

## Nesting density and breeding performance of the Pied Flycatcher *Ficedula hypoleuca* near the tree line in Swedish Lapland

Botäthet och häckningsframgång hos svartvit flugsnappare *Ficedula hypoleuca* nära trädgränsen i Lappland

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The Pied Flycatcher *Ficedula hypoleuca* is absent or very rare as a breeding bird in the subalpine birch forests in the Ammarnäs area of southern Swedish Lapland (ca 66° N). By introducing a surplus of nest-boxes the density was raised many times. On average 20% and maximally 40% of the nest-boxes were occupied. There was no difference in breeding density between the coniferous zone at 430-600 m, and the birch zone at 600-760 m., nor between different elevations within the birch zone. The flycatchers never bred in the transition zone to the alpine heath (at this site this zone is several hundred metres wide with birch groves and single birches). Thus, up to the border of closed forest the scarcity of nest sites limited distribution, whereas above that border some other, unknown factor prevented breeding. Possibly, this zone is too exposed to winds to allow a "flycatching" bird to collect enough food. No difference in clutch size or breeding success between elevations was observed. Average clutch size was 5.41 and the number of fledged young 4.43, suggesting that recruitment may balance mortality. Clutch size declined at a rate of 0.5 eggs per week and along a regression line common with that of populations in South Scandinavia.

Den svartvita flugsnapparen saknas eller är mycket sällsynt som häckfågel i de subalpina björkskogarna i Ammarnäsområdet i södra Lappland. Genom att sätta upp holkar i överskott höjdes tätheten många gånger. I genomsnitt 20% och upp till 40% av holkarna blev bebodda i fattiga björkskogar nära trädgränsen. Det fanns ingen skillnad i häckningstäthet mellan barrskogszonen på 430-600 m höjd och björkskogszonen på 600-760 m höjd, och inte heller mellan olika nivåer inom björkzonen. Däremot häckade flugsnapparen aldrig i övergångszonen till fjällheden (på denna plats flera hundra meter bred med björkdungar och enstaka björkar). Upp till gränsen för den slutna skogen var det alltså avsaknaden av bohål som begränsade utbredningen, medan det ovanför denna gräns var någon annan, okänd faktor som förhindrade häckning. Förslagsvis kan det vara den öppna och vindexponerade situationen som gör det omöjligt för en fågel med flugsnapparens jaktmetod att försörja sig där. Ingen skillnad i kullstorlek eller häckningsframgång mellan olika nivåer observerades. I medeltal var kullstorleken 5,41 ägg och antalet flygga ungar 4,43, vilket innebär att produktionen möjligen balanserar dödligheten. Kullstorleken minskade med 0,5 ägg per vecka under säsongen och minskningen följde samma regressionslinje som hos populationer i södra Skandinavien.

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## Introduction

Over considerable parts of its range the availability of suitable nest cavities is an important limiting factor determining the occurrence and breeding density of the Pied Flycatcher *Ficedula hypoleuca*. This is clearly demonstrated by results obtained in numerous nest-box experiments. When boxes are put up, the Pied Flycatcher increases in number. This was the case in the subalpine birch forests of the Ammarnäs area, upper Vindel River valley in southern Swedish Lapland. By the introduction of nest-boxes, the breeding density increased many times in rich and moist birch woodlands on the lower slopes of the mountains at Ammarnäs (Enemar & Sjöstrand 1972). The average density without nest-boxes was 1.5 pairs per 10 ha, whereas it increased to about 25 pairs per 10 ha with a surplus of nest-boxes.

When nest-boxes were supplied the Pied Flycatcher also reached a considerable density in poorer forests at higher elevations. The normal density in this type of woodland and at this elevation is zero or close to zero. No breeding pairs were recorded in a study of 14.3 ha over a period of 10 years (Hanson et al. 1966 and the LUVRE archives). In an adjacent similar plot of 14.5 ha with boxes an average of about 9 pairs per 10 ha was observed over a period of several years. The natural scarcity of Pied Flycatchers in poorer birch woods at higher elevations was also confirmed by line transect censuses. Only 0.3 singing males were recorded per hour in comparison with 3.1 in the meadow birch woods at the lower elevations (Enemar 1964). Similar results in forest near the tree line were obtained by, for example, Meidell (1961), Valane et al. (1968) and Pulliainen (1977) who were all able to raise the number of Pied Flycatchers considerably from levels close to zero by erecting nest-boxes.

