Growth of nestling Pied Flycatchers *Ficedula hypoleuca* in northern Lapland

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The growth of nestling Pied Flycatchers was studied on 37 broods and 159 nestlings in northern Finnish Lapland (69°N) during three years (1980, 1982, 1983), attention being paid to annual growth differences and the effect of (1) hatching date, (2) weather, (3) egg volume and (4) brood size. The wing length and body weight of the nestlings varied significantly between years. Nestlings in early broods were better developed than those in late broods. Wing length correlated positively with the mean air temperature during the nestling period. Large egg size had significant positive effects on nestling growth in the late breeding season of 1982. Brood size affected nestling weight towards the end of the nestling period. Well-developed nestlings left the nest first. The influence of the weather on the production of northern bird populations is stressed.

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Introduction

The availability of food for the laying female (Perrins 1970) and nestlings (Lack 1966) determine the breeding seasons of birds. In many species the production of young declines as the season progresses, often due to the seasonal decline of clutch size (for a review, see Klomp 1970). Thus early breeding is often advantageous, provided that cold spells do not occur in spring (Järvinen & Väisänen 1984).

Growing nestlings require appreciably more energy than is needed in maintenance of adults (e.g. Ricklefs 1968, Kendeigh et al. 1977). Therefore, the growth pattern can be expected to be influenced by external factors (weather; see e.g. Lindén et al. 1984) and the availability of food during the nestling period. Some authors have attributed the lower weight of nestlings in late broods to quantitative or qualitative deterioration of the food supply in late summer, which would also favour early breeding (e.g. Lack et al. 1957, Perrins 1965). Moreover, the growth and probability of survival of nestlings have been found to be positively correlated with egg size (e.g. Schifferli 1973, Parsons 1975, Lundberg & Väisänen 1979).

Our purpose is to describe the general growth pattern of Pied Flycatcher *Ficedula hypoleuca* nestlings in extreme northern conditions and to identify the main factors that control nestling growth in different years. More specifically, we evaluate the extent to which the growth of the nestlings is affected by (1) the date of hatching, (2) weather conditions, (3) egg volume and (4) brood size. There are several studies on the growth of nestling Pied Flycatchers from the southern and central parts of the species range (von Haartman 1954, Tompa 1967, Askenmo 1973, Rheinwald 1975, Schoppe 1977), but no comparable studies have been performed in the northern parts of the range.

Study area, material and methods

The study was conducted in a mountain area in northern Finnish Lapland (about 69°03'N, 20°50'E) in 1980 and 1982–1983. The area is among the most "arctic" places in Fennoscandia (for details, see Järvinen 1983, 1984a).

In 1980 the weather conditions were more favourable than in 1982–1983 (Table 1). The breeding season of 1982 was clearly the coldest, and during an exceptionally cold period between 5 and 26 June there was often snow and frost. The cold weather culminated between 21 and 23 June, when the study area was covered by 20 cm of snow. The breeding season of 1983 was an average one. The annual differences in weather conditions were more pronounced during the egg-laying and incubation periods (late May and June) than during the nestling period (July; Table 1).

Table 1. Mean air temperature (°C) and precipitation (mm) in May–July during the study years. Data from a meteorological station in the study area (alt. 480 m).

	May		June		July	
	°C	mm	°C	mm	°C	mm
Long-term mean	+1.1	21	+8.0	37	+10.9	63
1980	+2.4	21	+10.1	52	+11.8	9
1982	+1.3	40	+3.6	45	+10.7	41
1983	+2.7	31	+6.6	15	+10.4	94

All the nests were in nest-boxes in mountain birch *Betula pubescens* ssp. *tortuosa* woods (elevation 480–560 m). In 1980 the local population comprised 35 pairs, in 1982 20 pairs and in 1983 22 pairs. In each year the growth of nestlings was measured in the nests situated nearest the Kilpisjärvi Biological Station: in 1980 8 nests (N = 44 nestlings), 1982 18 nests (N = 67), and in 1983 11 nests (N = 48). At all nests the young were fed by both parents.

The nests were visited almost daily throughout the breeding season. Egg volume was estimated from the maximum egg length and maximum egg breadth, using the regression model of Ojanen et al. (1978), which explains 96 % of egg volume variance in the Pied Flycatcher. In 1982 and 1983 eggs were marked individually according to the laying sequence. The hatching order was determined, and we also recorded from which egg a particular chick hatched (nests were visited once every 30 min during the time of hatching). The hatchlings were marked individually.

