Body mass and wing length of nestling Redstarts *Phoenicurus phoenicurus* in a harsh northern environment

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Using mean brood values, the growth of nestling Redstarts was studied in relation to reproductive and environmental variables in a northern marginal area (Finnish Lapland). During three years the mean values of the growth variables did not vary significantly annually. The asymptote and the growth constant of the logistic body-mass curve correlated significantly with each other. Nestlings from large eggs reached the inflection point of the logistic body-mass curve sooner than nestlings from small eggs. Large egg size and warm weather during the nestling period had positive effects on wing growth. Brood size and the date of hatching did not affect the growth of nestlings. The results are compared with growth data on Pied Flycatcher *Ficedula hypoleuca* nestlings from the same area.

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Introduction

Here I will describe the growth of nestling Redstarts *Phoenicurus phoenicurus* in a harsh northern environment in relation to the year, hatching date, egg size, brood size and weather during the nestling period. My aim is to show how the pattern of growth of a northern altricial passerine is shaped by various abiotic and biotic factors, and which growth parameters are most sensitive to external factors. I will also discuss what biologically meaningful differences exist between different species.

As a basis for the interspecific comparisons, I will use data on another hole-nesting passerine, the Pied Flycatcher *Ficedula hypoleuca*, from the same study area (Järvinen & Ylimaunu 1984, 1986). Both species breed in nest-boxes and are migrants which winter in Africa. In northern conditions the nesting success of the Redstart is high compared with that of the Pied Flycatcher (Järvinen 1983). Therefore, it may be hypothesized that the growth of Redstart nestlings is less strongly affected by environmental factors than that of Pied Flycatcher young.

Study area, material and methods

The data were collected near Kilpisjärvi Biological Station (about 69°03'N, 20°50'E) in NW Finnish Lapland in 1981–1984. The study area is a mountain birch wood 475–600 m above sea level. The mean daily air temperature and precipitation (alt. 480 m) during the study years and in 1951–1985 were as follows (Järvinen 1987; precipitation for 1961–1985):

	Mean temperature, °C		Precipitation, mm	
	June	July	June	July
1981	4.3	10.2	29	122
1982	3.6	10.7	45	41
1983	6.6	10.4	15	94
1984	8.0	9.0	57	69
Long-term	7.2	10.6	39	64

In all, the data comprise 113 nestlings from 20 nests in nest-boxes. In 1981 there was one nest (6 nestlings), in 1982 there were 6 (brood size 4.7±1.2, SD), in 1983 there were 5 (6.2±0.4) and in 1984 there were 8 (6.0±1.2). All the nestlings in this study fledged and they were fed by both parents.

All eggs were measured to the nearest 0.01 mm with sliding calipers. Egg volume (EV) was calculated for each egg from the maximum egg length (EL) and breadth (EB) with the formula (Ojanen et al. 1978):

$$EV=0.044 + 0.4752 \times EL \times EB^2 ,$$

where EV is given in cm^3 and EL and EB in cm. This formula explains about 97% of the egg volume variance in the Redstart (Ojanen et al. 1978).

The nests were visited and the nestlings were measured daily at the same time of the day (between 09.00 and 14.00). To prevent heat loss, the nestlings were held in a woollen cloth and measured in about 30 seconds. Small young (0–4 days) were weighed with a 10-g Pesola spring balance (accuracy 0.05 g) and large young with a 50-g Pesola spring balance (accuracy 0.1 g). Wing length was measured by the maximum chord method (Svensson 1975) to the nearest 0.5 mm. The hatching day of the young is called day 0. Some nestlings hatched a day later than the other chicks in the brood and their body-size values were scored in the group corresponding to their real age. To simplify the analyses, nestling body mass and wing length are usually given for three different phases of the nestling period, i.e. day 1, day 6 and day 12 (nestlings fledged at the age of 12–14 days).

To facilitate intra- and interspecific comparisons of growth, a logistic equation (e.g. Hunt 1982)

$$W = A/(1 + Be^{-KT})$$

was fitted to the body-mass data. Here W = body mass in g at time T, A = the upper asymptote (or the final body mass) of the growth curve, B = measure of the starting size of the system, e = the base of natural logarithms, K = the growth constant (or the "intrinsic rate" at which the asymptotic body mass is being attained), T = age in days (day 0 is the day of hatching). The age I at the maximum absolute growth rate (determined by the inflection point of the curve, and representing the age at which 50% of the asymptotic body mass is attained) was solved from the equation $I = \ln B/K$.