Thus, the absence of suitable nesting cavities limits the altitudinal as well as the spatial distribution of the Pied Flycatcher in North Scandinavia. The following questions were posed: (1) At what elevation would the Pied Flycatcher cease to breed if there were nest-boxes available right up to the tree-line? (2) If the Pied Flycatcher did not breed at the high-

est elevations, would there be a continuous decline of density or an abrupt one at a certain elevation? (3) Would there be any measurable altitudinal decline in clutch size or breeding success, or a delay in the onset of breeding, as one moved up the slope? (4) How would density, breeding date, clutch size and breeding success vary between years?

I will also treat the seasonal decline in clutch size, the so called "calendar effect" of Haartman (1967), and the length of the breeding season in relation to the possible time constraints in a northern area.

## Study areas, methods and material

The study area, "Kraipe", is located on the north-facing slopes of the Vindel River valley between the villages of Djupfors and Kraddsele about 15 km southeast of Ammarnäs (65° 51' N, 16° 23' E; Fig. 1).

The first part of the study was carried out in 1971-1973. Nest-boxes were put up along a road, the lowest ones at 430 m (close to the valley bottom at 400 m) and the highest ones in the last scattered birches at 770 m, above the line of closed forest which runs here at about 750-760 m. The nest-boxes were put up alternately on both sides of the road every 25 m and at 5-25 m from the roadside, some at the forest edge and some within the forest. The uppermost nest-boxes were placed in four parallel rows 100 m apart (all in trees) and perpendicular to the forest line, and with the boxes 50 m from each other in each row (Fig. 1).

The results from 1971-1973 showed that the most interesting zone was the uppermost part of the birch belt close to the forest line. Accordingly, in 1974-1976 the boxes were moved and placed in two lines running closely below and parallel with the forest line (A and B in Fig. 1).

Before the breeding season of 1980 all the boxes were put up again, now in area C (Fig. 1) and spread between an elevation of about 700 m and the forest line at about 760 m. They remained there through 1985 and served to increase the sample size for the study of between-year variation.

In all years (except 1973) I also checked 41 nest-boxes in a permanent plot in the birch

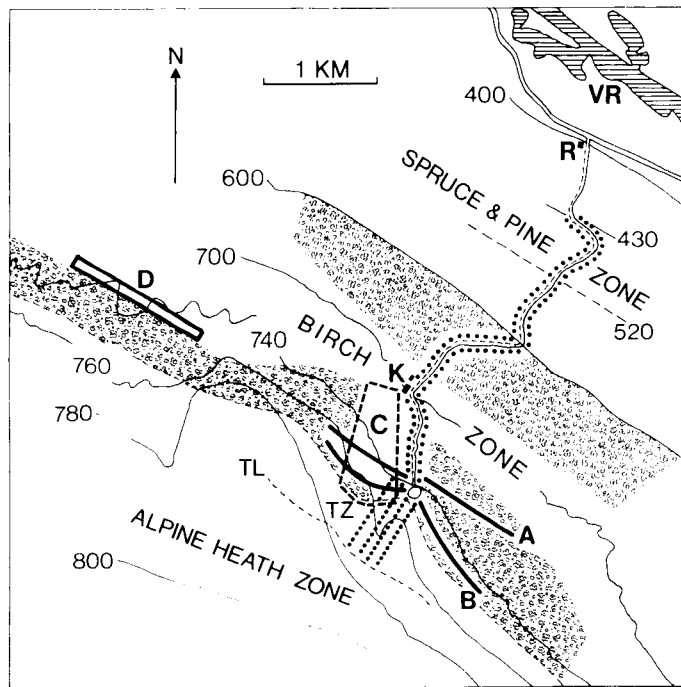


Fig. 1. Map of the study area. VR = the Vindel River in the valley bottom. R = Räftemyra. K = Kraipe reindeer butchery. TZ = Transition zone with clumped and scattered birches between the birch zone and the alpine heath. TL = Tree line. The figures give elevation in metres above sea level. Nest box locations: The dots along the road and in the transition zone show the location of the nest-boxes in 1971-1973 (the dots do not show the precise location and number of boxes in different parts of the lines). A and B is the upper and lower line of nest-boxes in 1974-1976. C is the area with nest-boxes in 1980-1985. D is the area with nest-boxes through the whole period 1971-1985. The Kraipe reindeer butchery has the coordinates 65° 51' N, 16° 23' E.

zone about 2 km west of the reindeer butchery (D in Fig. 1). In this plot there were also 10 boxes with 50 mm entrance holes for Redstarts *Phoenicurus phoenicurus*, but they were never used by the flycatchers (cf. Enemar 1980, who also found that the flycatchers in this area avoid boxes with large holes).