The nestlings were weighed and their wing length measured daily between 0900 and 1400 (the same nests were visited at the same time of the day). Nestlings 0–5 days old were weighed with a 10-g Pesola spring balance (accuracy 0.05 g) and nestlings more than 5 days old with a 50-g Pesola spring balance (accuracy 0.1 g). The wing length was measured by the maximum chord method (Svensson 1975) to the nearest 0.5 mm. Our analysis is based both on brood means and on data from individual nestlings. The weight data were fitted to the logistic function by Crossner's (1977) method.

Results

General features of the breeding seasons. Every year the timing of breeding in the measured broods was representative of the whole population (Fig. 1). This is important, because the weather was variable and of different character each year.

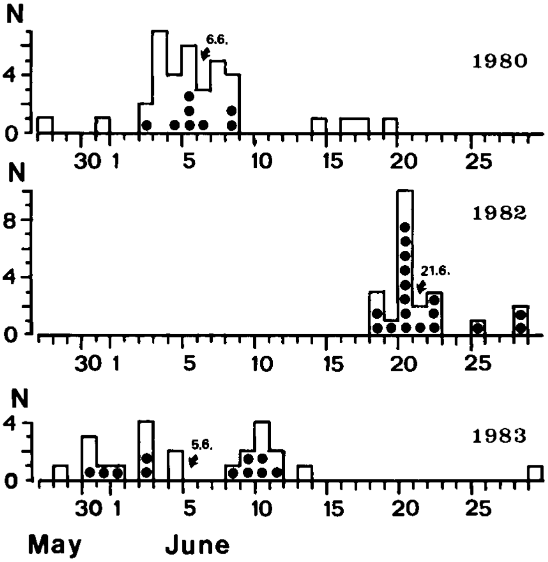

Fig. 1. Date on which the first egg was laid in the three study years. Black dots = measured broods, arrows = mean date of egg-laying in the whole population, N = number of broods.

In 1980 and 1983 the egg-laying of the Pied Flycatcher was somewhat ahead of the long-term mean (Fig. 1; mean 1966–81 13 June, Järvinen 1983). In 1982 very cold weather between 5 and 24 June caused an interruption of egg-laying and desertion of all nests. Egg-laying started again on 18 June (Fig. 1) after temporary amelioration of the weather between 15 and 18 June, when the mean daily air temperature rose to + 3°– + 6° C. It is not known whether the same females laid replacement clutches or whether new females settled. Both clutch and brood sizes were smaller and breeding success poorer in 1982 and 1983 than in 1980 (Table 2).

Table 2. Egg size (cm^3), clutch size and numbers of hatched and fledged young per brood (mean ± SD) in the whole Pied Flychatcher population at Kilpisjärvi (A) and in the measured broods (B). N = number of broods. None of the within-year differences between A and B are significant (t-tests).

	Egg size	Clutch size	Hatched	Fledged	N
1980					
A	1.59 ± 0.09	6.2 ± 0.8	5.8 ± 1.2	5.6 ± 1.2	35
B	1.61 ± 0.10	6.1 ± 0.6	5.5 ± 0.9	5.5 ± 0.9	8
1982					
A	1.55 ± 0.12	4.6 ± 1.1	3.7 ± 1.4	3.3 ± 1.6	21
B	1.55 ± 0.11	4.7 ± 1.0	4.0 ± 1.3	3.7 ± 1.2	18
1983					
A	1.55 ± 0.09	5.7 ± 0.8	4.5 ± 1.8	3.3 ± 2.2	22
B	1.58 ± 0.08	5.6 ± 0.5	4.5 ± 1.0	4.2 ± 0.9	11

The effect of the breeding season. The relationship between nestling growth and the timing of breeding was examined by studying both annual differences and the variations within a single season.

The growth of the wings of nestlings was more rapid in 1980 than in the other years, especially for nestlings older than 3 days (Fig. 2, Table 3). In the late season of 1982, wing length at hatching was significantly shorter than in other years, but at the age of 1–2 days the difference was not significant (Fig. 2, Table 3). Later the differences between years increased and the wings of nestlings grew more slowly in 1982 than in other years.

