Avian Ecol. Behav. 5: 79-104

Spring ambient temperature as an important factor controlling timing of arrival, breeding, post-fledging dispersal and breeding success of Pied Flycatchers *Ficedula hypoleuca* in Eastern Baltic

Leonid V. Sokolov

Abstract: Sokolov, L.V. (2000): Spring ambient temperature as an important factor controlling timing of arrival, breeding, post-fledging dispersal and breeding success of Pied Flycatchers *Ficedula hypoleuca* in Eastern Baltic. Avian Ecol. Behav. 5: 79-104.

Inter-annual fluctuations of timing of migration, breeding, post-fledging dispersal and breeding success in the Pied Flycatcher *Ficedula hypoleuca* on the Courish Spit on the Baltic in 1980-2000 appeared to be considerable, even though this species is single-brooded. Median date of spring passage varied within a month (28 April – 24 May) in different years. Median hatching date varied between 7 – 25 June. Median date of post-fledging dispersal of juvenile Pied Flycatchers ringed as pulli varied between 6 – 27 July. Median date of autumn passage was between 22 August and 11 September in different years. Breeding success and numbers of breeding and passage populations were also due to a pronounced inter-annual variation. Timing of breeding was significantly linked to the timing of spring migration, and the former was positively related to the timing of post-fledging dispersal and autumn migration. Numbers of local juveniles captured during post-fledging period was negatively correlated with the timing of spring migration, breeding and dispersal, but positively related to the number of broods, total number of ringed nestlings and the number of juveniles without rings captured in stationary traps. Numbers of autumn migrants and of local Pied Flycatchers captured during post-fledging period were positively related. Timing of migration, breeding and dispersal, and numbers estimates were significantly correlated with mean monthly temperatures of April and May: timing was correlated negatively, and numbers positively. Spring air temperatures (in April and May) have a strong indirect impact on the timing of spring migration, breeding, post-fledging dispersal and autumn departure of Pied Flycatchers, from one side; and on the breeding success of this species and thus on numbers of juveniles during post-fledging period and autumn migration, from the other side.

Key words: ambient temperature, climate, timing of spring and autumn migration, timing of breeding and post-fledging dispersal, breeding success, numbers of local and passage birds, Pied Flycatcher, passerines.

Address: Biological Station Rybachy, Zoological Institute, 199034 St.Petersburg, Russia. E-mail: LSok@bioryb.koenig.su

Received: 15 September 2000 / Received in revised form: 5 October 2000 / Accepted: 21 November 2000.

1. Introduction

Impacts of spring ambient temperature on arrival of different avian species were not infrequently reported (see reviews: Gauthreaux 1982, Sema 1989, Alerstam 1990, Richardson 1990, Žalakevicius 1997, Moos 1998, Sokolov et al. 1998). Less frequent are the reports of influence of spring temperatures on the timing of nesting and breeding success (Rytkönen et al. 1993, Cramp & Perrins 1994, Nager & Noordwijk 1995, Ravussin & Neet 1995, Zając 1995, Järvinen 1996, Mikhantiev & Selivanova 1996, Perrins 1996, Thingstand

1997, Sokolov & Payevsky 1998, Crick & Sparks 1999). And quite scarce is evidence of indirect impact of spring ambient temperature on the timing of dispersal and autumn migration of juveniles and adults, and on their numbers in these periods (Ellegren 1990, Morton 1992, Ryzhanovsky 1997, Sokolov & Payevsky 1998, Sokolov 1999, Sokolov et al. 1999).

The aim of this study of the Pied Flycatcher *Ficedula hypoleuca* is (i) to estimate the degree of dependence between arrival, breeding, dispersal, autumn departure and breeding success in one area; (ii) to estimate the impact of spring and summer ambient temperatures on the dynamics and inter-annual variation of these parameters.

2. Material and methods

2.1. Study area

The study was done on the Courish Spit on the Baltic Sea near field station "Fringilla" (55º05' N, 20º44' E) in 1980-2000. In a stripe along the spit, 10 km long (5 km each direction from stationary Rybachy-type traps) and 300 m wide, 350 new nest-boxes were added in 1981 to the existing 50. The next large-scale replacement of nest-boxes was done in spring and early summer 1996 when in essentially the same area (12 km long) 330 new nest-boxes were added to remaining 70 old ones. In August 1998, 50 old nest-boxes were replaced by 54 new ones. Thus, each year ca. 400 nest-boxes suitable for Pied Flycatchers and titmice were present in the study area.

2.2. Spring trapping

Spring (and autumn) trapping of passage Pied Flycatchers was done in stationary Rybachy-type traps which are annually in use on the Courish Spit between 1 April – 1 November. Timing of spring migration was estimated by the first capture and by median capture date in spring (before 1 June). Numbers of spring migrants were estimated by numbers of birds captured in two traps used simultaneously (traps # 4 and # 5) with entrance to the NE and SW, respectively. Day-to-day capture pattern was analysed in years for which the data on air temperature at noon were available. To study the relationship between daily trapping figures and air temperature at noon (or mean daily temperature), in each year periods of peak captures were defined.

2.3. Trapping during the breeding season

Trapping and marking of adult males usually started in early May in empty nest-boxes before the onset of nest construction. This method permits to increase the proportion of annually controlled males by about 25% (Sokolov et al. 1990). Females were captured in nest-boxes usually during incubation. Adult birds were also captured during feeding the young.

Timing of breeding was estimated by median and mean hatching dates (Sokolov et al. 1990). Practically all birds in the study area were regularly checked. Brood size was usually noted during ringing the pulli, normally at the age of 6-10 days. In most cases, fledging success was controlled for.

Numbers of Pied Flycatchers breeding in the study area were estimated by numbers of broods in nest-boxes. In the first two years (1980-1981), number of nests and ringed nestlings was low, as only 50 nest-boxes were available at the study site. In the study area, the number of nests found in natural cavities was always low, ca. three per year. However outside the borders of the study area, numbers of Pied Flycatchers breeding in natural cavities on the Courish Spit are considerably higher.

2.4. Trapping of juveniles during post-fledging dispersal

Timing of post-fledging dispersal was estimated by first captures of juveniles (incl. those ringed as pulli) in large traps, and by median capture date of local Pied Flycatchers (marked in nests). Dates of last captures of marked local birds, hatched within 1 km from the traps, were used as estimates of leaving the immediate natal site.

Numbers of juvenile Pied Flycatchers during post-fledging period were estimated by (i) number of birds ringed as pulli and captured in two traps (# 4 and # 5); (ii) numbers of unmarked juveniles trapped before 20 August. Last captures in "late" years suggest that to this date, the vast majority of marked juveniles leave the study area.

2.5. Estimating breeding efficiency

Breeding success was estimated by mean brood size, number of nestlings ringed in the study area, proportion of ringed nestlings that were recaptured during post-fledging period, and by the total number of captured local juveniles. I also analysed return rate of birds ringed as pulli to the natal and dispersal area in subsequent years.

2.6. Autumn trapping

As estimate of the timing of autumn migration used median trapping date of juvenile Pied Flycatchers after 20 August. Only birds trapped in the trap # 5 which was always in operation until late October, were considered.

3. Results

3.1. Timing of spring migration

First spring captures and median dates of spring passage show considerable interannual variation (Tab. 1). Earliest passage was recorded in 1983 and 2000, when 50% of all spring captures occurred in late April (Tab. 2). Latest passage was recorded in 1980 and 1991 when 50% of birds were not captured until 17 May and 24 May, respectively. Date of the first capture was significantly related to the median passage date, in spite of large interannual variation of the latter (Tab. 3).

Both first capture date and median passage date are significantly related to the mean air temperature in April and May (Tab. 3). First Pied Flycatchers arrive to the Courish Spit earlier if mean April temperature is high (Fig. 1A). Mean May temperatures to a large extent govern the schedule of passage through the Courish Spit in this month (Fig. 1B). During mass migration of Pied Flycatchers, most birds were captured in days when temperature at noon (or mean daily temperature) were high at the study site (Tab. 4, Fig. 2).

Table 1. Parameters of seasonal events in Pied Flycatchers on the Courish Spit included in the analysis.

	Parameters	Mean ± SE	SD
A.	Mean air temperature in April	6.7 ± 0.35	1.46
B.	First capture date on spring	24/04	4.32
C.	Mean air temperature in May	12.1 ± 0.35	1.45
D.	Median date of spring migration	10 /05	5.71
E.	Number of spring migrants	58 ± 7.9	36.6
F.	Mean air temperature in June	15.3 ± 0.23	0.94
G.	Number of broods	50 ± 3.8	16.7
H.	Median hatching date	14/06	4.84
I.	Brood size	5.5 ± 0.5	0.24
J.	Number of ringed nestlings	266 ± 21.2	89.4
K.	Mean air temperature in July	17.5 ± 0.33	1.4
L.	First capture date of a juvenile	14/07	7.99
M.	First capture date of a marked juvenile	6/07	7.15
N.	Median capture date of a marked juveniles	15/07	4.88
O.	Number of marked juveniles	27 ± 4.9	22.7
P.	Age of juveniles at last capture, days	33 ± 0.5	2.28
Q.	Recapture rate of marked juveniles in the same season	10.4 ± 1.18	5.41
R.	Return rate in subsequent years	7.3 ± 0.42	1.73
S.	Number of unmarked juveniles	42 ± 6.6	30.2
T.	Total number of captured juveniles	66 ± 9.4	42.1
U.	Number of autumn migrants	51 ± 7.3	33.7
V.	Median date of autumn migration	31/08	5.97

Notes: SE – standard error. SD – standard deviation.

