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Weather and breeding success at high latitudes — the Pied Flycatcher *Ficedula hypoleuca* and the Siberian Tit *Parus cinctus*

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The breeding success of the migratory Pied Flycatcher (*Ficedula hypoleuca*) and the resident Siberian Tit (*Parus cinctus*) were studied during 1986–1994 in Finnish Lapland. In the Pied Flycatcher, 15% of eggs did not hatch. In spells of cold weather, during the nestling period, Pied Flycatchers tried to compensate for the inactivity of winged insects (main food items) by altering their foraging niches and diet. However, low temperatures greatly decreased the feeding frequency of the Pied Flycatcher. The incapability to feed the young in cold and rainy conditions negatively affected nestling growth and fledging success in the Pied Flycatcher. In the Siberian Tit, neither the foraging strategy, nor the feeding frequency changed in relation to temperature. The hatching success of the Siberian Tit was very good in spite of early breeding, but 22% of nestlings died during the nestling period. We could not link nestling mortality with any climatic factors.

1. Introduction

Adaptedness to breeding conditions differs among species (e.g. Begon et al. 1986). Within an area, one species may be well adapted to the local situation while another may live at its margin. Poor breeding conditions may have an effect on clutch size, egg hatchability, feeding frequency, nestling growth, nestling mortality or adult mortality (Bryant 1989, and references therein). Cold weather, which is typical on the northern breeding areas, may decrease the breeding success in many ways. First, the lower the temperature, the greater is the need for high energy food (Tinbergen & Dietz 1994). Second, the availability of food for insectivorous birds declines during cold weather (Taylor 1963, Avery & Krebs 1984). Greater energy demand, lower food availability, and competition for survival for the young and the parents may retard the growth of nestlings or even cause them to starve (Murphy 1986). The effects of bad weather on the breeding success has been described in many species (e.g. Hildén et al. 1982, Grant 1986, Moreno 1989, Sørensen et al. 1990). However, the means by which poor weather conditions affect breeding success (see e.g. McNamara & Houston 1987), and the factors which explain the different behaviour among species during bad weather are unclear.

In this paper, we present the effects of weather on the breeding behaviour and breeding success of two hole-nesting passerines, which have different life histories in northern Lapland. The Pied Flycatcher (*Ficedula hypoleuca*) is a newcomer in Lapland (the archives of Kevo Subarctic Research Institute) and lives there at the northern-most border of its range, while the Siberian Tit (*Parus cinctus*) is a native species of the area, well adapted in many ways to the harsh conditions (Haftorn 1973).

The breeding success of the Pied Flycatcher has been shown to depend on the warmth of the summer (Järvinen & Väisänen 1984, Lundberg & Alatalo 1992). Likewise, in the Siberian Tit weather conditions affect breeding success, at least in some years (Saari et al. 1994). However, the means by which weather conditions affect (e.g. does cold weather reduce nestling survival directly or indirectly?) the breeding success are unclear. The question we wanted to answer was whether there are differences between two hole-nesting passerine species with different kind of life-history in their ability to cope with harsh weather conditions during egg-laying and nestling phases. First, we studied the foraging behaviour, feeding frequency and diet in different weather conditions to determine the functional responses of the two species to weather. Second, we analysed the dependence of losses in the egg-laying and nestling phases on weather factors.

2. Material and methods

The study was carried out in 1986–1994 in mixed deciduous–coniferous woodland in Finnish Lapland (lat. 69°N, long. 27°E). We distributed 1 300 nest-boxes over a large area to avoid possible intra- and interspecific density effects. Most nest-boxes and nests were situated in the Utsjoki valley. During the years 1986–1992, data were also gathered from nest-boxes located along the Utsjoki–Kaamanen and the Kaamanen–Karigasniemi roads. A detailed description of the study area is found in Eeva et al. (1989).