Table 3. Differences in the mean nestling wing length between years (t-tests). Significance: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, ns = not significant, asterisk in parentheses = 5 % significance level almost reached.

age (days):	0	1	2	4	6	8	10	12	14
1980/1982	***	ns	ns	***	***	***	***	***	***
1980/1983	ns	ns	ns	***	***	***	***	***	***
1982/1983	***	ns	ns	ns	(*)	*	ns	(*)	ns

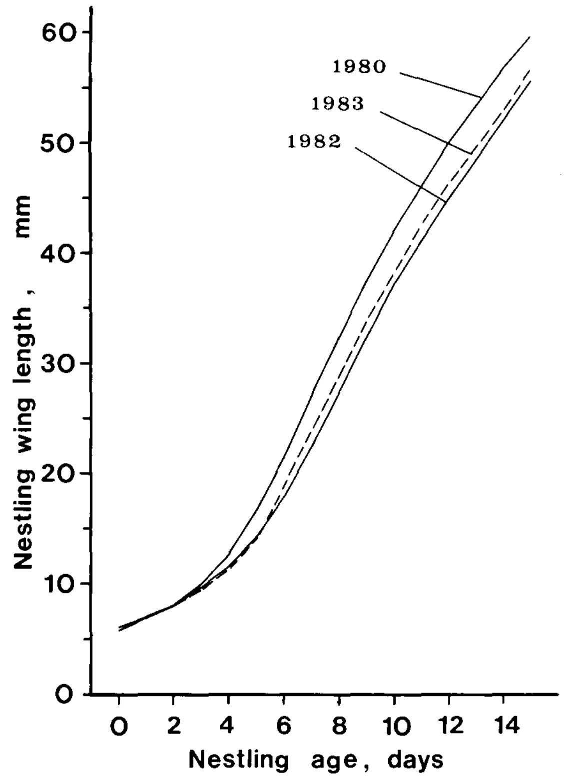

Fig. 2. Growth of nestling wing length in different years. The curves are mean values and the statistical significance of the differences between years is given in Table 3.

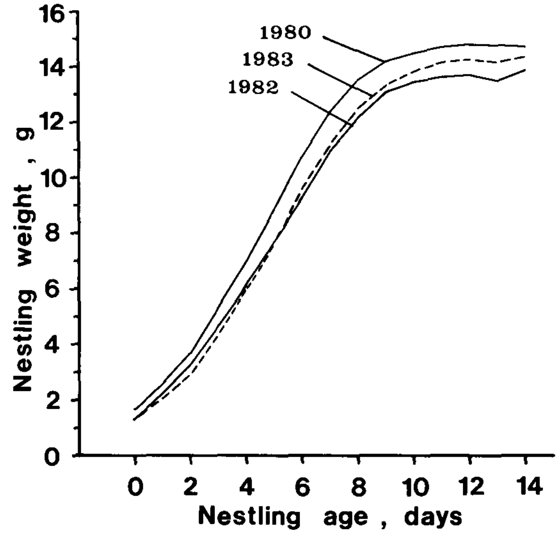

Fig. 3. Gain in nestling weight in different years. The statistical significance of the differences between years is given in Table 4.

The gain in weight of nestlings in 1980, 1982 and 1983 showed the same order as the growth of the wings (Fig. 3). However, in the warm summer of 1980 even the hatchlings (day 0) were significantly heavier than hatchlings in other summers (Fig. 3, Table 4).

The timing of breeding does not explain all between-year variation in the growth of nestlings, because in 1980 and 1983 clutches commenced at the same time had different growth rates. If the exceptionally small broods of 1–3 nestlings in 1982 are omitted, the relationship between the hatching day and the mean nestling weight at the age of 12.5 days is significantly negative (Fig. 4; r = –0.480, P < 0.01, N = 28 broods).