Overall number of Pied Flycatchers captured in spring in two traps, varied considerably – between 15 (in 1993) and 187 (in 1997) (Tab. 1, 2). No relationship between spring trapping figures and timing of migration or mean monthly air temperatures was revealed. However there is a weak trend to capture more birds at low May temperatures (Tab. 3).

3.2. Timing of hatching

Median hatching dates in the study area varied considerably, between 7 June (in 2000) and 25 June (in 1987) (Tab. 1, 2). Hatching dates are significantly related to mean April and May temperatures (Tab. 3). Early breeding is usually recorded in years with early and warm spring (Fig. 3A, B). No significant relationship between hatching dates and mean June temperature was found (Tab. 3).

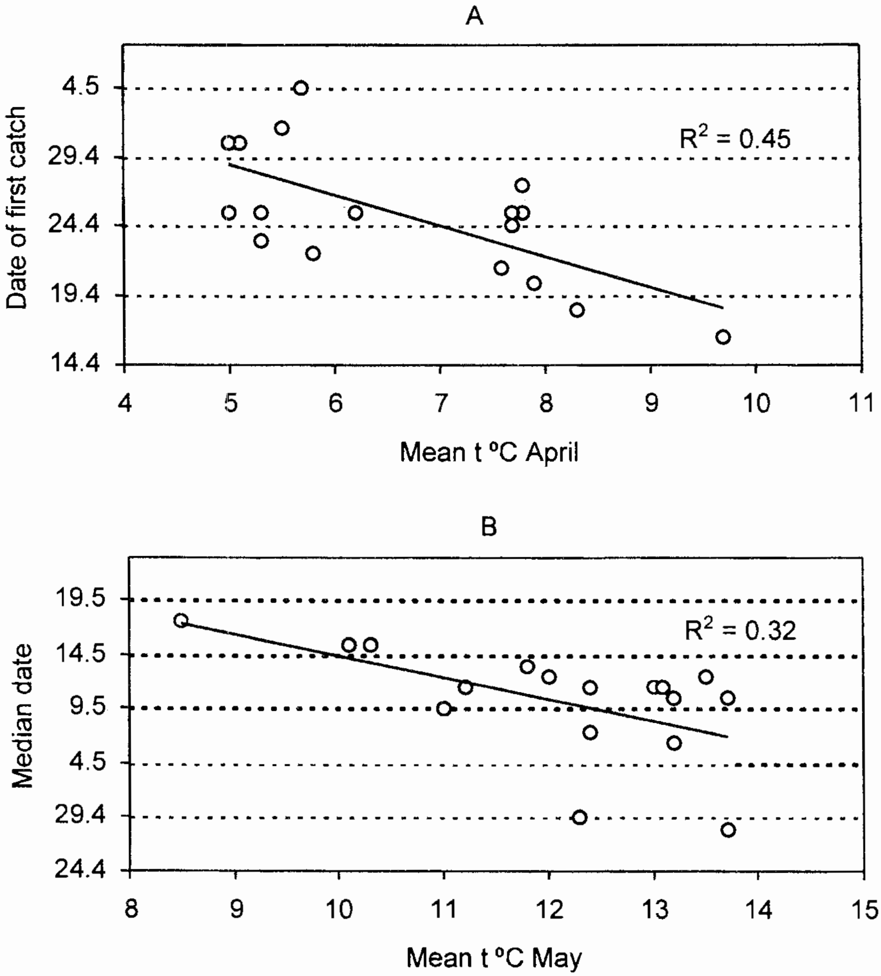

Figure 1. Dependence of the date of the first capture (A) of a Pied Flycatcher and of median date of spring migration (B) on mean air temperature in April and May.

I found a strong positive correlation between median hatching date and median date of spring passage (Tab. 3). In years when Pied Flycatchers arrive early they usually breed early (Fig. 3C).

Table 2. Inter-annual variation of spring and summer air temperature and parameters of seasonal events in Pied Flycatchers on the Courish Spit.

Index	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000
A	5.5	5.1	5.0	7.9	7.6	5.8	6.2	5.3	5.7	7.8	8.3					7.7	5.0	5.3	7.7	7.7	9.7
B	1/05	30/4	30/4	20/4	21/4	22/4	25/4	23/4	4/05	27/4	18/4	28/4	26/4	23/4	23/4	25/4	25/4	25/4	24/4	25/4	16/4
C	8.5	13.0	11.8	13.7	13.2	13.7	13.2	10.1	13.5	12.4	12.4					11.2	12.0	11.0	13.1	10.3	12.3
D	17/5	11/5	13/5	28/4	10/5	10/5	6/05	15/5	12/5	11/5	7/05	24/5	5/05	6/05	8/05	11/5	12/5	9/05	11/5	15/5	29/4
E	29	42	25	29	18	23	36	87	50	27	18	48	102	15	32	63	36	187	47	53	33
F	15.9	16.0	13.8	15.1	13.7	14.6	15.4	14.1	16.2	15.4	16.3					16.2	15.1	15.7	14.8	17.1	15.0
G	10*	11*	28	50	74	62	86	43	41	59	48	47	40	47	26	25	31	57	58	52	72
H	24/6	13/6	15/6	10/6	14/6	16/6	10/6	25/6	13/6	15/6	14/6	24/6	15/6	8/06	11/6	13/6	17/6	18/6	15/6	14/6	7/06
I	5.2± 0.36	5.8± 0.26	5.6± 0.28	6.0± 0.21	5.4± 0.19	5.6± 0.16	5.7± 0.16	5.1± 0.20	5.3± 0.22	5.6± 0.14	5.3± 0.18	5.6± 0.20	5.7± 0.25	5.3± 0.26	5.5± 0.32	5.6± .28	5.5± 0.26	5.4± 0.16	5.1± 0.20	5.6± 0.17	5.9± 0.15
J	52*	61*	160	295	382	329	470	220	214	333	252	256	224	236	144	139	169	308	275	254	400
K	16.4	16.5	18.2	18.0	15.6	16.6	17.6	16.5	18.7	18.0	16.9				20.6	18.5	16.1	18.5	16.0	19.8	16.2
L	20/7	17/7	16/7	6/07	9/07	11/7	10/7	15/7	8/07	6/07	4/07	24/7	23/7	8/07	8/07	22/7	1/08	26/7	16/7	16/7	3/07
M	20/7	13/7	3/07	1/07	4/07	8/07	25/6	9/07	3/07	3/07	1/07	12/7	19/7	25/6	5/07	8/07	16/7	7/07	6/07	10/7	30/6
N	22/7	15/7	17/7	14/7	15/7	18/7	15/7	27/7	16/7	16/7	18/7	19/7	21/7	6/07	9/07	11/7	16/7	18/7	12/7	21/7	8/07
O	6	8	22	64	55	22	88	7	24	53	42	21	3	24	13	14	2	27	16	15	46
P	30± 1.48	38± 3.39	31± 1.86	34± 1.04	35± 1.12	37± 2.43	33± 0.94	32± 4.48	31± 1.45	32± 1.58	35± 1.12	31± 3.07	30± 0.88	31± 2.93	35± 2.19	32± 2.68	34± 3.50	32± 1.48	33± 3.25	37± 2.70	34± 1.29
Q	9.6	13.1	13.8	21.7	14.4	6.7	18.7	3.2	11.2	15.9	16.7	8.2	1.3	10.2	9.0	10.1	1.2	8.8	6.0	6.0	12.0
R	5.8	8.2	7.0	10.5	8.4	8.8	10.9	5.0	7.0	7.2	4.4	6.3				6.5	5.9	7.4	6.9	8.0	
S	36	31	13	53	40	68	61	21	76	54	96	4	22	52	24	18	11	16	10	87	114
T	41	39	35	117	95	90	149	28	100	107	138	35	25	76	37	32	13	43	26	102	160
U	70	76	38	81	21	62	110	39	140	31	90	37	15	33	40	15	18	18	28	58	40
V	5/09	2/09	1/09	9/09	1/09	11/09	8/09	1/09	24/8	29/8	22/8	30/8	4/09	23/8	27/8	24/8	6/09	7/09	3/09	26/8	25/8

Note: * data incomplete due to a small number of nest-boxes.