The nest-boxes along the road in 1971-1973 were divided into groups according to habitat and elevation: the lower (430-520 m) and upper (520-600 m) coniferous zones, the lower (600-700 m) and upper (700-750 m) birch zones, the edge zone (750-760 m), and the alpine zone (760-770 m), the latter comprising the transition zone with scattered

groves and trees above the line of closed, continuous forest. The edge zone was arbitrarily taken as 50 m (horizontally) directly below the forest line.

In 1974-1976 the nest-boxes were divided into two groups corresponding to the upper (750-760 m) and lower (below 750 m) line, respectively. The results from area C, 1980-1985, were pooled since, as will be shown, there were no differences between elevations.

The coniferous zone is characterized by mixed pine *Pinus silvestris* and spruce *Picea abies* stands in the lower part and almost pure spruce forest in the upper part. A few birches occur among the conifers, particularly along

Tab. 1. Density (expressed as % occupied nest-boxes), clutch size and production of young in different zones of elevation and habitat (birch and coniferous) in 1971-1973, in the two lines at high elevation in 1974-1976, in Area C in 1980-1985 and in the permanent Area D in 1971-1985. — "N" for clutch size is sometimes smaller than "No. of nests" because a few clutches that were not completed are included in the latter figure.

Zone or area	No. of nest-boxes	No. of nests	Density % occupation	Clutch size											Mean	Hatched %	Fledged of hatched %	Fledged of eggs %
				2	3	4	5	6	7	8	9	10	11	12				
Coniferous, lower part	105	20	19.0	0	1	0	6	10	3	0	20	5.70	88.3	100.0	88.3			
Coniferous, upper part	84	18	21.4	0	1	0	5	8	3	0	17	5.71	76.7	100.0	76.7			
Birch, lower part	98	21	21.4	0	1	4	6	7	1	0	19	5.16	89.1	85.4	76.1			
Birch, upper part	116	23	19.8	0	2	2	7	8	4	0	23	5.43	88.7	100.0	88.7			
Birch, edge of closed forest	32	0																
Above edge of closed forest	74	0																
Coniferous, lower and upper	189	38	20.1	0	2	0	11	18	6	0	37	5.70	82.2	100.0	82.2			
Birch, lower and upper	214	44	20.6	0	3	6	13	15	5	0	42	5.31	88.9	94.6	84.1			
Birch, lower line (A)	120	31	25.8	0	0	7	10	12	2	0	31	5.29	85.2	96.2	82.0			
Birch, upper line (B)	120	25	20.8	0	0	5	12	7	1	0	25	5.16	92.1	86.1	79.3			
Birch, both lines (A+B)	240	56	23.3	0	0	12	22	19	3	0	56	5.22	89.2	90.2	80.4			
Birch, plot C	410	73	17.8	0	1	6	26	35	3	1	72	5.50	85.0	97.1	82.5			
Birch, plot D	563	136	24.2	1	5	11	36	38	17	2	110	5.49	87.4	93.7	81.9			
Birch, all plots and years	1427	309	21.7	1	9	35	97	107	28	3	280	5.41	87.3	93.7	81.8			

the roadsides. The border between the coniferous and birch belts is very distinct, and less than 50 m wide. The forest line is also very distinct. The closed birch forest abruptly changes into a patchy zone (TZ in Fig. 1) of alternating birch groves and open alpine heath or willow fields. The birch groves decrease successively in size and number until the last windblown birches give way to scrubs and other low alpine vegetation.

The birch belt is mostly not of the rich and luxuriant meadow type found, for example, west of Ammarnäs. It is dominated by a rather poor and dry type with Junipers *Juniperus communis*.