The relationship between the hatching day and the mean nestling wing length at the age of 12 days was also negative (r = –0.458, P < 0.01, N = 35); each day that the hatching date was advanced corresponded to a difference of –0.12 mm in the mean length. However, omission of the abnormally small broods of 1982 did not result in a higher coefficient of correlation, which suggests that the development of wings is more constant than the gain in weight. The date of hatching seemed to have a negative,

Table 4. Differences in the mean nestling weight between years. Symbols as in Table 3.

age (days):	0	1	2	4	6	8	10	12	14
1980/1982	***	***	***	***	***	***	***	***	***
1980/1983	***	***	***	***	***	***	***	***	**
1982/1983	***	***	***	ns	ns	ns	(*)	*	*

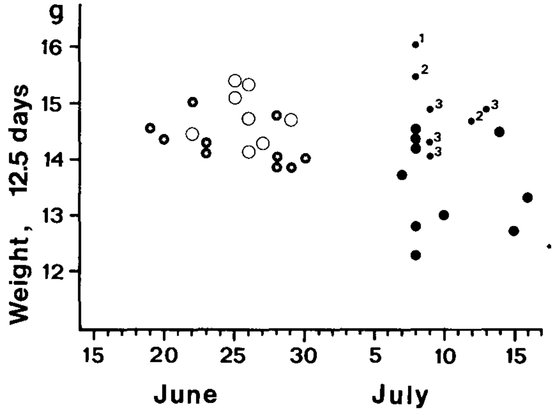

Fig. 4. The relationship between hatching date and mean nestling weight in broods at the age of 12.5 days in 1980 (open circles), 1982 (black dots) and 1983 (dots with stars). The unusually small broods (1–3 nestlings per brood) in 1982 are marked with small black dots.

though not significant, relationship with the growth of the nestlings within each study year, as well (Table 5, Fig. 4). The broods which were attended by females only were not included in the above analyses.

There was a close linear relationship between the weight of nestlings just before fledging (day 12.5) and the theoretical asymptotic weights derived from a logistic equation ($r = 0.970, P < 0.001$; asymptote $= 0.928x + 1.557$).

Table 5. Correlations of hatching date with mean weight and wing length of nestlings at end of nestling period (day 12).

	Weight	Wing
1980	–0.038 ns	–0.382 ns
1982	–0.175 ns	–0.195 ns
1983	–0.373 ns	–0.504 (*)

The effect of weather. Nestling weight correlated with the mean air temperature during the early part of the nestling period (Table 6). However, this correlation was mainly due to the year 1983, when cold weather retarded the growth of newly hatched young (some nestlings fell into hypothermia when the females left them unattended). Except in 1983, the weight did not correlate with the mean air temperature at the end of the nestling period (Table 6). The mean air temperature during the whole nestling period (days 0–13) did not correlate significantly with the final weight of the nestlings (Table 6).

In the combined material wing growth correlated positively and significantly with the mean air temperature during both the early part and the whole nestling period (Table 6, Fig. 5). The weight of birds is more sensitive than wing length to fluctuations in temperature and temporary shortage of food, which explains positive correlation in 1983 between nestling weight at the age of 12.5 days and the mean air temperature around this time (days 11–13; Table 6).

Table 6. Correlations of mean air temperature during nestling period with nestling wing length (day 12, brood means) and weight (days 4.5 and 12, brood means). Correlations given separately for 1983 and for total study years.

	Mean temperature			
Days:	0–5	6–10	11–13	0–13
Weight, 4.5 days				
1983	0.684*	–	–	–
Total	0.494**(*)	–	–	–
Weight, 12 days				
1983	–0.058 ns	–0.147 ns	0.746**	–0.549 ns
Total	–0.008 ns	0.010 ns	0.060 ns	–0.270 ns
Wing length, 12 days				
1983	0.739*(*)	0.781**	0.079 ns	0.761**
Total	0.578***	0.317(*)	0.003 ns	0.685***

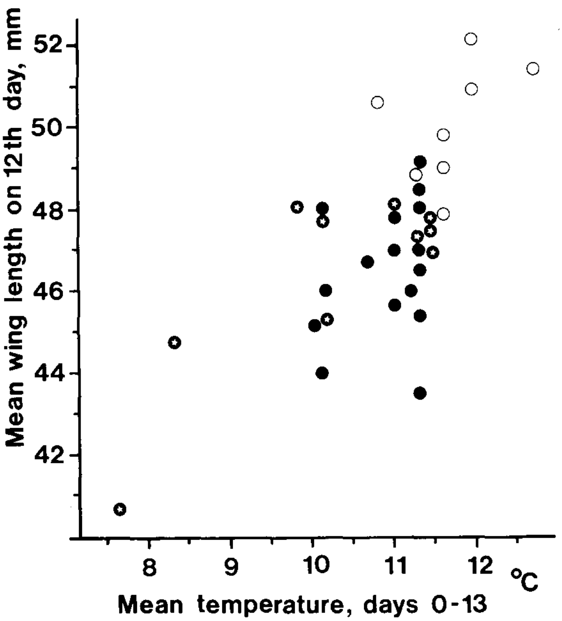

Fig. 5. The relationship between mean wing length (brood means) on the 12th day of the nestling period and mean air temperature during the nestling period (days 0–13).