Table 3. Correlations between analysed parameters (Spearman rank correlation coefficient: $^{1)}$ $p < 0.10$, $^{2)}$ $p < 0.05$, $^{3)}$ $p < 0.01$, $^{4)}$ $p < 0.001$).

Index	B	C	D	E	F	G	H	I	J	L	M	N	O	P	Q	R	S	T	U	V
A	-0.60$^{2)}$	0.27	-0.62$^{2)}$	-0.25	0.20	0.48$^{2)}$	-0.54$^{2)}$	0.24	0.51$^{2)}$	-0.70$^{3)}$	-0.57$^{2)}$	-0.42$^{1)}$	0.57$^{2)}$	0.25	0.42$^{1)}$	0.11	0.60$^{3)}$	0.67$^{3)}$	0.16	-0.53$^{2)}$
B			0.61$^{3)}$	0.36		-0.52$^{2)}$	0.34	-0.16	-0.49$^{2)}$	0.54$^{2)}$	0.46$^{2)}$	0.36$^{1)}$	-0.38$^{1)}$	-0.53$^{2)}$	-0.13	-0.12	-0.33	-0.34	-0.01	0.17
C			-0.60$^{2)}$	-0.42$^{1)}$	-0.21	0.46$^{1)}$	-0.51$^{2)}$	0.32	0.45$^{1)}$	-0.52$^{2)}$	-0.51$^{2)}$	-0.48$^{2)}$	0.59$^{2)}$	0.38	0.48$^{2)}$	0.62$^{3)}$	0.28	0.36	0.41$^{1)}$	0.11
D				0.25		-0.40$^{1)}$	0.66$^{4)}$	-0.39$^{1)}$	-0.45$^{2)}$	0.50$^{2)}$	0.58$^{3)}$	0.54$^{2)}$	-0.49$^{2)}$	-0.30	-0.39$^{1)}$	-0.55$^{2)}$	-0.37$^{1)}$	-0.43$^{2)}$	-0.04	0.05
E						-0.20	0.28	0.21	-0.17				-0.43$^{1)}$				-0.35	-0.42$^{1)}$	-0.27	0.18
F						-0.36	-0.25	0.03	-0.34	0.11	0.13	0.12	-0.14	-0.06	0.06	-0.19	0.34	0.24	0.32	-0.41
G								0.13	0.98$^{4)}$	-0.43$^{2)}$	-0.53$^{2)}$	-0.14	0.75$^{4)}$	0.31	0.25	0.57$^{2)}$	0.44$^{1)}$	0.62$^{3)}$	0.06	0.12
H								-0.43$^{2)}$	-0.17	0.62$^{3)}$	0.68$^{4)}$	0.79$^{4)}$	-0.47$^{2)}$	-0.29	-0.57$^{3)}$	-0.57$^{2)}$	-0.52$^{2)}$	-0.55$^{3)}$	-0.33	0.49$^{2)}$
I									0.25	-0.07	-0.09	-0.21	0.23	0.28	0.31	0.67$^{3)}$	0.24	0.29	0.10	0.12
J										-0.40$^{1)}$	-0.52$^{2)}$	-0.14	0.77$^{4)}$	0.30	0.28	0.59$^{2)}$	0.41$^{1)}$	0.62$^{3)}$	0.02	0.15
K										-0.06	-0.15	0.05	0.07	-0.13	0.08	0.16	0.14	0.13	0.17	-0.36
L											0.79$^{4)}$	0.43$^{2)}$	-0.65$^{3)}$	-0.26	-0.64$^{3)}$	-0.27	-0.73$^{4)}$	-0.74$^{4)}$	-0.51$^{2)}$	0.54$^{2)}$
M												0.59$^{3)}$	-0.84$^{4)}$	-0.13	-0.71$^{4)}$	-0.37	-0.47$^{2)}$	-0.68$^{4)}$	-0.32	0.42$^{1)}$
N													-0.36$^{1)}$	-0.22	-0.40$^{1)}$	-0.42$^{1)}$	-0.07	-0.20	0.05	0.32
O														0.13	0.78$^{4)}$	0.59$^{2)}$	0.52$^{2)}$	0.81$^{4)}$	0.30	-0.20
P															0.10	0.45$^{1)}$	0.34	0.30	0.28	0.03
Q																0.41$^{1)}$	0.47$^{2)}$	0.72$^{4)}$	0.48$^{2)}$	-0.30
R																	0.30	0.51$^{2)}$	0.21	0.39
S																		0.88$^{4)}$	0.64$^{3)}$	-0.38$^{1)}$
T																			0.62$^{3)}$	-0.28
U																				-0.11

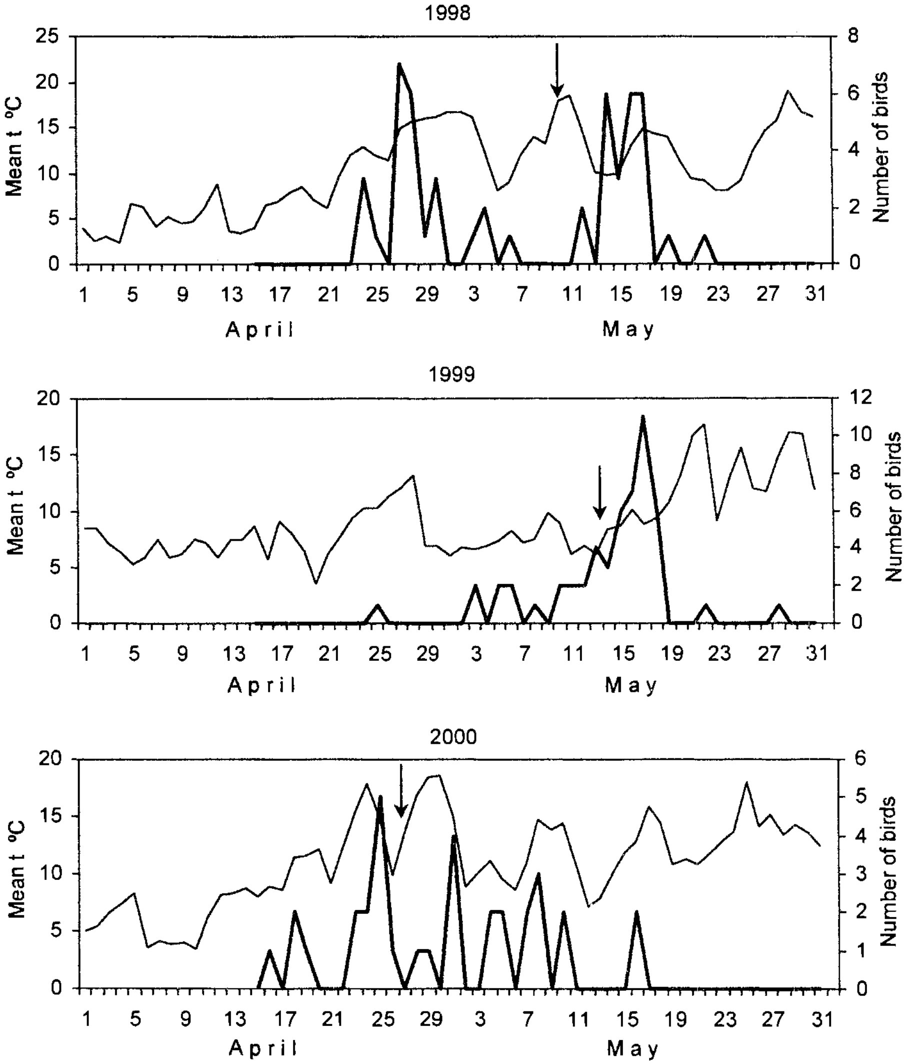

Figure 2. Day-to-day dynamics of mean daily temperature (thin line) and captures of Pied Flycatchers (thick line) during spring migration in some years. Arrows indicate the median date of passage.

3.3. Number of broods and brood size

Number of nests with broods varied considerably, between 25 (in 1995) and 86 (1986). The data from 1980-1981 are not considered, as in those years number of nest-boxes was low (Tab. 1, 2).

Number of nests with broods was positively correlated with mean April temperature, assumed that in first two study years the number of broods was also minimal, ca. 25 (Tab.

3, Fig. 4A). Relationship with May temperature was not significant, however a trend for more nests in years with warm May is recorded (Fig. 4B). No significant correlation with mean June temperature was revealed (Tab. 3). A negative relationship between number of nests and timing of spring migration, especially the date of the first capture, was revealed (Tab. 3, Fig. 4C).

Mean brood size varied from 5.1 (1981 and 1998) to 6.0 (1983), overall average 5.5 fledglings (Tab 1, 2). It was significantly related only to the median hatching date: in years with early breeding broods were larger (Tab. 3, Fig. 5).