The nest-boxes used in the two experimental areas in 1971-1973 and 1974-1976 and again in area C in 1980-1985 were of the "Boman" type from Hammarplast AB, i.e. made of a somewhat porous, grey-brown plastic material. The bottom area was circular and about 90 cm<sup>2</sup>. The entrance hole was 35 mm in diameter. The nest-boxes used in plot D were made of wood with a square bottom area of 100 cm<sup>2</sup> with an entrance hole of 35 mm diameter.

## Results

### Breeding density

The flycatcher density is expressed as the percentage of nest-boxes where at least one egg was laid. All data for different elevations are given in Tab. 1 whereas the data for the birch belt for the whole period 1971-1985 are shown in Fig. 2.

There was no change in density with altitude in 1971-1973 until close to the forest line where the flycatchers suddenly ceased to breed. This occurred about 200 m (horizontally) below the forest line (20 m vertically). The number of nest-boxes in this narrow zone was not high enough to tell precisely where the birds ceased to breed. There were two attempts (start of nest-building) 50-100 m below the forest line.

The two nest-box lines of 1974-1976, however, clearly showed that breeding ceased in a very narrow zone comprising the last 50 m (horizontally) below the forest line. This distance is well within a feeding territory. Thus, the Pied Flycatcher breeds all the way up to

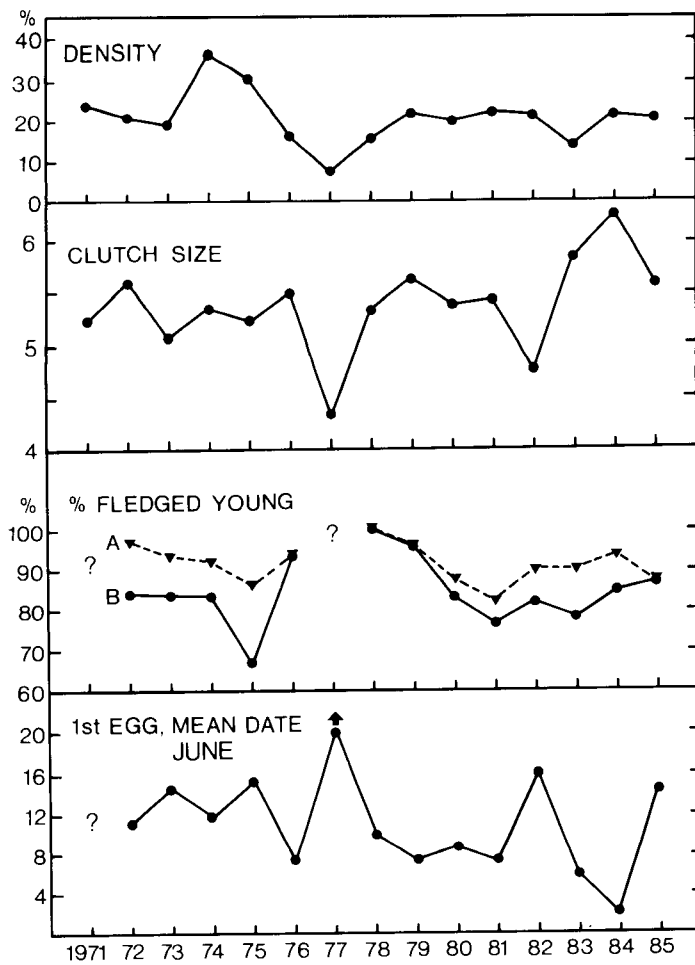


Fig. 2. Density (per cent occupied nestboxes), mean clutch size, production of young, and mean date for laying of the first egg (all nests in the birch zone, 1971-1985). The production of young is given as a percentage of fledged young: (B) including complete losses of clutches of broods and (A) excluding complete losses. The mean date for 1977 is uncertain but exceptionally late (probably around 27 June, 3 nests).

the border of closed forest, but above that border not a single breeding attempt was recorded.

The average density (box occupancy) for the whole birch zone in 1971-1985 was 21% (Fig. 2). The coefficient of variation was 33%. In most years the density deviated very little from mean density. Higher densities were recorded in 1974-1975 and lower density in 1977.

#### *Time of laying*

The start of laying (first egg) was usually determined by calculating the date back from hatching date using 14 days for the incubation period and a laying rate of one egg per day. For some clutches the time was calculated using an estimate of the age of the young.