Foraging behaviour was studied during the nestling periods in 25 territories of the Siberian Tit and in 51 territories of the Pied Flycatcher during 1986–1994. In the Pied Flycatcher, one catch was recorded as one observation. In the Siberian Tit, which regularly stayed longer periods at a site, one observation lasted less than one minute in a location. Observation periods lasted on average one hour, and 2–50 observations per individual were recorded. Average percentage distributions (birch, pine, ground layer, air) were calculated first for each observation period, and the statistical analyses were made using an observation period as a replicate. Because our sampling was conducted in many different weather conditions (e.g., individuals studied repeatedly were studied in different temperatures), we suggest that some unavoidable nonindependence in data does not affect the answers to our question (does the foraging behaviour of the species differ in relation to the ambient temperature?). The relation between temperature and foraging niche was analysed by compositional analysis (Aitchison 1986). First, the percentage use of the foraging niches was converted to log-ratios (e.g. Aebischer et al. 1993). After that, the differences of log-ratios in relation to the temperature were analysed by PROC GLM (SAS Institute Inc. 1989).

Clutch size, dates of hatching and death of nestlings, and the hatching and breeding successes were determined by weekly nest inspections. When a nestling disappeared, the occurrence of death was set at the midpoint between visits. Nest predation by weasels or voles (one nest of Siberian Tit, 0.7%, and six, 1.1%, nests of Pied Flycatchers) was omitted. The nests in which incubation never occurred were also omitted (2.8%, 4 out of 143, in the Siberian Tit; and 6.1%, 33 out of 544, in the Pied Flycatcher, respectively). Hatching dates for the broods were estimated using mean wing length of young nestlings compared with growth curves based on known hatching dates.

The nestlings were weighed and their wing length measured at least twice during the nestling period in the years 1986, 1987, 1989 and 1990 in the Siberian Tit and in 1987, 1989 and 1990 in the Pied Flycatcher. We were unable to measure the nestlings at a fixed age, and therefore we used mass residuals calculated in the following way. First, a logistic growth curve was fitted to the pooled data based on the formula (Ricklefs 1983):

$$M(x) = \frac{A}{1 + \frac{A-1}{1} \times e^{(-Kx)}}, \qquad (1)$$

where M(x) = mass at age x, A = asymptotic mass, I = initial mass, K = rate constant. A fixed initial mass of 1.8 g was used for both species. The curve was fitted by nonlinear least squares estimation with Axum (TriMetrix Inc. 1993). Then relative mass residuals were calculated as percentage deviations from the mass expected from the growth curve. Finally, mean mass residuals for each brood (MBMR) were calculated for ages 6 to 15 days in the Siberian Tit and between for ages 5 to 12 days in the Pied Flycatcher. By omitting measurements taken from the oldest nestlings, we wanted to prevent the confusing effect of weight recession near the time of fledging (Ricklefs 1968). Differences in growth for all years were studied by ANOVA, using MBMR as the dependent variable.

In addition, we measured the feeding frequency and collected data on nestling diet of the Siberian Tit at nine nests, and of the Pied Flycatcher at 13 nests by video cameras and binoculars near Kevo Subarctic Research Station during 1986–1991 and in 1994. Both parents fed the young actively at all studied nests. Each nest was observed for one to three hours between 8 a.m. and 5 p.m., when the feeding activity of the study species was fairly constant (Tuominen 1969, Hannila & Järvinen 1987).

Weather data were received from the Meteorological Station at Utsjoki Kevo (lat. 69°45´N, long. 27°01´E). The temperature sum at the onset of laying (TDD0, base of 0°C), daily mean temperature (°C) during incubation (ITEM) and nestling (NTEM) periods, frequency of cold days (days in which mean temperatures were < 5°C, DAYSB5, for the Siberian Tit and DAYSB7, < 7°C, for the Pied Flycatcher) and amount of rainfall (mm, NRAIN) during the nestling period were calculated separately for each breeding attempt. The temperature limit for a cold day corresponds to the lowest decile of daily average temperatures during the nestling period of the species. Basic data on weather in spring (May) and during egg and nestling phases of both species are shown for the years 1986 to 1994 in Table 1.