Total number of fledglings varied broadly, from 139 (in 1993) to 470 (in 1986), data from 1980 and 1981 excluded (Tab. 1, 2). Number of fledglings was positively related to April temperature and negatively – to the timing of spring migration, assumed that in two first years the number of fledglings in the study area was also low, ca. 140 (Tab. 3, Fig. 6A, B). A similar relationship with May temperatures was on the edge of statistical significance, no relationship was found with June temperatures (Tab. 3).

Table 4. Relationship between daily trapping totals of Pied Flycatchers in stationary traps and noon (or daily average, *) air temperature at Fringilla during mass migration in spring (r_s - Spearman rank correlation coefficient).

Year	Period	r_s	p
1980	1/05 - 24/05	0.49	< 0.05
1981	1/05 - 15/05	0.89	< 0.001
1982	1/05 - 15/05	0.46	< 0.10
1983	20/04 - 5/05	0.30	n. s.
1985	20/04 - 10/05	0.57	< 0.01
1986	20/04 - 10/05	0.75	< 0.001
1987	5/05 - 25/05	0.55	< 0.05
1990	28/04 - 10/05	0.49	n. s.
1995	28/04 - 15/05	0.18	n. s.
1996	25/04 - 15/05	0.52	< 0.05
1997	1/05 - 10/05	0.56	< 0.10
1998*	25/04 - 10/05	0.22	n. s.
1999*	1/05 - 15/05	0.27	n. s.
2000*	20/04 - 15/05	0.51	< 0.01

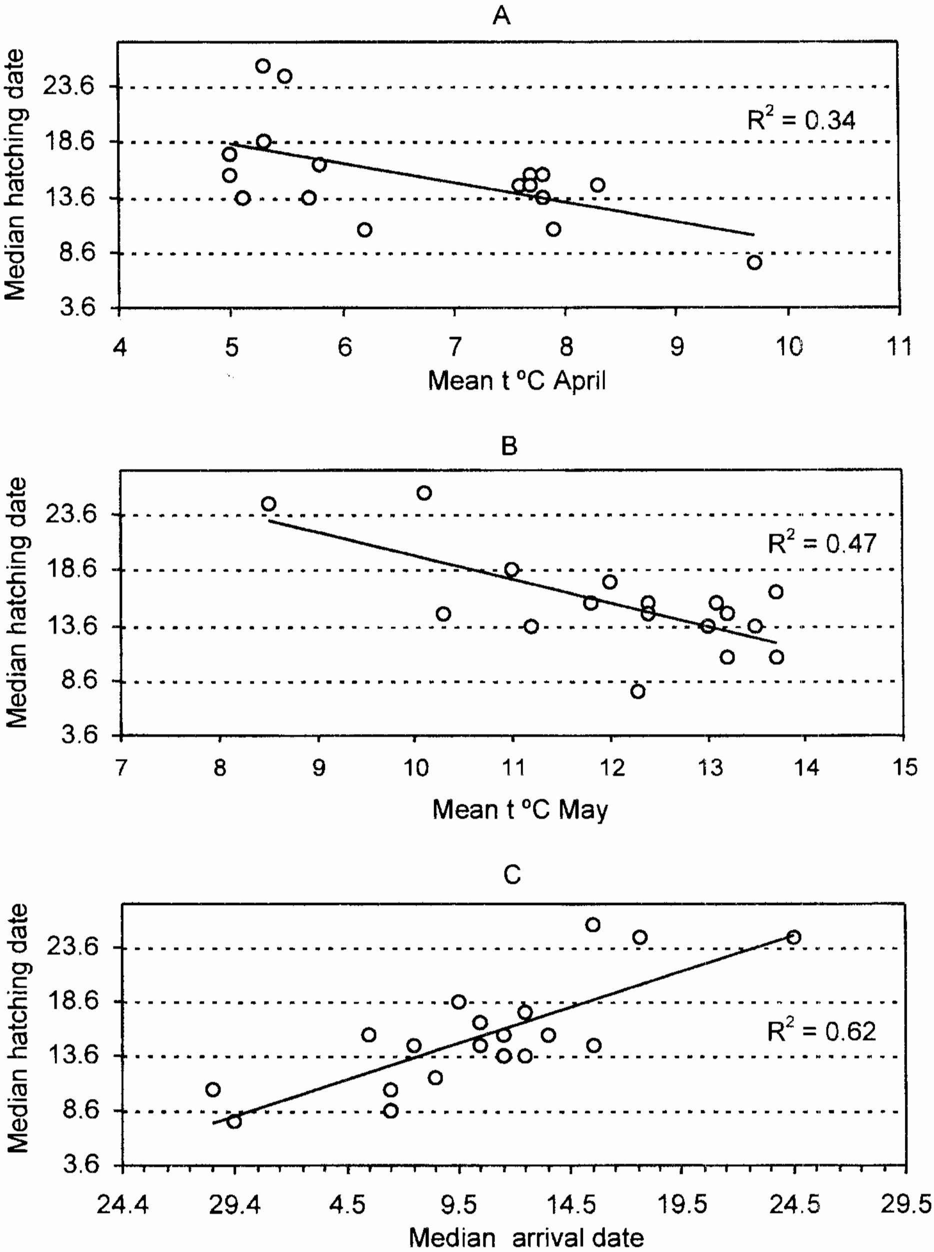

Figure 3. Dependence of median hatching date on mean air temperature in April (A), May (B) and median date of spring migration (C).

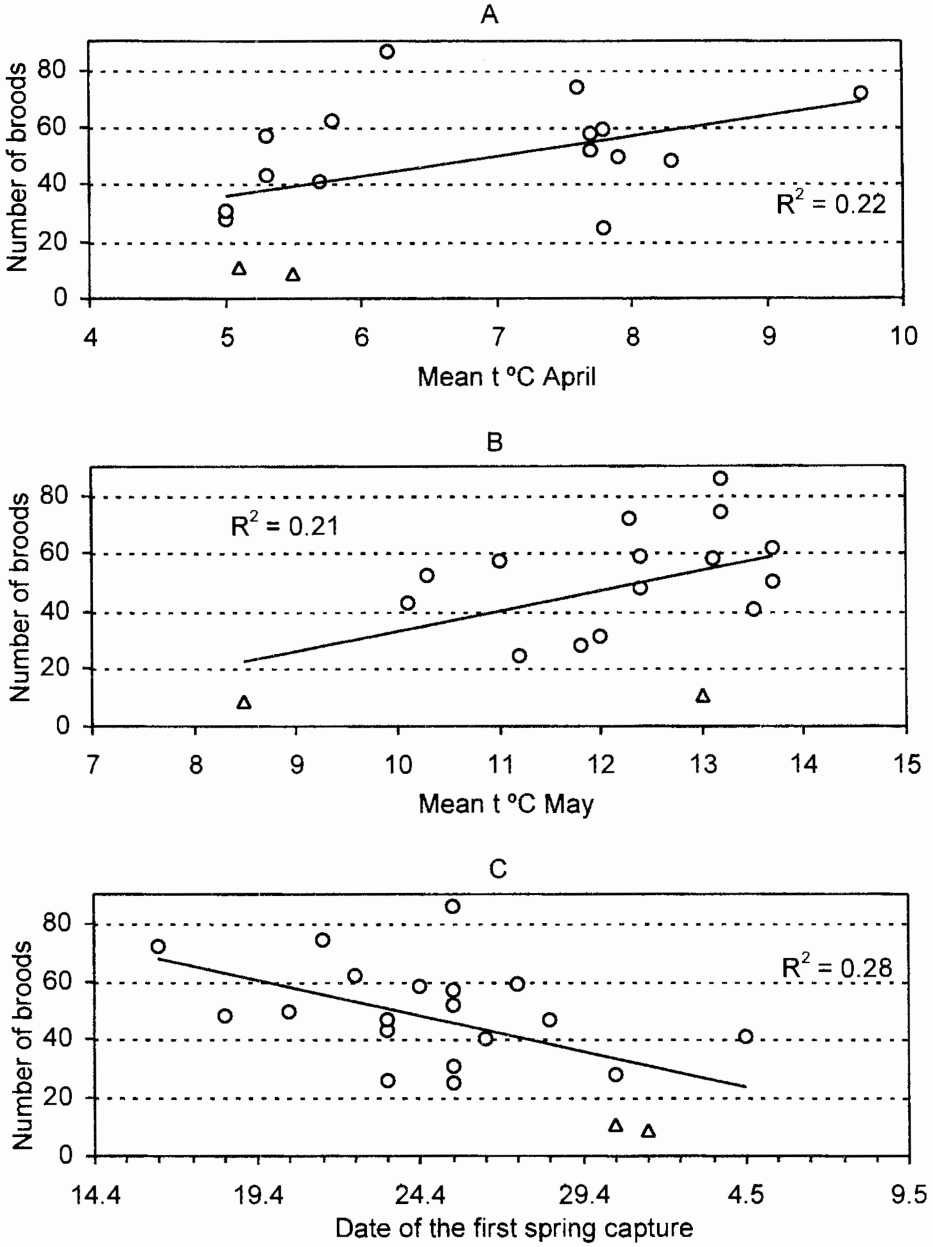

Figure 4. Relationship between the number of broods and mean April temperature (A), May temperature (B) and the date of the first spring capture (C). Triangles refer to years with low number of available nest-boxes (1980, 1981).