The start of laying was not determined in 1971. In 1972 and 1973 there was a small but insignificant difference (later in the birch

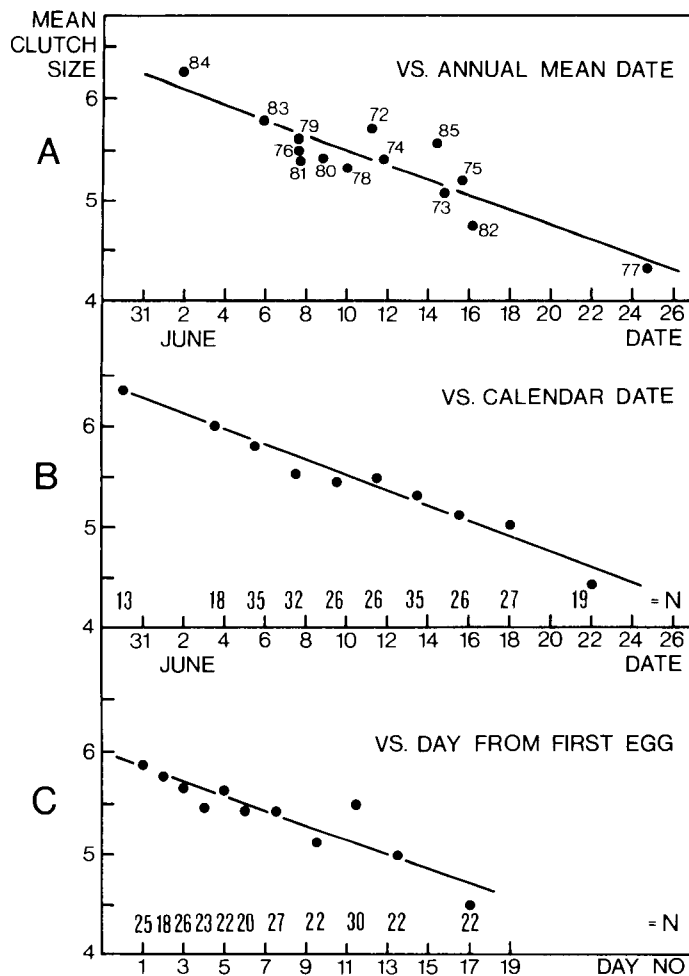


Fig. 3. Mean clutch size versus time of laying the first egg for all nests in the birch zone. The linear regression lines have the slopes -0.52 (A), -0.53 (B), and -0.49 (C) eggs per seven days. The correlation coefficients were: -0.90 (A), -0.98 (B), and -0.95 (C), all significant at the 0.1% level. Sample size for the different years were (1972 through 1985): 14, 12, 39, 18, 3, 23, 25, 21, 10, 22 and 21, respectively. Sample sizes for B and C are given in the figure.

zone) between the coniferous and birch zones, 2.4 and 3.4 days, respectively.

There was no difference between the two lines in 1974-1976: line A was 1.1 days earlier in 1974, 0.7 days earlier in 1975 and 1.5 days later in 1976.

The most pronounced differences were not between elevations but between years (Fig. 2). 1984 was the earliest year with the mean

start of laying on 2 June. Comparatively late years were 1973, 1975, 1982, and 1985 with a mean start of laying on 14-16 June. 1977 was an exceptionally late year (only three clutches, laid 20-30 June).

In each year the laying period varied in length but the number of days between the start of the first and last clutch was never longer than 23 days. The majority of the

clutches was started during a much shorter period. Taking all years together 50% of the clutches were started during the first six days and 75% during the first 11 days.

#### Clutch size

Clutch size in 1971-1973 did not differ between the lower and upper coniferous zones, nor between the lower and upper birch zones. There was a slight difference between the coniferous and the birch zones: 5.70 versus 5.31 eggs, which is not significant ( $0.05 < p < 0.10$ ). Perhaps the small difference can be explained by the slightly later laying date in the birch zone, although this difference was also not significant.

It was not possible to detect any difference in clutch size between the two lines close to the forest line in 1974-1976, the difference of 0.13 eggs being far from significant ( $p > 0.10$ ).