The effect of egg size. The mean egg volume of the broods correlated positively and significantly with their mean weight and wing length (Table 7), but this was mainly caused by the year 1982; there were no significant correlations in our data from 1980 and 1983. If we exclude the unusually small broods (1–3 nestlings) in 1982, the correlation in that year between egg volume and nestling weight at the age of 12.5 days is still high ($r = 0.610$, $df = 8$, $P < 0.1$), although not significant.

Table 7. Correlations of mean egg volume with some growth parameters of broods in 1982 and in the combined material.

	Weight at 4.5 days	Weight at fledging	Asymptotic weight	Wing length at fledging
1982	0.462*	0.590**	0.545*	0.477**
Total	0.334*	0.491**	0.392*	0.472**

In 1982 we examined the growth of individually marked nestlings in relation to the volume of the egg from which they hatched (the effects of brood size and hatching sequence were eliminated, see Järvinen & Ylimaunu 1984). This analysis and the analysis based on brood means and performed in the present study gave similar results, i.e. in 1982 egg volume was positively related to the growth of the nestlings.

Using linear regression models, we have estimated that in 1982 a difference of + 0.5 cm^3 in egg volume (1.9 cm^3 vs. 1.4 cm^3) resulted in 24.1 ± 3.5 % (SD, N = 8) greater nestling weight and in 13.7 ± 2.5 % greater nestling wing length during the first eight days (0–7) in the nest; during the last eight days (8–15) in the nest the differences were less pronounced, although still considerable: 10.4 ± 2.6 % and 7.7 ± 3.0 %, respectively. Thus, in the first half of the nestling period the benefit of hatching from a large egg was reflected more in the weight than in the size (wing length) of the nestlings.

The effect of brood size. The brood sizes differed between the years (Table 2). There was no straightforward relationship between brood size and the age at which the inflection point of the logistic weight curve was reached. Nor did wing length in the later part of the nestling period depend on brood size (Table 8). However, brood size seemed to have an effect on nestling weight just before fledging: the correlation between brood size and fledging weight was significantly negative (Table 8).

Nestlings in large broods were lighter than in small broods, especially in the late breeding season of 1982 (Table 8, Fig. 6). In this year brood size and egg volume correlated negatively. However, since egg volume has relatively little influence on the gain of weight at the end of the nestling period, it seems that the important factor towards the end of the period is brood size (cf. correlation coefficients in Table 8). In partial correlation analysis, when egg volume was kept constant, brood size in 1982 explained 9.6 % (N = 17, NS) of weight variance at the age of 4.5 days, but 42.8 % ($P < 0.01$) at the time of fledging.

The age at fledging in relation to growth. The age at fledging correlated negatively and significantly with the weight at the age of 12.5 days, with the theoretical asymptotic weight of the broods, and with wing length at the age of 12 days (Table 9). In other words, the data indicate that well-developed nestlings leave the nest first. The data for the separate years gave similar results (Table 9). A multiple linear regression analysis of the data for each year (egg volume, brood size, nestling weight and wing length as independent variables and fledging age as a dependent variable) did not give better results than the simple linear regression model.