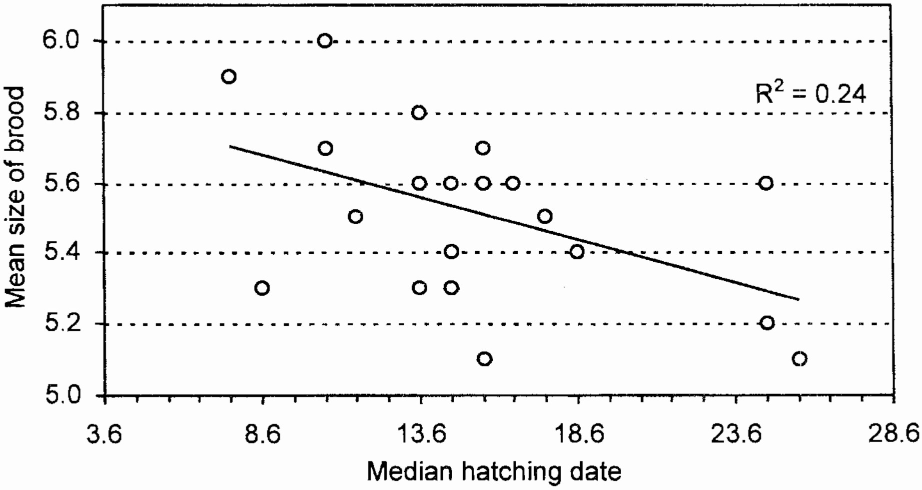

Figure 5. Relationship between the mean brood size and median hatching date.

3.4. Timing of post-fledging dispersal

As shown by first captures of juveniles and median capture dates of local juveniles in stationary traps, timing of post-fledging dispersal varies broadly from year to year (Tab. 1, 2). Earliest first captures of juveniles ringed in nests were recorded in 1986, 1993 and 2000. Latest first captures occurred in 1980 and 1997. First captures of marked and unmarked juveniles, and median trapping date of local birds are highly correlated (Tab. 3).

Dates of first captures of juveniles are significantly related to mean April and May temperatures (Tab. 3). Median date of post-fledging dispersal is also negatively related to the mean May temperature. Early dispersal usually occurs in years with a warm spring (Fig. 7A, B).

It was possible to show a strong positive dependence of the timing of post-fledging dispersal from the timing of spring migration and hatching (Tab. 3). Early arrival and breeding facilitate early dispersal of juveniles from their natal areas (Fig. 7C).

Age of last capture of juveniles ringed as pulli in the immediate hatching area varied between years, but less broadly than other parameters analysed, between 30-38 days (Tab. 1, 2). It was not dependent on any other parameter except for the first capture date in spring (Tab. 3).

3.5. Proportion of juveniles recaptured during post-fledging period and in subsequent years

Proportion of juveniles marked as nestlings and recaptured in stationary traps during post-fledging period varied considerably, between 1.2% in 1996 and 21.7% in 1983 (Tab. 1, 2). It was significantly related to May temperatures, hatching dates and timing of post-fledging dispersal (Tab. 3). Proportion of recaptured birds was higher in years with warm spring, early breeding and dispersal (Fig 8A, B). It was also higher in years with high numbers of local juveniles (Fig. 8C). Return rate in subsequent years was more stable, from 4.4% in 1990 to 10.9% in 1986 (Tab. 1, 2). It was positively dependent on May temperatures, negatively dependent on the timing of spring migration and breeding, positively dependent on the number of broods and brood size. It was also related to the number of marked fledglings and number of local juveniles captured in stationary traps (Tab. 3, Fig. 9A-D).

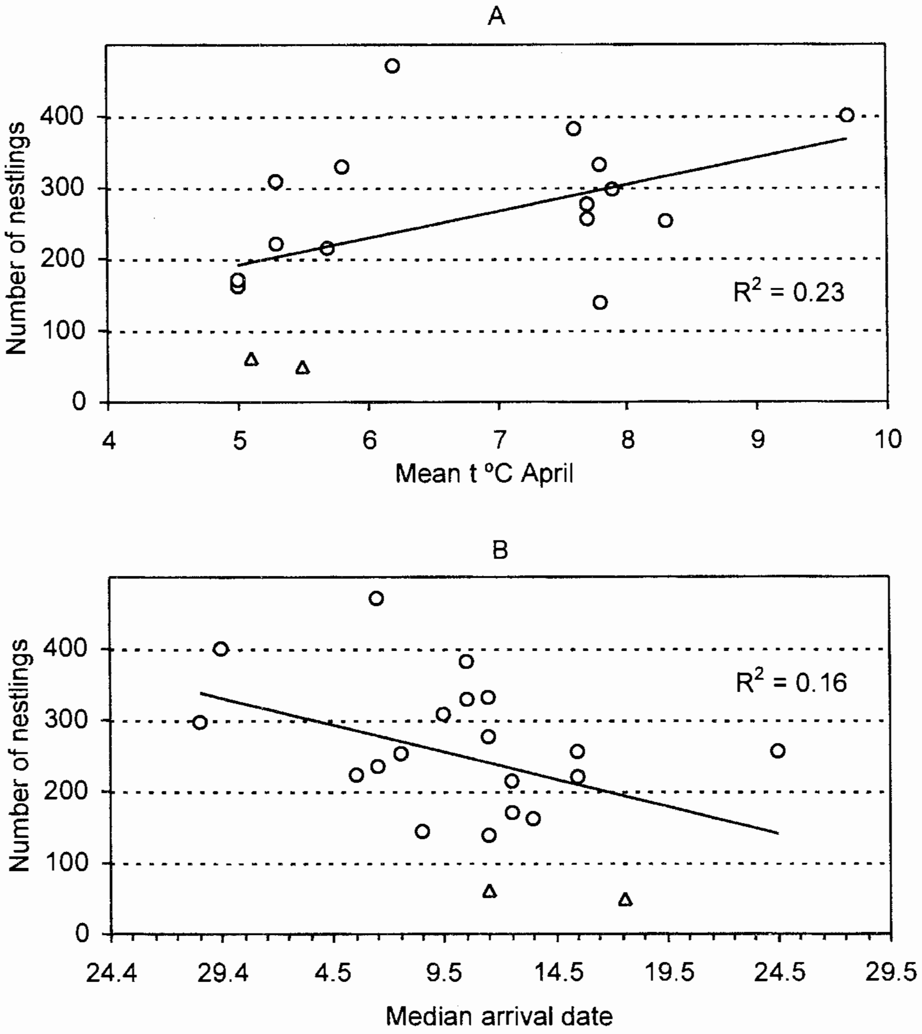

Figure 6. Dependence of the number of ringed pulli on mean April temperature (A) and on median date of spring migration (B). Triangles refer to years with low number of available nest-boxes (1980, 1981).