Calculations were made for each nest of the mean air temperature between 0 and 3 days, 0 and 6 days, and 0 and 12 days, and 7 and 12 days after the hatching of the young, and of the mean precipitation during the nestling period (days 0–12), using the records of the Kilpisjärvi Meteorological Station of the Finnish Meteorological Institute. This meteorological station lies within the study area.

As in studies of egg size (e.g. Järvinen & Väisänen 1984), the analysis of egg volume, body mass and wing length is based on clutch/brood means, for three reasons: (1) most nestlings could not be matched with certainty with a specific egg, (2) brood size was included as a study variable and (3) in the statistical tests, measurements of individual nestlings from the same brood were avoided, in order to eliminate pseudoreplication. The statistical methods used are explained in Conover (1980) and Hoaglin et al. (1983).

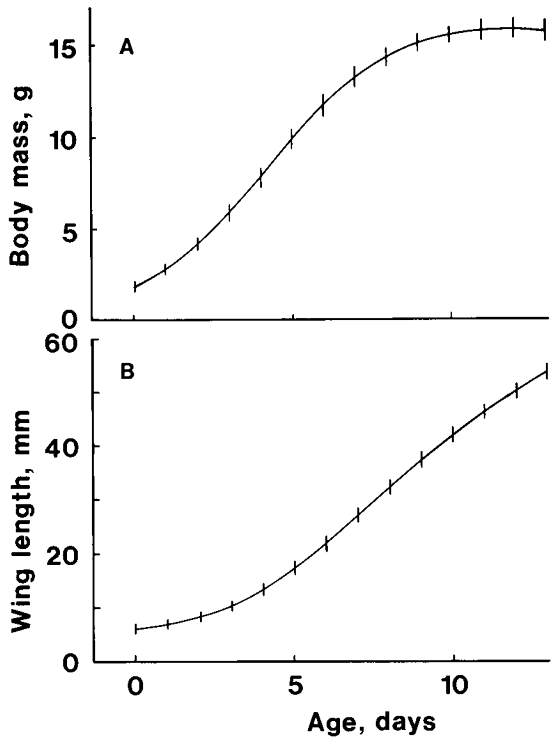

Fig. 1. Growth curves for nestling body mass (A) and wing length (B) of the Redstart in northern Lapland in 1981–84 (n=20 nests). Daily brood means and their 95% confidence limits are given. Day 0 is the day of hatching.

Results

Mean values of variables and their annual variation

On average, the nestlings reached their final body mass at the age of about 10 days (Fig. 1A), but at fledging (12–13 days) their wings were still growing (Fig. 1B) and averaged about 2/3 of the adult wing length. The inter-brood coefficient of variation in body mass decreased steadily as the nestlings grew (a slight increase around the time of fledging), but the CV of wing length seemed to reach another peak at the age of five days (Fig. 2). The CV of the mean daily body mass (days 0–13, n=14) was 8.7% and that of the wing length 7.3% (Wilcoxon signed-rank test, 2-tailed P=0.06). The mean brood size was smallest in 1982, the year when the hatching date was the latest, but the annual variation was significant only in the latter variable (Table 1).

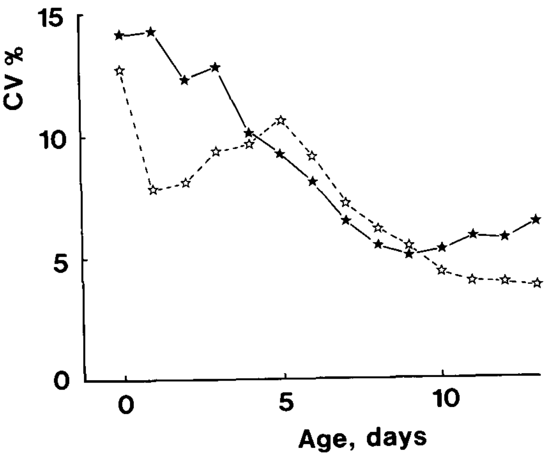

Fig. 2. Coefficient of variation in mean body mass (black stars) and wing length (white stars) of nestling Redstarts in northern Lapland in relation to the age of the nestlings. n=20 nests.