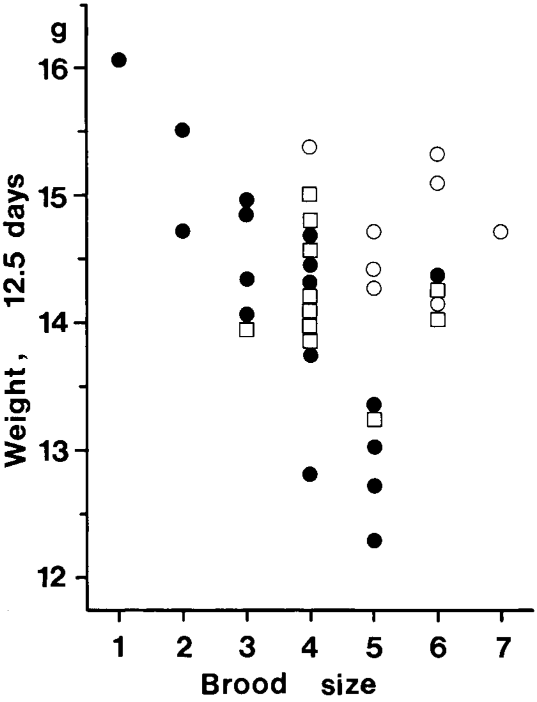

Fig. 6. The relationship between brood size and mean nestling weight at the age of 12.5 days when nestlings are usually heaviest. 1980 = open circles, 1982 = black dots, 1983 = squares.

Table 8. Correlations of brood size with some growth parameters of broods in 1982 and in the combined material.

	Mean egg volume	Weight at 4.5 days	Weight at fledging	Wing length at fledging
1982	-0.489*	-0.466*	-0.749***	-0.131 ns
Total	-0.110 ns	-0.090 ns	-0.387*	-0.004 ns

The correlation between weight and wing length at the age of 12 days was highly significant (r = 0.759, combined material, df = 35, $P < 0.001$). Annual variation also occurred in wing length just before fledging. In 1980, when growth was rapid, the nestlings were particularly heavy but young at fledging, and they had particularly short wings (Table 10).

Table 9. Correlations between fledging age (days) and some growth parameters of broods.

	Mean egg volume	Weight at 4.5 days	Weight at 12.5 days	Weight at fledging	Wing length at 12 days	Brood size
1980	-0.182	-0.283	-0.707*	-0.197	-0.359	0.612
1982	0.394	-0.053	0.088	0.208	-0.492*	-0.300
1983	0.044	-0.064	-0.465	-0.209	-0.650*	0.069
Total	0.206	-0.266	-0.407*(*)	0.004	-0.520***	-0.169

Discussion

Optimal growth and the timing of breeding. In arctic and subarctic areas the timing of breeding is crucial because of the short summer and the cold and unpredictable weather (Belopolskii 1957, Salomonsen 1972, Birkhead & Nettleship 1982, Järvinen 1983). In general, there are two major constraints which delimit the breeding seasons of northern bird populations. First, females should have sufficient food for egg production and incubation (e.g. Perrins 1979, O'Connor 1978). Second, nestlings should have sufficient food for growth and development (e.g. Lack 1966, Ricklefs 1973). However, if the favourable breeding season is short as in our study area, selection pressures may conflict and the penalty for breeding at a non-optimal time is heavy. For example, birds breeding early face a considerable risk of occasional cold weather spells, which may cause heavy nesting losses, whereas late breeders may lack food so that many young may starve.

In our Pied Flycatcher population a late cold spell in 1982 destroyed all early clutches with the result that in the remaining late clutches clutch size was smaller than in other years (Table 2). Similarly, in 1981 the cold and rainy early summer caused an almost complete nesting failure in the Pied Flycatcher (Järvinen 1983).

There is ample evidence in the literature that it is advantageous for a young nidicolous bird to grow rapidly and to be as heavy and well-developed as possible at fledging (Perrins 1965, Lack 1968, Ricklefs 1968, 1973). But why do the nestlings not grow optimally every year and in every brood? According to the present study, several ecological factors prevent the optimal growth of nestlings in the North. The weather is no doubt a major factor. For example, in 1980 breeding took place in very favourable conditions, the eggs were large and the nestlings presumably grew at a nearly maximal rate. In Central Finland nestling tits *Parus* spp. also grew faster in 1980 than in other years (Orell 1983). In 1983, however, a cold spell delayed nestling development (hypothermia in some broods). During the cold period the parents were not able to feed their young, probably because they had to spend more time foraging for their own survival.

Table 10. Fledging age, wing length and weight of young at fledging in different years (mean ± SD, last measurement of broods 5–15 hours before fledging). Symbols as in Table 3 (t-tests).