Logistic regression analyses were used to test the effects of bad weather on survival prospects of nestlings. The response variable was the occurrence of nestling deaths *[p(deaths occurred)]*. We made these analyses using: 1) a binary variable with two states: no nestlings died vs. one or more nestlings died; 2) a three-level response variable (no deaths, some deaths, all nestlings died); and 3) a multilevel response variable (number of nestlings that died as the variable value). Since more complicated multilevel models did not fit the data better (the slopes were homogeneous for all significant factors, p-values of score tests for proportional odds assumption varying from 0.2139 to 0.8495), we will present only the results of the binary responses. The analyses were made by entering the independent variables stepwise into the model (SAS LOGISTICS procedure).

3. Results

3.1. Foraging behaviour and diet

In the Siberian Tit, the use of foraging sites did not vary in relation to ambient temperature (Fig. 1, Table 2). The Pied Flycatcher foraged mostly on

Table 1. Temperature and precipitation in May and during egg and nestling phases of the study species in different years. The means for breeding phases are averages of mean temperatures and sums of precipitation calculated separately for each breeding attempt. Data from Kevo Meteorological Station.

	May		*P. cinctus*				*F. hypoleuca*			
			Egg phase	Nestling phase			Egg phase	Nestling phase		
Year	°C	mm	°C	°C	mm	n	°C	°C	mm	n
1986	4.1	18.3	8.1	11.7	11	21	12.1	10.7	23	119
1987	2.7	24.3	5.0	9.7	16	24	9.2	10.3	13	109
1988	3.3	16.9	5.6	12.8	41	11	11.1	13.8	86	85
1989	5.5	47.8	6.2	11.8	45	20	11.4	13.5	21	38
1990	3.0	14.7	4.6	10.1	15	26	9.2	14.4	20	42
1991	3.0	15.6	11.7	12.4	39	20	12.4	11.5	22	17
1992	5.6	26.0	8.2	12.2	60	13	13.0	7.9	85	16
1993	3.7	28.8	·	·	·	·	7.4	12.2	13	21
1994	3.1	9.9	·	·	·	·	8.8	12.1	21	27
86–(92)94	3.7	22.5	6.9	11.3	29	135	10.6	11.8	33	474

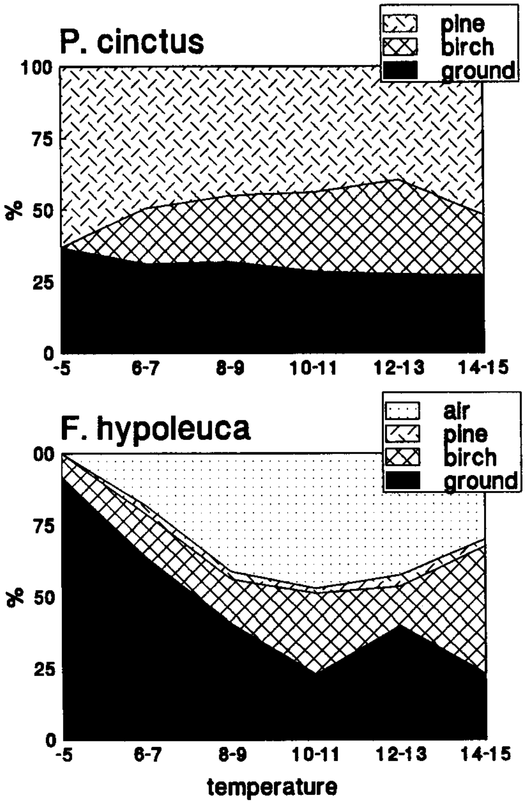

Fig. 1. Variation of foraging sites of *P. cinctus* (n = 54 observation periods) and *F. hypoleuca* (n = 40) in relation to ambient temperature (°C) during the nestling period.

winged insects in the air and from the ground layer in favourable conditions (Fig. 1, Table 3). When temperatures dropped, Pied Flycatchers shifted most of their foraging to the ground layer (Fig. 1, Table 2).