The mean values of all the weather variables included in this study varied significantly annually, but there was no corresponding variation in the growth variables (Table 1). In fact, the mean body mass at fledging (day 12), the mean nestling wing length at fledging, the growth constant, and the asymptotic body mass of the logistic curve showed remarkably little annual variation (Table 1).

Factors affecting growth

I compared the growth parameters of the Redstart nestlings in relation to the mean egg volume/clutch by dividing the material into two groups, nestlings hatched in nests with small eggs (n=10 nests, mean egg volume 1.560–1.799 cm^3) and in nests with large eggs (n=10, 1.805–2.137 cm^3). The mean hatching day and brood size were the same in the groups. The nestlings from large eggs reached the inflection point of the logistic curve sooner and developed longer wings than nestlings from small eggs (Table 2).

Table 1. Mean breeding parameters (based on brood means) of the Redstart at Kilpisjärvi in 1982 (6 nests with 28 nestlings), 1983 (5/31) and 1984 (8/48), and in 1981–1984 (20/113). Annual differences (1982–84) are tested by the Kruskal-Wallis test.

Variable	1982 n=6 nests		1983 n=5 nests		1984 n=8 nests		1981–84 n=20 nests		Kruskal-Wallis
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	P
Brood size	4.67	1.21	6.20	0.45	6.00	1.20	5.65	1.18	0.074
Egg volume, cm^3	1.82	0.17	1.79	0.14	1.80	0.11	1.81	0.13	0.92
Hatching day	6 Jul	8	23 Jun	2	24 Jun	11	27 Jun	10	0.024
Mean °C 0–3 days after hatching	10.8	2.6	7.7	1.1	8.9	0.9	9.1	2.0	0.027
Mean °C 0–6 days after hatching	11.0	0.8	8.4	1.1	8.9	0.7	9.3	1.5	0.002
Mean °C 0–12 days after hatching	10.6	0.6	9.8	0.9	8.7	0.6	9.5	1.1	0.002
Mean °C 7–12 days after hatching	10.2	1.8	11.4	0.5	8.4	1.4	9.6	1.9	0.024
Precipitation, mm 0–12 days after hatching	21	6	24	3	39	14	30	13	0.021
Wing length, mm, day 1	7.0	0.6	6.8	0.6	7.3	0.3	7.1	0.6	0.37
Wing length, mm, day 6	23.2	2.1	21.6	2.4	21.9	1.8	22.4	2.1	0.37
Wing length, mm, day 12	50.2	2.6	49.5	2.3	49.8	1.5	49.9	2.0	0.53
Body mass, g, day 1	2.8	0.5	2.6	0.4	2.6	0.3	2.7	0.4	0.83
Body mass, g, day 6	12.0	1.1	12.0	1.1	11.2	0.6	11.7	0.9	0.24
Body mass, g, day 12	16.0	1.0	15.9	1.0	15.8	0.9	15.8	0.9	0.92
Asymptote, g	16.1	1.0	16.2	1.1	16.1	1.0	16.1	1.0	0.99
Growth constant	0.54	0.03	0.54	0.03	0.51	0.04	0.53	0.04	0.29
Inflection point, days	3.95	0.39	4.01	0.36	4.23	0.46	4.05	0.43	0.41

Table 2. Comparison of the growth variables of Redstart nestlings hatched in nests with small (1.560–1.799 cm^3) and large (1.805–2.137 cm^3) mean egg volumes at Kilpisjärvi in 1981–1984.

Variable	Small eggs n=10 nests Mean	SD	Large eggs n=10 nests Mean	SD	Mann-Whitney test 2-tailed P
Egg volume, cm^3	1.72	0.09	1.89	0.10	–
Brood size	5.30	1.25	6.00	1.05	0.23
Hatching day	26 June	7	28 June	12	0.68
Wing length, mm, day 1	6.9	0.5	7.3	0.5	0.21
Wing length, mm, day 6	21.2	1.4	23.5	2.0	0.013
Wing length, mm, day 12	48.8	1.9	51.0	1.3	0.016
Body mass, g, day 1	2.5	0.2	2.9	0.5	0.14
Body mass, g, day 6	11.3	0.4	12.0	1.2	0.070
Body mass, g, day 12	15.9	0.8	15.8	1.0	0.62
Asymptote, g	16.2	0.9	15.9	1.0	0.52
Growth constant	0.52	0.03	0.54	0.04	0.13
Inflection point, days	4.30	0.26	3.80	0.42	0.021