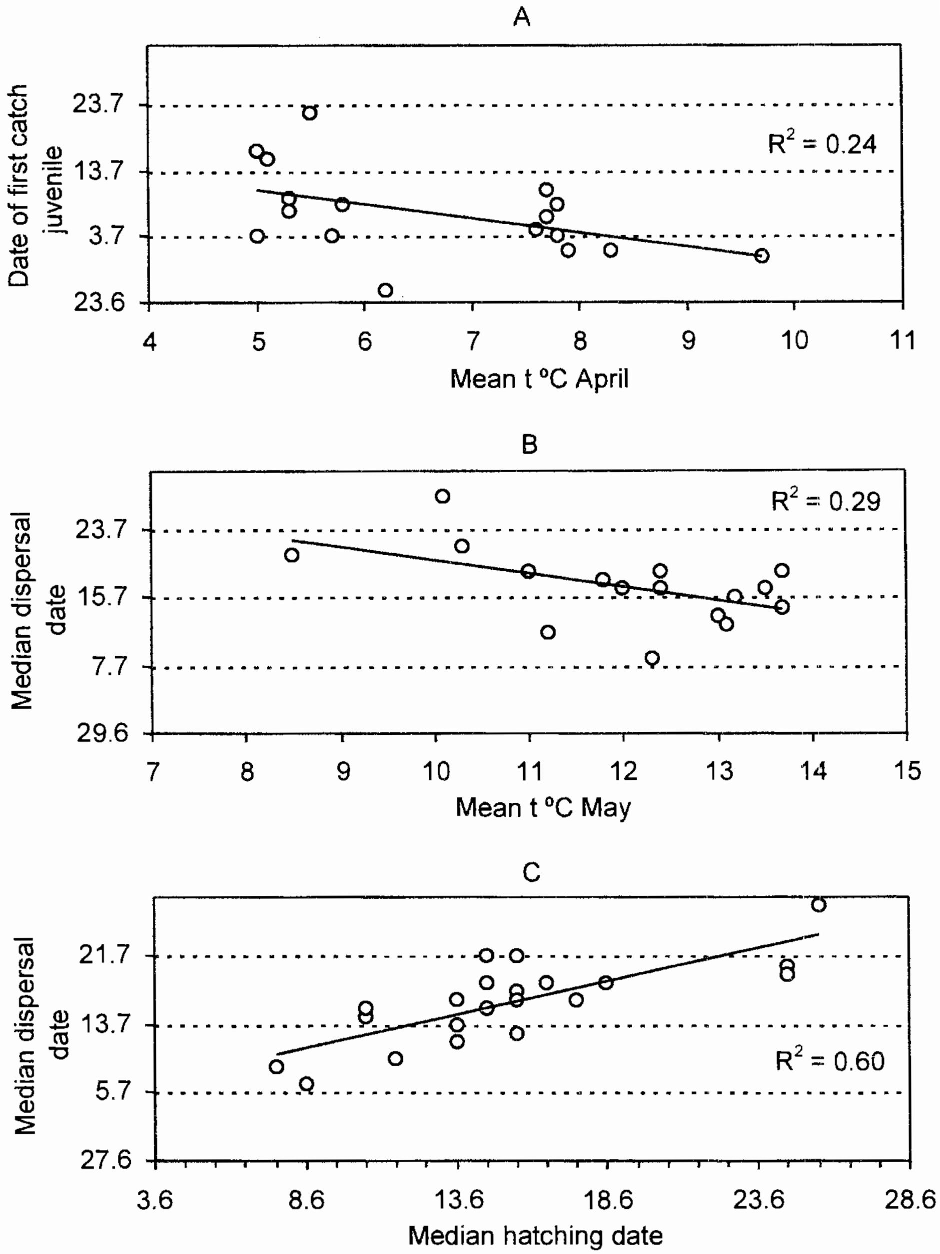

Figure 7. Dependence of the first capture date of juvenile and of median date of juvenile dispersal of Pied Flycatchers on mean temperature of April (A) and May (B), and on median hatching date (C).

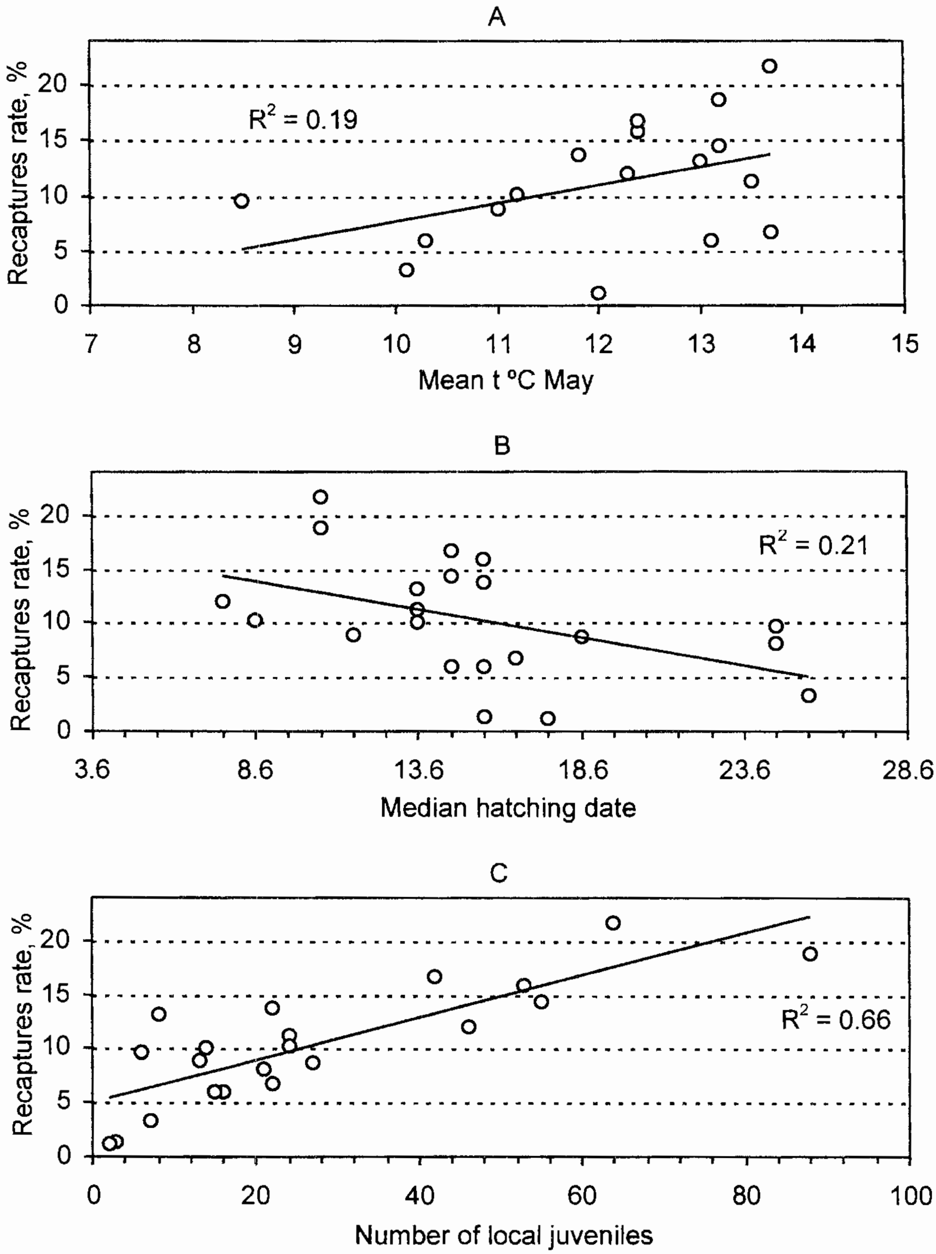

Figure 8. Dependence of the proportion of juveniles ringed as pulli and recaptured during post-fledging period on mean May temperature (A), median hatching date (B) and number of local juveniles (C).

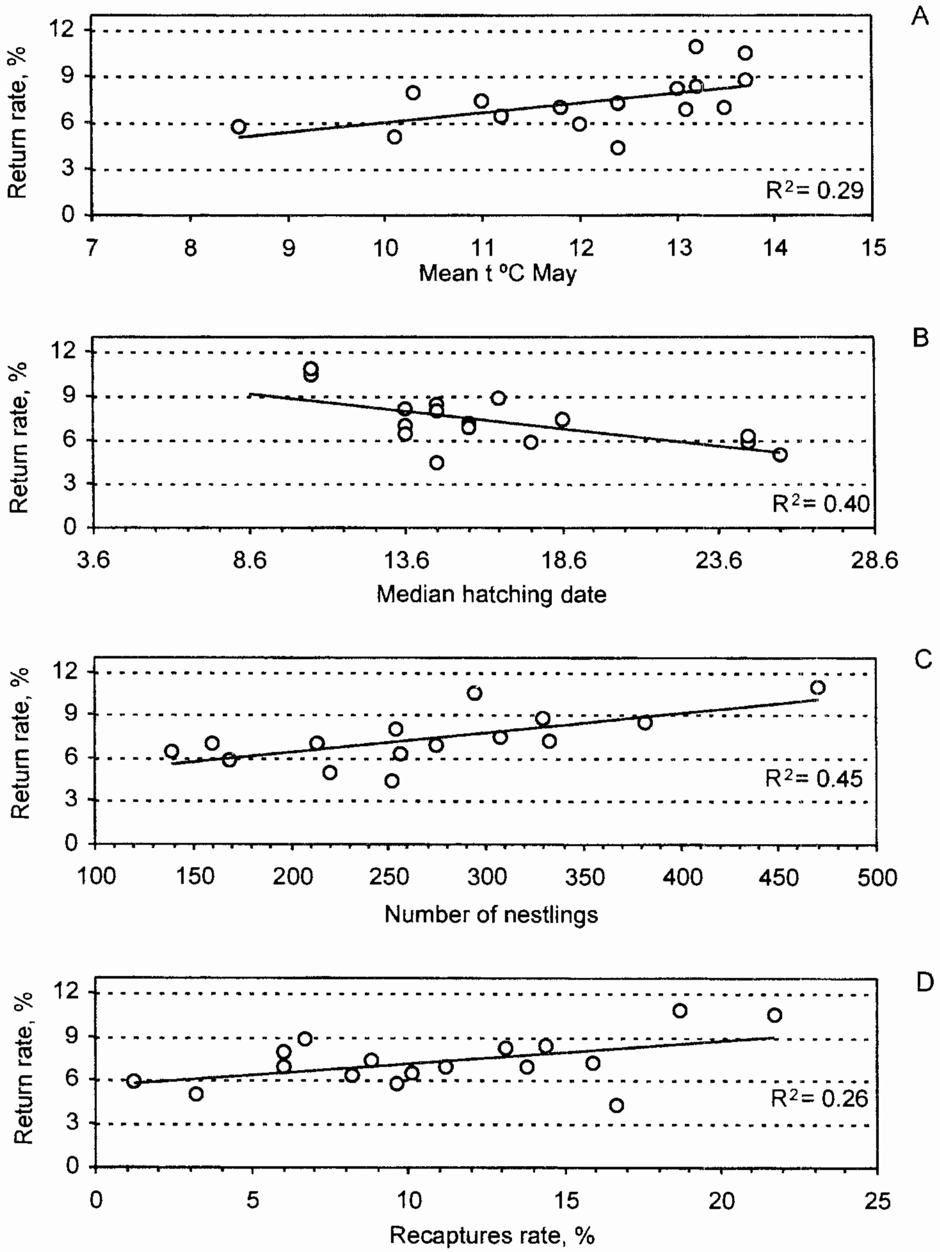

Figure 9. Dependence of the return rate of Pied Flycatchers on mean May temperature (A), median hatching date (B), number of ringed pulli (C) and recapture rate (D).