In the Siberian Tit, the proportion of winged insects among all food items rose as temperatures decreased (Table 3). We did not find any obvious changes in the diet of the Pied Flycatcher in relation to ambient temperature (Table 3). However, the proportion of winged insects in food loads tended to be lower at low temperatures.

3.2. Feeding frequency

The mean feeding frequency was 2.1 visits/nestling/h (S. D. = 2.12, n = 159 observation periods) for the Siberian Tit and 4.4 (S. D. = 3.61, n = 147) for the Pied Flycatcher. We first tested the effect of age of nestlings on feeding frequency within broods by the homogeneity of slopes model of GLM in SAS. For both species the dependence of feeding frequency on age was similar among broods (nonsignificant interactions between brood and age). The effect of brood size on feeding frequency was then analyzed using feeding frequencies corrected for age of nestlings. In both species, the frequency of feeding per nestling decreased with an increase in brood size (Table 4). Further, the Siberian Tit did not increase its feeding frequency with the age of the young, while the Pied Flycatcher did (Table 4).

In the Siberian Tit, temperature did not affect the feeding frequency (linear regression [effects of nestling age and brood size were removed]: $y = 0.02x - 0.21$, F = 0.98, p = 0.32, $r^2 = 0.01$, n = 158, Fig. 2a). In the Pied Flycatcher, the feeding frequency decreased as temperatures dropped (linear regression [effects of nestling age and brood size were removed]: $y = 0.15x - 2.15$, F = 15.97, $p < 0.001$, $r^2 = 0.10$, n = 153, Fig. 2b). During

Table 2. Compositional analysis of the effects of ambient temperature (°C) on foraging behaviour (ANOVA on log-ratios, see Material and methods).

	P. cinctus				*F. hypoleuca*			
Log-ratio	df	MS	F	p	df	MS	F	p
Birch/ground	1	114.8	0.66	0.421	1	650.7	5.46	0.025
Error	52	174.3			38	119.2		
Pine/ground	1	298.5	1.61	0.209	1	1005.2	8.95	0.005
Error	52	185.1			38	112.3		
Air/ground	·	·	·	·	1	1029.7	9.92	0.003
Error					38	103.8		

rainy and cold periods, which occurred in some years, the Pied Flycatcher did not feed or warm its nestlings at all. For instance, in eight of ten studied broods the young were without brooding from 9 a.m. to 3 p.m. on 10 June 1987.

3.3. Growth rates of the young

In both species, the growth of nestlings varied among study years (ANOVA: Siberian Tit: $F = 3.74$, $p = 0.0184$, $n = 4$ years; Pied Flycatcher: $F = 6.06$, $P = 0.0046$, $n = 3$ years). In the exceptionally good year of 1986, the nestlings of Siberian Tits grew faster than in other years (Tukey's test, $HSD = 3.8$, $df = 40$, $p < 0.05$). In the Pied Flycatcher, the gain of mass was less in the colder summer of 1987 than in the summers of 1989 and 1990 (Tukey's test, $HSD = 3.4$, $df = 46$, $p < 0.05$).

3.4. Egg and nestling loss

Nests with no hatchlings were uncommon in the Siberian Tit (three nests, 2.6%), while in 26 nests (5.8%) of the Pied Flycatcher no eggs hatched. The mean hatching success of the Siberian Tit was good; only 8% of eggs did not hatch (Fig. 3). In the Pied Flycatcher, the hatching success was 85%. It was very poor in 1993, when the temperature during the egg-laying phase was lowest (3.2°C below the average, Fig. 3, Table 1). In logistic regression analyses (binary response variable: one or more unhatched eggs), however, none of the weather variables explained hatchability significantly (p for temperature during incubation 0.1277).