It can be concluded that there is no difference or only a very small difference in clutch size between different elevations.

Fig. 2. shows that mean clutch size varied little during the 15-years period, with three exceptions: lower in 1977 and 1982 and higher in 1984.

Fig. 3. presents clutch size versus time in three different ways. All three give a clutch size decline of 0.07-0.08 eggs per day or about 0.5 eggs per week, very similar to the seasonal rate of decline in other populations of Pied Flycatchers.

From my data the best fit to a straight line is obtained for clutch size versus calendar date but the fit is almost as good for clutch size versus the number of days from the first egg. The fit is less good for the annual mean clutch size versus annual mean date. Within a rather long time period, at least the 10 days between 6 and 15 June (i.e. excluding 1977, 1982, 1983 and 1984) there is little or no decline (slope -0.029/day,  $r = -0.48$ , N.S.). The slope of the regression line is mainly determined by the very early year of 1984 and by the very late year of 1977 (with only 3 clutches). Excluding these two years provides, however, a slope of -0.056/day ( $r = -0.70$ ,  $0.01 < p < 0.02$ ).

#### Breeding success

Breeding success (per cent fledged young of eggs laid in completed clutches) did not differ between the coniferous and birch zones, being 82% and 84%, respectively. Breeding success was also the same in the two lines of 1974-1976 and in plots C and D.

Breeding success was better than 75% in all years with the exception of 1975 when it was 67%, still a fairly high figure. This lower figure was mainly caused by complete losses of clutches and broods; excluding these the figure raises to 86%. Thus, breeding success was high and varied little from year to year (Fig. 2). I have no data on breeding success for 1977 but judging from what happened to other species it ought to have been low.

Breeding success may have been slightly overestimated in some years because I could rarely follow the broods until they fledged. In a few years a late visit was made to the boxes after fledging, in order to determine the number of dead young. In other years some of the broods could not be followed for more than a few days and I had to rely upon inspection of the nest-boxes in the next year. Some small dead young may have disappeared during the winter. Therefore I did not include late broods with small young at the time of the last visit when calculating fledging success. Since late broods suffer a higher mortality than early ones, these cases may have contributed to a small overestimation of survival. However, this error is marginal because there were few late broods.

## Discussion

#### Density

The study showed that density was about the same up to the border of closed forest but then fell to zero. Why did the flycatchers not breed in the patchy transition zone between the forest line and the open alpine heath? The rest of the bird fauna in the lower part of that zone (100-300 m wide) was a typical forest fauna with almost no alpine birds. For example, Willow Warblers *Phylloscopus trochilus*, Bramblings *Fringilla montifringilla*, Redwings *Turdus iliacus* and Dunnocks *Prun-*

*nella modularis* bred there and, superficially at least, the birch groves looked suitable also for flycatchers. But, on no occasion, did they breed in this zone, in fact they did not even attempt to breed.

The explanation cannot be that the Pied Flycatcher is not attracted to breed in a habitat of that physiognomy. At lower elevations and in South Scandinavia it is a common breeder in gardens, parklands and mosaic habitats with copses and small trees.

Järvinen (1984) found that Pied Flycatchers preferred more productive parts of the birch forests at Kilpisjärvi (but without any difference in breeding performance). Since I have no data on the productivity of the transition zone in relation to that of the closed forest nearby I cannot tell if food production as such is a key factor.

A possible explanation is that the area beyond the closed forest is too exposed to winds to make feeding profitable for a bird with a "flycatcher" mode of hunting. In order to resolve this question further studies are necessary.

My results seem to be different from those obtained by Pulliainen (1977) in an experiment similar to mine. Pulliainen put up nest-boxes at different elevations at 67°N in Finland, including the almost treeless alpine zone and the subalpine birch belt. For the alpine zone Pulliainen's result was the same as mine: no flycatchers occupied the nest-boxes. But during his four years study period Pulliainen obtained only one breeding flycatcher in the subalpine birch zone (390-408 m., 36 boxes in 1973 and 51 boxes 1974-1976) which is only 0.4% occupation. In the coniferous zone below 375 m the frequency of occupation was 14.5%, only slightly lower than at Kraipe. Pulliainen states that the subalpine zone is very narrow so that the birds can fly from the alpine to the coniferous zone in a few minutes thus being able to really select between the different zones and habitats. This explanation does not hold since in my area it would also be no problem for the flycatchers to move between the different zones although the birch zone is about 2 km wide.