	Fledging age (days)	Wing length at fledging (mm)	Weight at fledging (g)	N
1980	14.5 ± 0.8	50.1 ± 1.4	14.5 ± 0.6	8
1980/82	ns	***	ns	
1982	15.1 ± 1.6	55.7 ± 4.8	14.2 ± 1.0	18
1982/83	ns	ns	ns	
1983	15.5 ± 0.8	57.4 ± 1.6	14.1 ± 0.5	10
1980/83	*	***	ns	

In our material early broods were heavier than late broods (Fig. 4; see also Perrins 1970, Ricklefs 1968, Askenmo 1973, Orell 1983). The reason for this trend was not energetic losses due to cold weather (the temperature was rising at the time), but probably poor or insufficient food in late June and July (cf. Perrins 1970). Several other studies (e.g. Gibb 1950, Lack 1966, Orell 1983) have pointed out a similar conclusion, although direct evidence is lacking. The poor growth of nestlings in 1982 was presumably mainly due to food shortage, though the weather was relatively favourable during the nestling period. The cold and snowy period in June, in particular, may have destroyed a substantial proportion of the insect food.

Variation of growth curves. The form of the growth curve is typical of each bird species (Ricklefs 1968). The heritability of growth patterns is low (Ricklefs & Peters 1981) because different external factors are involved in different seasons (e.g. Bryant 1978). In our material both the weight and wing length curves differed significantly between years (Tables 3 and 4). Similar annual differences are known, for example, among tits (Orell 1983). In rainy and cold breeding seasons, nestlings grow slowly and the mortality after fledging is probably high. For example, in the Great Tit *Parus major* mortality after fledging correlated negatively with the weight at the age of 15 days (Perrins 1965). These facts support the conclusion that in northern areas weather factors are selective and important for nestling growth, and that irregular "ecological crunches" (Wiens 1977) cause high mortality and reduce population size (see also Järvinen 1984a, 1984b, Järvinen & Väisänen 1984).

The growth rate also seems to affect the time of fledging: nestlings leave their nest earlier if they have grown fast (Table 9). In northern areas the selection pressure for rapid growth and early fledging may be considerable, due to the shortness of the favourable season. However, we need more data to be able to compare growth parameters in different populations. At least in one species, the Shore Lark *Eremophila alpestris*, the nestlings of an arctic race grow faster than those of temperate races (Maher 1980).

The mean maximum weight of Pied Flycatcher nestlings in our population (14.0 g) was about the same as in two populations in southern Finland (von Haartman 1954, Tompa 1967). In Germany the mean maximum weight was rather low (12.3 g), but according to the author this was caused by food competition due to densely placed nest-boxes (Rheinwald 1975). In a population in southern Finland there was no direct relationship between population density and nestling growth (Tompa 1967).

Effects of egg size and brood size. The correlation between egg volume and nestling growth varied annually. In 1982 nestlings hatched from large eggs grew better and were bigger at fledging than nestlings from small eggs. In 1980 and 1983 egg volume was not a very important factor affecting nestling growth. Many studies have demonstrated that nestlings from large eggs develop and survive better than nestlings from small eggs (Skoglund et al. 1952, Parsons 1970, Schifferli 1973, O'Connor 1975, Howe 1976, Nisbet 1978, Lundberg & Väisänen 1979, Williams 1980, Moss et al. 1981, Järvinen & Ylimaunu 1984). The weight of hatchlings seems to be chiefly determined by egg volume (e.g. Davis 1975, Furness 1983).

Hatchlings from small eggs have often caught up with hatchlings from large eggs by the end of the nestling period, but in late breeding seasons (as in 1982 in our study area) and when food supplies are poor, the advantage of hatching from a large egg is of longer duration (Schifferli 1973, Birkhead & Nettleship 1982, Järvinen & Ylimaunu 1984). With larger reserves, the nestlings can better tolerate the stress of food shortage prevailing during cold periods in the North.

As egg volume is largely determined genetically (e.g. Ojanen et al. 1979), it is natural to expect strong selection pressure for large egg size due to the better growth and survival of nestlings from large eggs. However, there are no observations of rapid evolution of egg size in our study or in other studies of natural bird populations (for a review, see Ojanen 1983). Therefore, some counteracting selection pressures must be involved. Laying large and qualitatively good eggs probably increases the female's stress and decreases her chances of future breeding. Females laying small eggs may have an advantage, especially under poor conditions in spring, because they are able to breed early and lay relatively large clutches (Perrins 1970).