The numbers of fledglings and fledging success varied among years in the Siberian Tit (Fig. 3). On average, 22% of nestlings died. In the pooled data, mortality was greatest among newly hatched and very large young (Fig. 4). In a stepwise logistic regression model (binary response variable (one or more nestlings died vs. no deaths), none of the independent variables explained the occurrence of nestling mortality. In the best, forced model, temperature during incubation improved nestling survival nearly significantly (ITEM, Table 5).

In the Pied Flycatcher, 84% of nestlings fledged. Almost all Pied Flycatcher young fledged in the years of 1986, 1991, 1993 and 1994 (Table 1, Fig. 3). The four years with good fledging success were not the most favourable breeding seasons according to the mean temperature and rainfall during the nestling period (Table 1). The fledging success was lowest in 1987, 1988 and 1992 (Fig. 3). Most deaths occurred on cold and rainy days in 1987 (86.8%) and 1988 (64.5%). Of all deaths of nestlings (pooled data 1986–1992), the cause of which we were able to identify ($n = 337$ dead nestlings), at least 80% were due to starva-

Table 3. The diet of nestlings in relation to the ambient temperature. G-test. The number of food items n(items) are given.

	Tipula (larvae), %	Araneae, %	Caterpillars[1], %	Winged insects[2], %	n(items)
P. cinctus					
7°C	12.7	35.2	4.2	47.9	71
8–11°C	18.3	46.0	17.5	18.3	126
12–15°C	20.6	44.1	11.8	23.5	68
			$G = 23.879$, $p < 0.001$, d. f. = 6		
F. hypoleuca					
7°C	·	36.2	20.7	43.1	58
8–11°C	·	31.1	9.4	59.4	106
12–15°C	·	25.7	21.1	53.2	109
			$G = 9.038$, $p = 0.060$, d. f. = 4		

[1] Includes larval Lepidoptera and Hymenoptera (Symphyta).

[2] Includes adult Coleoptera, Diptera, Ephmeroptera, Hymenoptera (Symphyta), Lepidoptera and Plecoptera.

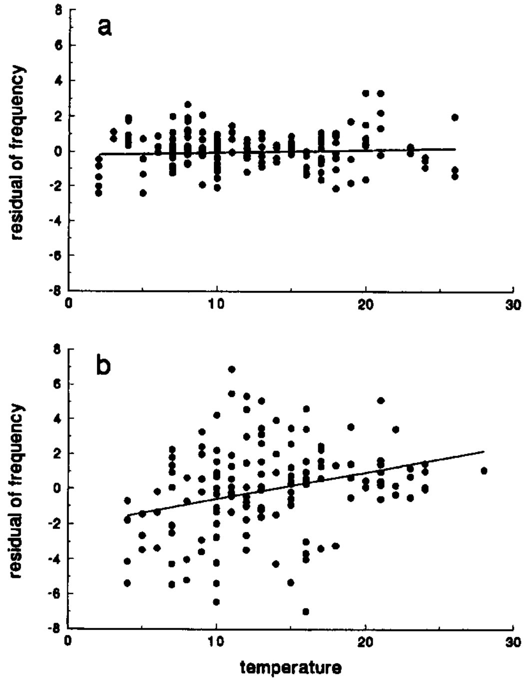

Fig. 2. Residual feeding frequency per nestling in *P. cinctus* (a, n = 158 study periods) and *F. hypoleuca* (b, n = 153) in relation to ambient temperature (°C). Effects of nestling age and brood size were removed.

tion in the Pied Flycatcher. The mortality rate of nestlings was highest among mid-aged nestlings in the Pied Flycatcher (Fig. 4). The number of cold days and the amount of rainfall during the nestling period affected nestling survival (Table 5).

Table 4. The dependence of feeding frequency (visits per nestling) on nestling age (days) and brood size. Observation periods were used as replicates.