In general, there was a better correlation between egg volume and wing length at fledging (day 12; Spearman's rank correlation coefficient, r_s = 0.424, P=0.06) than between egg volume and body mass at fledging (r_s= –0.030, P=0.90). Initially heavy nestlings seemed to reach the inflection point sooner than light nestlings (Fig. 3). The mean temperature for 0–6 days after hatching correlated with wing length on day 6 (r_s=0.571, P=0.007) and on day 12 (r_s=0.561, P=0.009). The asymptote and growth constant correlated significantly negatively (r_s= –0.539, P=0.013).

When the data were divided into two groups according to brood size (small broods 3–5 young, n=7; large broods 6–7 young, n=13), or according to hatching day (early hatched clutches 14–23 June, n=10; late hatched clutches 24 June – 16 July, n=10), no significant differences in the growth parameters emerged between these groups (Mann-Whitney tests, all P-values ≥ 0.2).

In body mass v. body mass correlations the strength of the positive relationship decreased as the nestlings grew, but in wing v. wing correlations it increased (Table 3). Initially heavy nestlings also had longer wings at fledging than light nestlings.

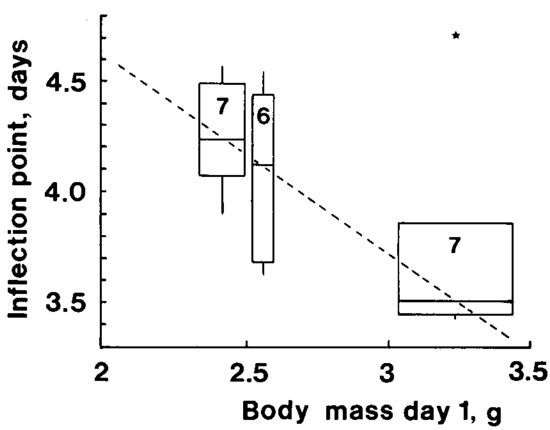

Fig. 3. Best-fit three-group resistant line (broken line) through the group medians of Redstart nestling body mass day 1 versus inflection point of the logistic body-mass curve. Equation: inflection point=–0.898 × body mass day 1 + 6.413 (goodness of fit = 0.9998). The box plots show the median (horizonal lines), the central 50% of the data (rectangles), adjacent values (vertical bars), and a possible outlier (star). The numbers denote the number of nests in each group.

Table 3. Spearman's correlation coefficients and their 2-tailed probabilities (in parentheses) between body mass and wing length in the Redstart nestlings aged 1, 6 and 12 days (n=20 nests).

	Body mass day 6	Body mass day 12	Wing day 1	Wing day 6	Wing day 12
Body mass, day 1	0.732 (<0.001)	0.360 (0.121)	0.608 (0.004)	0.577 (0.007)	0.453 (0.044)
Wing, day 1	– –	– –	– –	0.377 (0.102)	0.423 (0.063)

Discussion

In northern Lapland the Redstart starts to breed about five days earlier than the Pied Flycatcher (Järvinen 1983). The growth constant of the logistic body mass curve of the Redstart nestlings (0.53±0.04) is higher and they reach the inflection point sooner (4.05±0.43 days; Table 1) than the Pied Flycatcher nestlings in the same area (0.50±0.04, and 4.48±0.51, n=45 nests; Mann-Whitney tests, P=0.043 and P=0.004, respectively; A. Järvinen, unpubl.), even though the asymptotic body-mass of Redstart nestlings is higher (16.1 g) than that of the Pied Flycatcher nestlings (14.4 g; Järvinen & Ylimaunu 1984).

The age at fledging averaged 15 days in the Pied Flycatcher (Järvinen & Ylimaunu 1986), compared with 13 days in the Redstart. The relative body mass and wing length differences between the Redstart broods decreased towards the end of the nestling period (Fig. 2), a pattern resembling that of the Pied Flycatcher (Järvinen & Ylimaunu 1984). Sibling competition (brood size) seemed to play a small role in the determination of nestling growth in the Redstart. In the late breeding season of 1982, brood size had negative effects on the growth of Pied Flycatcher nestlings (Järvinen & Ylimaunu 1986).