In some other species, e.g. the Herring Gull *Larus argentatus* and Kittiwake *Rissa tridactyla*, the success and survival of the chicks do not depend on egg size, but on the quality and experience of the parents (Parsons 1970, Davis 1975, Barrett & Runde 1980). Using extensive material from northern Lapland, Järvinen & Väisänen (1983, 1984) were able to demonstrate that heavy Pied Flycatcher females are better producers than lean females, and that heavy females lay the largest eggs and clutches.

In our material sibling competition (brood size) seemed to play a role in the determination of nestling weight in the late breeding season of 1982 (Fig. 6). In tits the weight of nestlings seems to depend on brood size only when food supplies are poor and unstable (Lack et al. 1957, Perrins 1965). In other studies of the Pied Flycatcher a correlation has rarely been observed between nestling weight and brood size, which may be partly due to small brood size variation (Tompa 1967, Askenmo 1973). The decreasing feeding rate of parents just before fledging (our own observations) together with sibling competition may be responsible for the negative correlation between fledging weight and brood size (Table 8). When only the female was feeding the young, the growth of nestlings was poor and the youngest nestlings usually died due to sibling competition (unpubl.).

Conclusions

Our results support the view that physical factors, especially the weather conditions, have a strong influence on the reproduction and productivity of bird populations in subarctic areas (see also Jehl & Hussel 1966, Birkhead & Nettleship 1982, Järvinen 1984a, b). Factors such as the weather and the food supplies cause great annual variation in the patterns of nestling growth and fitness, and partly for this reason considerable fluctuation occurs in the densities of bird populations in extreme northern environments (Wiens 1974, O. Järvinen 1979, Järvinen 1983). The stability of populations is greater in predictable and biologically more productive environments (as in temperate bird populations, where the densities can also be high, see O. Järvinen 1979).

Cold weather during the nestling period may act on nestling growth by (1) hampering food gathering by the parents and thus lowering the amount of food the nestlings receive and by (2) increasing the maintenance costs, which decreases the proportion of energy invested in growth. In extreme cases decreased food resources may lead to a conflict between the parents and the nestlings. This happened during a cold spell in 1983, when some females sacrificed their broods for their own survival. In less extreme cases points (1) and (2) may lengthen the nestling period, which may increase the risk of predation or force the nestlings to fledge in undernourished condition.

The individuals living at the boundary of a species range usually face different environments and other selection pressures than individuals in the central parts of the range, to which the species has adapted. As the nesting place fidelity of Pied Flycatchers is low and the gene flow between local populations is high (Järvinen 1983), we cannot expect rapid evolution in our population (e.g. in egg size or growth pattern), although strong selection pressures may prevail.

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Selostus: **Kirjosiepon poikasten kasvusta Pohjois-Lapissa**

Kirjosiepon poikasten vuotuisia kasvueroja tutkittiin Enontekiön Kilpisjärvellä 1980, 1982 ja 1983. Tutkittuja pesyeitä oli 37 ja niissä oli yhteensä 159 poikasta. Taulukossa 1 on esitetty tutkimusvuosien sääolot, taulukossa 2 ja kuvassa 1 tärkeimmät kirjosiepon pesintää kuvaavat tunnusluvut. Lähemmin selvitettiin (1) kuoriutumisjärjestyksen, (2) sääolosuhteiden, (3) munan tilavuuden ja (4) poikuekoon vaikutuksia poikasten kasvuun ja kehitykseen.

Poikasten siiven pituus ja paino kehittyivät eri vuosina erilailla (taulukot 3–4, kuvat 2–3). Varhain keväällä munituissa pesyeissä poikaset kehittyivät paremmin kuin myöhään munituissa pesyeissä (kuva 4). Siiven pituus korreloi positiivisesti pesäpoikasaikana vallinneen ilman keskilämpötilan kanssa (taulukko 6, kuva 5). Myöhäisenä pesimäkautena 1982 suuri munan koko edisti poikasten kasvua, muina vuosina munan koon merkitys oli vähäisempi (taulukko 7). Pesäpoikasajan loppupuolella pesyekoko oli tärkeä poikasten kasvuun vaikuttava tekijä (taulukko 8, kuva 6). Hyvin kehittyneet poikaset lähtivät pesästä ensimmäisinä maailmalle (taulukot 9–10). Ulkoisten säätekijöiden vaikutusta linnunpoikasten kasvua ja kehitystä rajoittavana tekijänä pohjoisessa korostetaan.

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