Variable	Beta	S.E.	p
P. cinctus[1]			
Intercept	1.864	0.21	0.0001
Age of nestlings	0.031	0.02	0.177
Brood size	– 0.105	0.04	0.022
F. hypoleuca[2]			
Intercept	5.787	0.78	0.0001
Age of nestlings	0.345	0.81	0.0001
Brood size	– 1.350	0.17	0.0001

[1] Multiple regression: n = 158, R^2 = 3.2%, $F_{2,156}$ = 5.32, p = 0.022

[2] Multiple regression: n = 146, R^2 = 29.4%, $F_{2,144}$ = 60.51, p < 0.0001

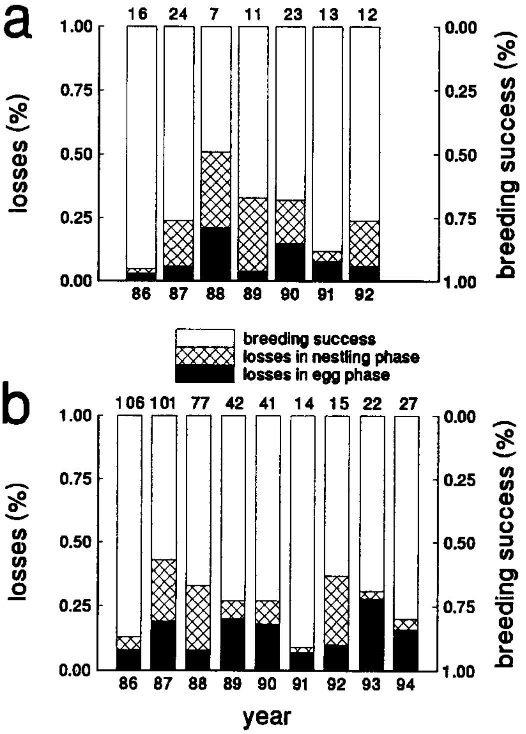

Fig. 3. Losses (%) in egg and nestling phases and breeding success (fledglings per egg) in *P. cinctus* (a) and in *F. hypoleuca* (b). Numbers of nests are given.

Breeding success is affected by low temperatures and too much rain, but these stress factors occur only rarely together in our area. There was only one summer (1992) when both low temperatures and rain occurred frequently together during this nine-year study (Table 1).

4. Discussion

We found that weather influences breeding success of the sedentary Siberian Tit (which has been present for a long time in Lapland) and the newly settled and migratory Pied Flycatcher at this high latitude breeding area in several ways.

Among Siberian Tits, normally over 90% of eggs hatch despite the very early breeding start (this study, Saari et al. 1994). The adaptations to low temperature such as courtship feeding and a well-insulated nest (Haftorn 1973) ensure good success during incubation and hatching. Similarly, cold periods had hardly any effect on nestling survival of this species. Neither the foraging strategy and diet, nor the feeding frequency changed at temperatures below 10°C. It is interesting, however, that the proportion of winged insects in nestling's diet is greater in cold temperatures. We propose that the Siberian Tit is better at catching inactive winged insects at low temperatures, than catching flying ones in warmer conditions. Although we could not observe an effect of cold conditions on behaviour, nestlings grew faster in the favourable summer of 1986.

Although weather conditions seem to affect breeding success in some years in the Siberian Tit (also Järvinen 1982, Saari et al. 1994), we could not link nestling mortality with any climatic factors. Even though nestling mortality is over 20% in Lapland (see also Saari et al. 1994), the Siberian Tit produces 5–8 fledglings per nest in Lapland (this study, Saari et al. 1994).

The egg-laying phase seems to be a bottleneck for the success of the Pied Flycatcher in its marginal breeding areas (see also Siikamäki 1995). In the north, the mean hatching success is poorer (Järvinen 1990, this study) than in its main breeding areas (e.g. Lundberg & Alatalo 1992). Hatching success is greater in our area than in the higher altitude study area of Järvinen, but in the worst cases 20% or more of eggs remained unhatched. We observed that the capability to find food declines in low temperatures. Then, the male is not able to feed his mate successfully during the incubation period (own obs., see also Lifjeld & Slagsvold 1986) and the female has to interrupt incubation for long periods, which decreases the egg hatchability (see Järvinen 1983, 1990, Lundberg & Alatalo 1992, Siikamäki 1995).