In the Pied Flycatcher, a southern newcomer which started to breed in the area in the 1950s (Järvinen 1983), annual variation (1980, 1982–83) in the growth parameters was more pronounced than in the Redstart (Järvinen & Ylimaunu 1986; Table 1). The late breeding season of 1982 was an especially poor year with respect to flycatcher growth, but for the Redstart this year was as good as the others. Thus, in this northern area weather factors may be more selective and important for the growth of the Pied Flycatcher nestlings. This is in accordance with the fact that the breeding success of the Redstart fluctuates less annually than that of the Pied Flycatcher (Järvinen 1983).

In both species wing length, but not body mass, at fledging was significantly correlated with the mean temperature during the early part of the nestling period. In the Pied Flycatcher, the nestlings benefited from a large egg size only in the late breeding season of 1982 (Järvinen & Ylimaunu 1986; for the Great Tit *Parus major*, see Schifferli 1973). In that year, according to partial correlation analyses, hatchlings from large eggs had larger food or energy reserves than hatchlings from small eggs, but their wing length was not greater (Järvinen & Ylimaunu 1984). Toward the end of the nestling period the larger reserves of nestlings from large eggs apparently accelerated the growth of the young and this was manifested in better developed young at fledging (longer wings; Järvinen & Ylimaunu 1984). The small size of the Redstart material does not allow a meaningful correlation analysis for the separate years.

It may be advantageous for a young altricial bird to grow rapidly and to be as heavy and well developed as possible at fledging (Perrins 1965, Ricklefs 1968, 1973). In the north, weather is no doubt among the factors which prevent the nestlings from growing optimally (Orell 1983, Järvinen & Ylimaunu 1986). The daily growth of Swift *Apus apus* nestlings is favoured by warm or sunny weather (Lack & Lack 1951), and the wing length of the Pied Flycatcher nestlings is positively correlated with the mean air temperature during the nestling period (Järvinen & Ylimaunu 1986). Low temperatures are also important for their effect on brooding: the demands of brooding may conflict with the nestlings' food needs. In a small passerine like the Redstart, thermoregulation (physiological heat production) is attained about 8–10 days after hatching (O'Connor 1984:123).

The post-natal growth and survival of nestlings have been found to be positively correlated with egg size (e.g. Parsons 1970, Schifferli 1973, Lundberg & Väisänen 1979, Järvinen & Ylimaunu 1984). In the parameters of the logistic equation, large egg size seems to have positive effects on the asymptote in the Pied Flycatcher (Järvinen & Ylimaunu 1984), and also on the inflection point in the Redstart (Table 2).

Intraspecific variation in growth rates of birds usually does not correlate at all with variation in nestling asymptotic body mass, which is in sharp contrast to the interspecific situation (Ross 1980, O'Connor 1984:91). As pointed out by O'Connor (1984:91), one likely reason for this is that the growth rate and asymptote may be independent parameters of the individual bird's development, coupled only with external factors such as the nutritional level. In the Redstart nestlings, growing in harsh northern conditions, the growth rate and asymptote seem to be adjusted to environmental pressures in a similar way, i.e. they are significantly correlated.

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Selostus: **Leppälinnun poikasten kasvusta Kilpisjärvellä**

Leppälinnun poikasten painon lisäystä ja siiven kasvua tutkittiin Kilpisjärvellä 1981–1984. Analyyseissä käytettiin 20 pesyeen keskiarvoja (yht. 113 poikasta; kuva 1).

Poikasten kasvussa ei ollut tilastollisesti merkitseviä vuotuisia, muninta-aikaan tai poikuekokoon liittyviä eroja (taulukko 1). Suuresta munasta kuoriutuneet poikaset saavuttivat painokäyrän inflektiopisteen nopeammin ja olivat pitempi siipisiä kuin pienestä munasta kuoriutuneet poikaset (taulukko 2, kuva 3). Myös lämmin sää pesäpoikasaikana edisti kasvua. Tuloksia verrataan Kilpisjärven kirjosiepon poikasten kasvuun.

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