Instead I think that the difference is only

apparent. What Pulliainen calls "mountain birch forest" corresponds to what I call the transition zone, which is clear from his photograph B in Fig. 1 of Pulliainen (1977). The habitat shown in that picture looks very similar to my transition zone. The dense, closed birch forest zone in my area seems to have no correspondence in Pulliainen's area. So, it seems that our results do agree in that both indicate that the Pied Flycatcher breeds with about the same density up to the border of closed forest, whether this is formed by pure birch, coniferous or mixed birch/coniferous forest.

Järvinen (1983) concluded that the density of the Pied Flycatcher is much higher in southern (Ammarnäs) than in northern (Kilpisjärvi) Lapland. This is an erroneous conclusion drawn from a comparison between the rather poor high elevation woods at Kilpisjärvi and the very rich woods at a relatively lower elevation (below 600 m) on the south-facing slopes of the mountains Gaisatjåkko and Valle at Ammarnäs where the forest line runs at 800 m and the border between coniferous and birch woods at 520 m. When comparing instead the data from the birch belt at Kraipe with that from Kilpisjärvi I found about the same densities, perhaps, even, a slightly higher one at Kilpisjärvi: 22% and 29% occupancy, respectively. This shows that when comparing densities (and other properties of populations) at different localities it is necessary to account for habitat differences.

For the period 1971-1979 there is a good correlation ( $r=0.84$ ,  $0.01 < p < 0.05$ ) between the densities at Kraipe and Kilpisjärvi, located about 340 km apart. This means that perhaps two thirds of the density fluctuation might be explained by some common factor that operates over a large geographical area. Events in the African winter quarters or during migration, or spring weather in the breeding area, constitute such factors. Järvinen's (1978) findings that density is significantly correlated with spring temperature ( $r=0.75$ ) makes the last factor most likely to be a key factor. Events in Africa can be ruled out since they would have affected also populations in southern Scandinavia but these



populations have been stable during this period (Svensson 1984).

Several authors have suggested that density fluctuations should be more extreme in the north (or at the margins of a population's range). Järvinen (1984) found this to be the case for the Pied Flycatcher (coefficient of variation at Kilpisjärvi was 50%). He proposed that this increase was not gradual but very abrupt near the northern border of the range. Whether or not this is the case deserves further analysis since the coefficient of variation at Kraipe (33%) lies between that observed at Kilpisjärvi and those found in South Scandinavia (CV=5-20% in a number of plots in South Sweden; personal data).

#### *Time of breeding and clutch size*

The decline in clutch size with the date of breeding is a well-known feature for many species of birds. The decline seems to be unusually steep in the Pied Flycatcher (von Haartman 1967). My data from Ammarnäs (Fig. 3) show the same clutch size decline as do other sets of data (e.g. Järvinen 1980).

If we combine clutch size data from the northern areas of Kilpisjärvi and Ammarnäs with data from areas in southern Scandinavia, for example those reported by von Haartman (1969) and Källander (1975), the different sets of data regress along a common line with a slope of about 0.08 eggs per day. Von Haartman suggested that a stable clutch size may prevail before 25 May and this was accepted by Järvinen (1983) who proposed that this allows the southern flycatchers to postpone laying until mean air temperature has reached about +10°C without losing anything by the calendar effect. It is not clear, however, whether there is a maximum clutch size at this level. Källander's (1975) data still show some decline from May 18 at a mean clutch size level of 7 eggs, and the data given by Lack (1966) show a decline from a mean clutch size of above 7.5 eggs on April 30. Thus, all data sets show larger clutch size early in the season, and there is no indication of smaller clutches on very early dates.

The calendar effect is still much of a mystery. Lack (1966) suggested that the decline (within the same year) was an adaptation to

the declining food resource at the time of feeding young. Since this cannot explain the fact that there is also a decline of the same magnitude for years with different mean laying dates Lack was "extremely uneasy about this explanation"

The length of the laying period at Kraipe means that it is more compressed in the north than in the south. Pasanen (1977) found a range of laying dates of 35 days (mean of four years) at Lieksa at 63° N and I found a range of 33-34 days (two years) in population near Karlshamn (56° N). Considering the much larger number of years of observation at Kraipe and Kilpisjärvi, this means that the laying period is about twice as long in southern populations. This indicates that it is important for northern flycatchers to finish breeding as soon as possible, a situation faced by many species in northern habitats.