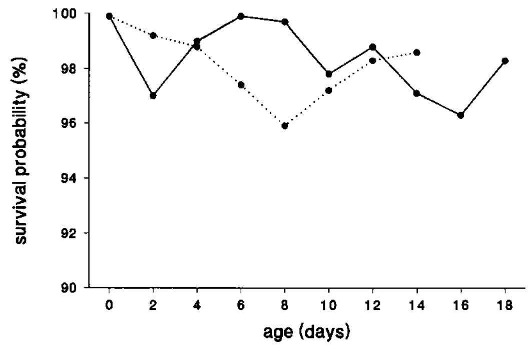

Fig. 4. The survival probability of nestlings from time *t* to time *t* + *2*. Solid line = *P. cinctus* (n = 601 nestlings), dotted line = *F. hypoleuca* (n = 1677 nestlings). Data from 1986–1991.

If hatching success depends so much on the temperature, it would be greater, if the Pied Flycatcher laid eggs later in the north. Pied Flycatchers lay their first eggs, on average, on 7th June (unpubl. data), when the mean temperature is only 7°C. For instance, the mean temperature of the laying date is ca. 15°C in Harjavalta, SW Finland (T. Eeva & E. Lehikoinen, unpubl. data 1991–1993). The Pied Flycatcher perhaps does its best in Lapland, but still has to start laying in too cold conditions. We suggest that early breeding is forced by time constraints — at the northern border of their breeding range the summer is simply too short for females to wait for better conditions

Table 5. Logistic regression models for the dependence on weather factors of the probability to breed without nestling deaths. In *P. cinctus* the variable that explained most of the survival probability was forced into the model (although not quite significant), in *F. hypoleuca* stepwise approach was applied. ITEM = daily mean temperature (°C) of incubation, NRAIN = amount of rainfall (mm) during the nestling period, DAYSB7 = number of days in which mean temperatures were < 7°C.

Variable	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square	Standardized Estimate
P. cinctus (n = 106)					
INTERCPT	– 0.6887	0.6107	1.2718	0.2594	·
ITEM	0.1501	0.0794	3.5777	0.0586	0.220618
F. hypoleuca (n = 413)					
INTERCPT	1.6571	0.2088	63.0005	0.0001	·
NRAIN	– 0.0114	0.00370	9.5261	0.0020	– 0.191064
DAYSB7	– 0.2036	0.0546	13.8977	0.0002	– 0.228760

(Perrins 1970). The low hatchability of eggs indicates that the Pied Flycatcher is at the upper limit of its range in Finnish Lapland.

In the Pied Flycatcher, foraging behaviour, diet and fledging success were clearly connected with the weather conditions. It forages mostly on winged insects (Lundberg & Alatalo 1992). When temperatures drop below 10°C, winged insects hide themselves in the vegetation (see Taylor 1963), and their availability as a food source for Flycatchers decreases. During a cold period, the Pied Flycatcher shifts to foraging on the ground layer (cf. Alatalo & Alatalo 1979). A more remarkable phenomenon, however, is the low feeding frequency of the Pied Flycatcher in cold conditions. That is why the nestling mortality is high in years with rainy and cold periods (also Pullianen 1977, Järvinen & Väisänen 1984, Sørensen et al. 1990, Lundberg & Alatalo 1992, Siikamäki 1996). However, our data does not support the findings of Järvinen and Väisänen (1984), who stated that the mean temperature and/or rainfall during the breeding season indicates the quality of the year. We emphasize that one or two rainy and cold days, which do not affect greatly the mean temperature or the amount of total rainfall during nestling period, may cause high nestling mortality. For instance, the nestling period of 1988 was warm, but nestling mortality was high on 4th and 5th July, when it rained 69 mm in two days (Veistola 1989). Especially the middle-aged nestlings are sensitive to poor conditions (this study) because of their partly naked body and high energy demand.