3.6. Numbers of juveniles during post-fledging period

Numbers of marked and unmarked juveniles (re)captured in stationary traps during post-fledging period (before 20 August) varied from 13 in 1996 to 149 in 1986 (Tab. 1, 2). Numbers of juveniles captured with and without rings were strongly correlated (Tab. 3).

Numbers of marked juvenile Pied Flycatchers recaptured in stationary traps during post-fledging period are significantly related to mean April and May temperatures (Tab. 3). After a warm spring generally more local juveniles are present at the study site in this period (Fig. 10A). Numbers of marked juveniles are also dependent on the timing of spring migration, breeding and post-fledging dispersal (Tab. 3, Fig. 10B, C). Early breeding promotes increase in numbers of juveniles during post-fledging season (Fig. 10 B).

Numbers of unmarked juveniles captured during post-fledging period are significantly positively correlated with mean April temperature and proportion of marked juveniles recaptured in the same season; and negatively correlated with median hatching date and dates of first captures of juveniles (Tab. 3).

If juveniles (re)captured during post-fledging period, marked and unmarked, are pooled, correlations of their numbers with mean April temperature (positive), timing of spring migration, breeding and post-fledging dispersal (negative), number of broods and overall number of ringed nestlings, and with proportion of recaptured local birds (positive) are revealed (Tab. 3).

3.7. Numbers of autumn migrants

Numbers of first-autumn Pied Flycatchers captured after 20 August in the trap # 5, with the entrance to the NE varied between different years from 15 in 1992 and 1995 to 140 in 1988 (Tab. 1, 2). Autumn trapping figures were not significantly related to spring temperatures in our study area, however a weak trend for higher numbers in years with high May temperatures could be noted (Tab. 3, Fig. 11A).

Numbers of autumn migrants were negatively correlated with the first capture date of an unringed post-fledging juvenile and positively correlated with recapture rate of marked juveniles in the same season (Tab. 3, Fig. 11B). Strongest relationship was however found between numbers of autumn migrants and numbers of unmarked juveniles or pooled number of all juveniles trapped in the post-fledging period (Tab. 3, Fig. 11C).

3.8. Timing of autumn migration of juveniles

Median date of autumn migration of young Pied Flycatchers on the Courish Spit varied between 22 August (in 1990) and 11 September (in 1983) (Tab. 1). The year with the latest autumn migration (1983) excluded, timing of autumn passage in our area is significantly negatively related to the mean April temperature (Tab. 3, Fig. 12A). Besides, timing of autumn migration was significantly positively related to the hatching dates at our site, and to the timing of post-fledging dispersal (Tab. 3, Fig. 12B, C).

No significant relationship between the timing of autumn migration of Pied Flycatchers and their post-fledging and autumn numbers was recorded, even though a weak correlation between numbers during post-fledging period and timing of autumn passage does exist (Tab. 3).

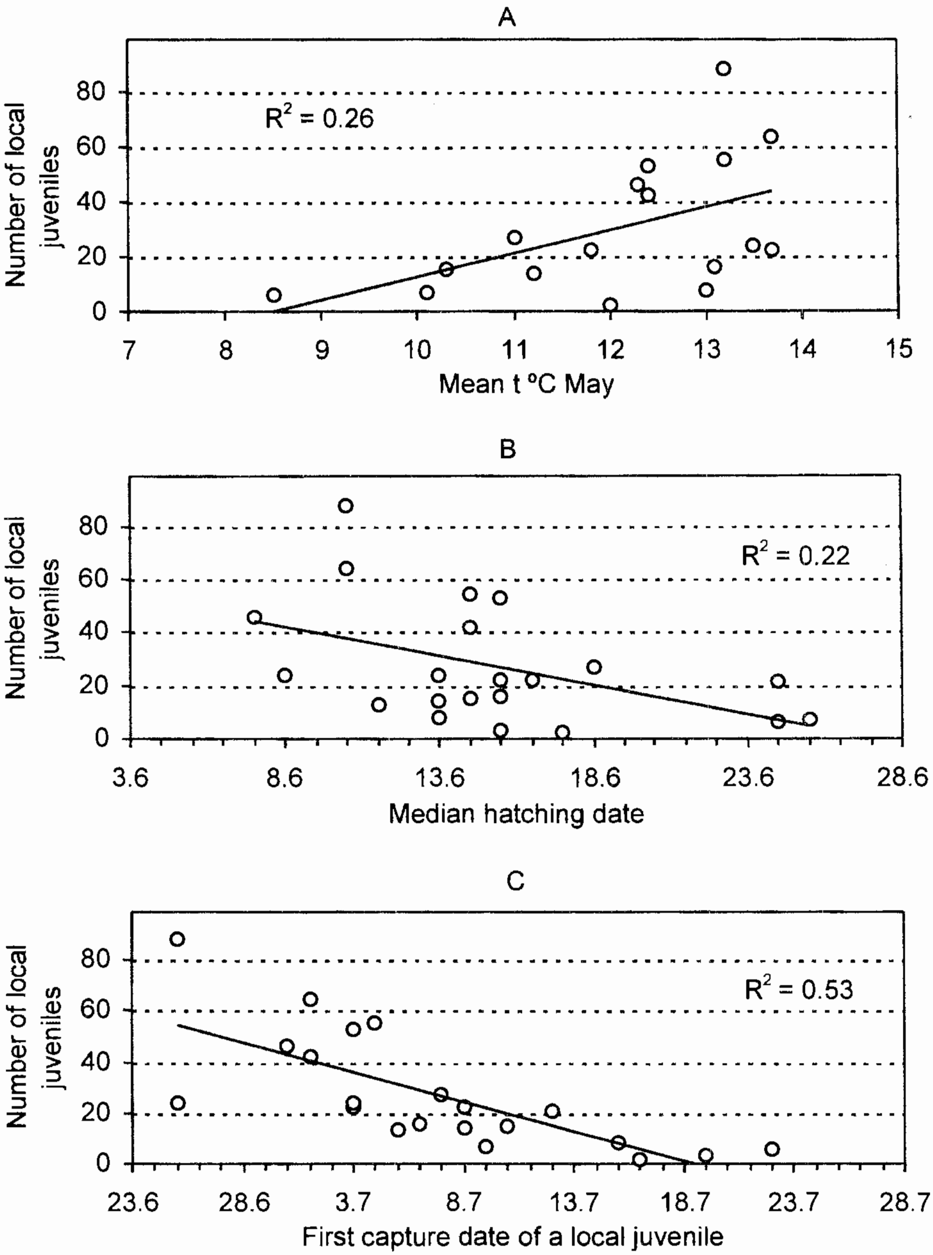

Figure 10. Relationship between the number of juveniles ringed during post-fledging period on mean May temperature (A), median hatching date (B) and the date of the first capture of a juvenile (C).

