1986), and more protein and calcium are lost at low temperatures (Scott & Balnave 1991). Thus, even though the levels of airborne pollutants are thought to be low in this marginal habitat, the synergetic effects of climatic stress and reduced availability of calcium and protein may be serious during long spells of bad weather, giving a result similar to that described as an acidification effect (Scheuhammer 1991, Tyler 1992, Nyholm 1994). As adult birds normally forage near their nests (but see Lennerstedt 1983), breeding deficiencies noted in populations nesting close to large lakes may primarily be caused by the harsher, local climatic conditions in this edge habitat.

### 4.3. Weather conditions and breeding success

A highly varying reproductive success was found during this study. Rough comparison with weather conditions in May and June (Table 1 and Fig. 1) seems to show some correlations between the breeding and weather parameters. It was shown, by means of some more detailed analyses, that weather conditions in the early breeding season were important and explained most of the variations, particularly the mean numbers of eggs laid and hatched. As the physiological condition of females during the egg-formation period is essen-

tial for the clutch sizes, bad weather during this period is known to have catastrophic consequences, far exceeding the "calendar effect" (cf. Haartman 1967, Källander 1975) for breeding Flycatchers in northern habitats (Järvinen & Lindén 1980, Järvinen & Väisänen 1983, Lundberg & Alatalo 1992: 64–65). The annual start of egg-laying can consequently be predicted by the weather conditions during the pre-breeding period (Slagsvold 1976). Egg-laying normally starts about five days after a particularly warm, sunny period. Thus, the mean date for the first egg laid varied from 28 May to 15 June in another subalpine birch forest at Nerskogen in Central Norway during 1989–92 (Thingstad 1992). A great variation has also been noted in this Lierne area, but precise records are lacking. However, this weather response might have weakened the correlations between breeding parameters and pentads. Nevertheless, broadly speaking, the first two pentads used in the analyses represent the establishment phase of the local population of the Pied Flycatcher, the next two the egg-laying phase, pentads 5–7 the incubation phase and pentads 8–10 the nestling phase.

Tompa (1967) and Borgström (1983) found that cold, wet weather during the nestling phase gave the most significant losses, but at Lauvsjøen this was only the case in the last year. Instead, the losses in the clutches were normally most pronounced during the incubation phase (cf. the small divergence between the mean number of nestlings and fledglings in Table 2), and were particularly great in the lower transect. The mean temperature and precipitation between 27 and 31 May (T2 and P2), together with the mean temperatures between 6 and 10 June (T4) and 21 and 25 June (T7), seem to have been the critical factors for production of young in the lower transect (Table 3). This indicates that most eggs were laid in years when there were warm, dry conditions during the establishment phase, and that the greatest hatching success was attained in years with relatively warm weather during the later parts of the egg-laying and incubation phases (see also Järvinen 1989b). These results may to some extent reflect a "calendar effect", since cold conditions during the later part of the normal egg-laying phase delayed egg-laying and thus reduced clutch sizes.

In addition, the number of caterpillars was another important factor explaining the variations



in the total production of young in the two transects combined. The production of young the previous year, particularly in the upper transect, seemed to be yet another factor of importance. It went a long way towards accounting for the number of established pairs (and consequently also the number of eggs laid) in the lower transect. However, this probably only reflects the influx of more immigrants to this marginal habitat in years following surplus production in more optimal surrounding habitats.

#### 4.4. Consequences of the “lake effect”

Although dynamics in a limited area are most likely to be linked to events happening on a much greater scale (breeding success in more optimal areas, events in distant wintering areas and so on), the variations in most of the breeding parameters used in this study can be largely explained by the weather conditions during the breeding seasons, and to some extent also the breeding success the previous year and/or caterpillar irruptions.

The suitability of the lower transect was decreased by the “lake effect” (Järvinen 1982), which means that a zone close to lakes has lower early summer temperatures and is more exposed to wind from the open water surface than a more sheltered area at higher altitudes further from the shore (Skaar 1986, Utaaker 1992). However, pairs of Pied Flycatchers established in a nest-box transect close to a lake seem to start their egg laying at the same time as those breeding in a more sheltered area; hence, there is probably no “calendar effect” between the two transects (Thingstad 1993: 38, but see Järvinen 1982).

Great variations in density and breeding success are known to exist among birds in harsh northern environments where physical factors such as wind and low temperatures prevail (Whittaker 1972, Järvinen & Väisänen 1984, Svensson et al. 1984, Järvinen 1989a, Thingstad 1995). This fits well with the results from this study, where the variation was great, in particular in the transect close to the lake (cf. the CV values). According to Virolainen (1984), self-maintenance for a local Pied Flycatcher population requires 4.6 fledglings per successful brood. On average, only 3.8 fledglings were produced in the lower transect in

this study area. Therefore, in many ways, the lower transect seemed to behave as a “sink” habitat, its breeding population of Pied Flycatchers only being maintainable through a surplus of individuals from some “source” habitat (cf. Wiens & Rotenberry 1981, Wiens 1989: 173).

This study emphasizes that just a few natural physical and biological factors might explain a considerable proportion of the annual and local variations in the breeding success of a Pied Flycatcher population located close to a large subalpine lake. In many ways, the local breeding deficiencies for the pairs nesting close to the shore of Lauvsjøen, situated in an area with low levels of airborne pollutants, are similar to those previously reported to be caused by pollutants (low breeding success, many deserted clutches, and so on). However, as much as 97.7% of the variation in the number of fledglings for the successful pairs in the nest-boxes located near the shore of Lauvsjøen was explained by climatic parameters alone. The local reductions in the number of successful breeding pairs, clutch sizes and young produced were most pronounced in years with bad climatic conditions. This “lake effect” might not have been noticed during a study period that was too short, as shown by the breeding success (e.g. given as BrS), which was greatest in the lower transect in 1992, a year with particularly good weather conditions during the breeding season.

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#### Sammanfattning: Årlige och lokale reproduksjonsvariasjoner i en Svarthvit Fluesnapper populasjon ved en subalpin innsjø i Midt-Norge

I løpet av 10-års perioden 1986–1995 ble hekkesuksessen til svarthvit fluesnapper *Ficedula hypoleuca* undersøkt i et subalpint skoghabitat i Midt-Norge. Data ble samlet fra to kassefelter, der det ene fulgte stranda til en innsjø og det andre var utplassert i et mer skjermet område et stykke fra sjøen. Det ble påvist: 1) signifikante årlige varias-

joner i hekkesuksess, men likevel en negativ trend i hekkebestandens størrelse, 2) gjennomgående dårligere hekkesuksess og større årlige variasjoner hos de parene som hekket nede ved innsjøen enn hos de som hekket i et mer skjermet område innenfor det samme skoghabitatet, 3) ulempene med å hekke nede ved innsjøen var spesielt merkbare i år med kaldt og vått vær under de tidligste fasene av hekkesesongen.

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