Weather conditions strongly affect nestling growth in the Pied Flycatcher (Askenmo 1973, Järvinen & Ylimaunu 1986, Siikamäki 1996, this study). Because nestling weight affects survival of fledglings (e.g. Tinbergen & Boerljist 1990, Magrath 1991, Lundberg & Alatalo 1992), and the nestlings are lighter at fledging dates in 'bad years' than in 'normal years' (Järvinen & Ylimaunu 1986), we suggest that the effects of spells of bad weather are more pronounced than the results of nestling mortality show. In our study situation it was, however, impossible to monitor postfledging survival or recruitment rate.

Summarising, we believe that the differences in nestling mortality between the species are caused by different abilities to feed the young during spells of bad weather. Differences in the ability to find food are caused by different morphologies and life histories. The Siberian Tit searches effectively carefully food items on the ground layer and from trunks and branches. To find immobile food items is an indispensable trait for the Siberian Tit, because it also overwinters in the harsh environment (Haftorn 1973, 1994). The Pied Flycatcher is not able to hang on trunks and branches because of its structure. Thus, it is dependent on mobile insects, that it catches while flying (own obs.). The Pied Flycatcher, which is a newcomer in Lapland, has not evolved to cope with very cold conditions, because the temperature normally is greater than 10°C in its primary breeding area. We suggest that ambient temperatures, activity of arthropods and the foraging abilities of the species all affect the timing of breeding. The dependence of the Pied Flycatcher on warm conditions (via activity of arthropods) prevents successful early breeding in the north, while the Siberian Tit has evolved in cold climates and it starts to breed before arthropods are available (Veistola, Eeva & Lehikoinen, unpublished).

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Selostus: **Sään vaikutus kirjosiepon ja lapintiaisen pesimämenestykseen Inarin Lapissa**

Monissa tutkimuksissa on osoitettu, että säätekijät (erityisesti kylmät ja sateiset kesät) vaikuttavat monen varpuslintulajin pesimä-menestykseen. Kuitenkin on ollut epäselvää, onko esim. kylmän sään vaikutus suoraa (esim. kylmyys tappaa poikaset) vaiko epäsuoraa (esim. kylmyys heikentää mahdollisuuksia ravinnon hankintaan). Toisaalta eri lajien sopeutumiskyky huonoihin sääoloihin voi vaihdella. Tässä tutkimuksessa vertaillaan uudistulokkaan kirjosiepon ja alueella kauan pesineen lapintiaisen sopeutumiskykyä huonoihin sääoloihin. Tutkimus on tehty vuosina 1986–1994 Inarin Lapissa.

Huonot sääjaksot vaikuttivat monella tavoin kirjosiepon käyttäytymiseen ja pesimä-menestykseen. Kun pesäpoikasaikana ilma viileni, kirjosieppo etsi ruokaa enemmän maasta sekä saalisti enemmän hämähäkkejä ja vähemmän lentäviä hyönteisiä kuin lämpimällä ilmalla. Vastaavasti poikasten ruokintatiheys laski ilman viiletessä. Kirjosiepon poikasten kasvunopeus oli hitaampi kylmänä pesäpoikaskautena (1987) kuin kahtena lämpimämpänä tutkimusvuotena (1989 ja 1990). Pesäpoikasten kuolleisuus oli selvästi sidoksissa säätekijöihin: sekä pesäpoikaskauden keskilämpötila että sademäärä selittävät poikaskuolleisuutta.

Lapintiainen selviytyi hyvin kylmistä sääjaksoista. Munien kuoriutuvuus lapintiaisella oli hyvä, vaikka munavaiheessa ilman keskilämpötila on vain n. 7°C. Kylmä ilma pesäpoikasvaiheessa ei muuttanut lapintiaisen poikasten ruokintafrekvenssiä. Mikään säätekijä pesäpoikaskaudella ei selittänyt pesäpoikasten kuolleisuutta.

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