In northern areas it is essential for flycatchers to finish breeding early enough to be able to moult before starting migration in early August (Järvinen 1983). With, say, up to ten days dependence of the young on their parents after fledging, a 15 days feeding period, a 14 days incubation period and one day per egg when laying it seems impossible to raise broods successfully if they are started later than in the last week of June. This fits well with the data from both Ammarnäs and Kilpisjärvi. In none of the areas were any clutches started later than 30 June. At Ammarnäs only three clutches were started after 24 June.

I do not know if the Pied Flycatcher is territorial in Africa. This seems likely, however, since it occupies territories during stopovers in Portugal (Bibby & Green 1980). Then it will have to travel to its winter quarters as early as possible to settle in the most profitable territories. This will add to the time constraints to which the birds are exposed.

Thus, it is not difficult to find a number of different explanations for the seasonal decline in clutch size, provided that one accepts that it is important for a late layer to shorten the breeding period even by only 1-3 days. It is more difficult to identify the proximate cue or cues that the birds use in order to determine how many eggs that are to be laid if the

clutch is started at a certain date. At least three possibilities exist: (1) immediate environmental cues, for example amount of food for egg formation or for feeding the young (it may be possible for a bird to have already experienced the future amount of food for the young at the time of leaf formation since many larvae hatch at this date or soon after), (2) an internal clock that is set at birth or before arrival in the breeding area, perhaps in the African winter quarters (it is known that birds in Africa are able to tell the date precisely: they are able to start their northward migration on almost the same date every year, e.g. the morphologically distinguishable subspecies of Yellow wagtails *Motacilla flava*; Curry-Lindahl 1958), or (3) a response to some cue in the breeding area that is independent of weather (such a cue could be the sun arch in combination with a magnetic latitude determination). These possibilities have yet to be tested.

#### *Breeding success and recruitment*

When analysing the dynamics of marginal populations a key question is whether the number of fledged young is sufficient to maintain a constant population level. Järvinen (1983, p. 136) estimated the minimum number of fledglings per nest to be 4.4 on the assumptions that the survival of juveniles was 30%, that of adults 50%, and that only 50% of the one year old females bred. At Kilpisjärvi the number of fledglings per nest was only 2.3, which is thus not enough to maintain the numbers. At Ammarnäs the mean number of fledglings per nest was 4.43. The assumptions are too uncertain to determine whether this figure is high enough.

The fact that the population was fairly stable throughout the fifteen years is weak evidence for self-maintenance, since stability also can be explained by assuming an annual influx of birds from more southerly areas. The correlation between spring weather and density (Järvinen 1978) speaks in favour of this idea even if it is not an argument for stability.

The most important limiting factor was the absence of nesting cavities. But why did the nest-box occupancy stay at about 20% (never

above 40%)? A straightforward explanation is that the occupancy rate simply reflects the number of flycatchers arriving in the area each spring. If so, the number of flycatchers is determined by the spring weather, the most important correlate, i.e. a density independent factor. But the critical experiment is lacking. What would have happened if the number of nest-boxes and the area covered by nest-boxes had been many times larger, for example thousands of nest-boxes over several tens of square kilometres in the birch woods? Would the occupancy rate have remained the same or would it have declined because of a lack of flycatchers? Before this question has been answered the possibility remains that some factor other than the available number of flycatchers sets the upper limit. The possibility that territorial (food) competition is important remains to be determined (perhaps by feeding experiments).

#### **Conclusion**

The present study shows that the density of the Pied Flycatcher can be increased considerably even at the very limits of its natural altitudinal distribution close to the forest line. In fact, no significant differences in density or breeding performance could be detected for flycatchers breeding in forests at different elevations. This shows that the absence of nesting cavities limited the population level. However, only 20% (and never more than 40%) of the nest-boxes were occupied. The factor (limited number of flycatchers arriving in spring, local habitat/food conditions, competitive interactions) that set this limit is still unknown. Furthermore, it is not possible to determine with certainty whether the average production of young is sufficient to compensate for average mortality.

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