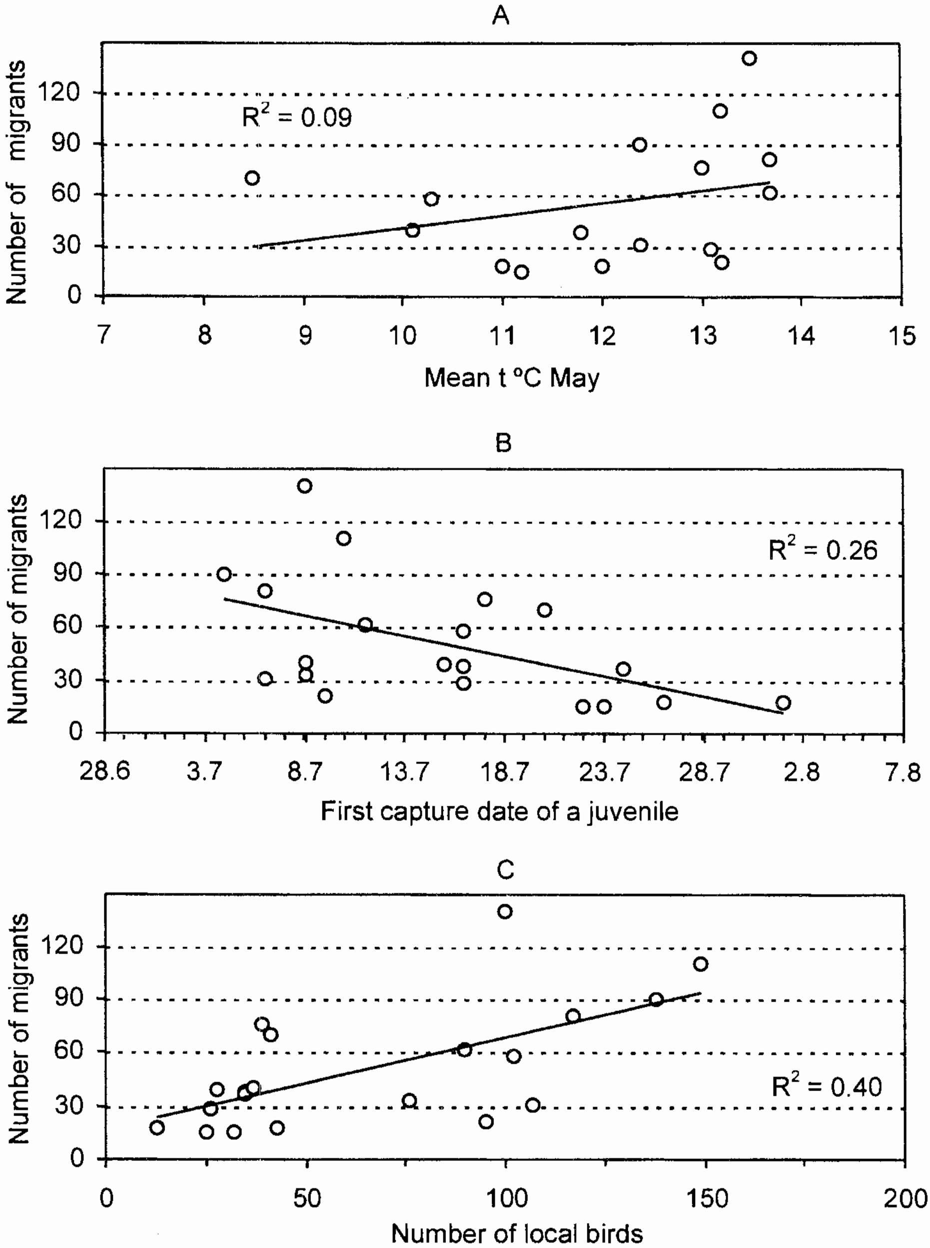

Figure 11. Dependence of the number of Pied Flycatchers captured during autumn passage in trap # 5 on mean May temperature (A), the date of the first capture of a juvenile (B) and numbers of local juveniles during post-fledging period (C).

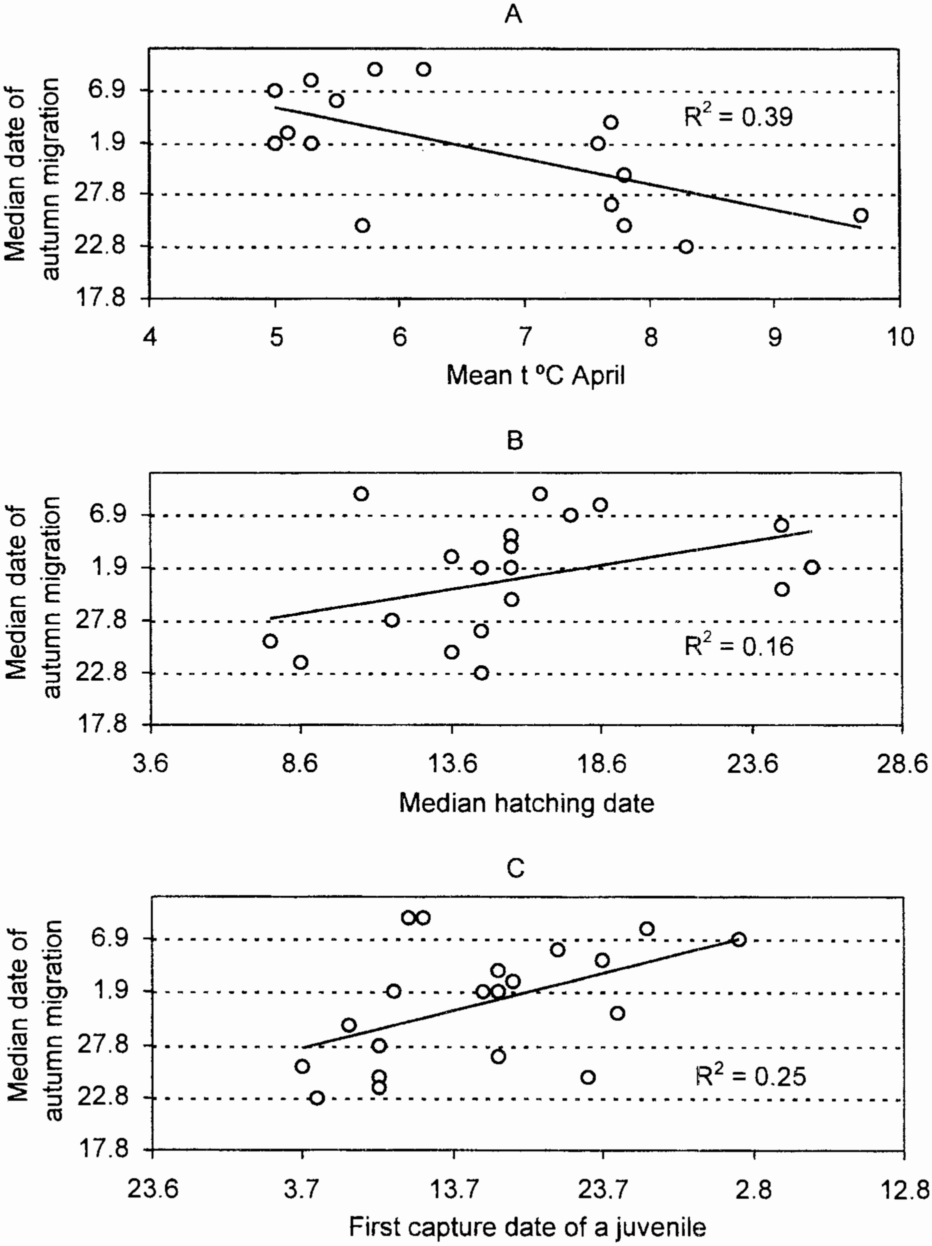

Figure 12. Relationship between the median date of autumn passage and mean air temperature in April (A), median hatching date (B) and the date of the first capture of a juvenile (C).

4. Discussion

This study shows that in the Pied Flycatcher which is a long-distance migrant (Cramp 1992, Lundberg & Alatalo 1992), schedules of different annual events are subject to considerable inter-annual variation (Tab. 1). In years with an early and warm spring median date of spring passage through the Courish Spit occurs in late April, whereas in years with late and cold springs it may be as late as the second half of May (Tab. 2). Strong negative correlation is found between the timing of spring passage and mean monthly temperatures of both April and May (Tab. 3). April temperatures are most important for the birds arriving first, as suggested by the daily capture pattern in Rybachy-type stationary traps (Fig. 2, Tab. 4). May temperatures influence mainly Pied Flycatchers that migrate later. This trend has been already shown in other passerines arriving to the Courish Spit early, or, respectively, late (Sokolov et al. 1998).

Significant inter-annual variation in the timing of arrival to the breeding grounds should by no means be interpreted as evidence of similar variation in the timing of departures from tropical Africa. Long-term (1950-1986) monitoring of departure schedules of Spotted Flycatchers *Muscicapa striata* from a wintering site in Bloemfontein (South Africa) showed, that inter-annual variation is small, birds depart within a time-span of ten days (17-26 March) (Kok et al. 1991). Most birds that spend their winter in the tropics, including Pied Flycatchers, probably annually start spring migration within a narrow temporal window following an endogenous stimulus (Dolnik 1975, Berthold 1996, Gwinner 1996). When birds reach Southern Europe, their may either continue their northward movement if weather conditions are favourable, or stop over in this region for some time (which probably may be rather long in some cases) if the weather is not suitable for further migration (Sokolov et al. 1998).

Based on this hypothesis, I suggest that inter-annual variation in arrival dates of a long-distance migrant, Pied Flycatcher, that we record at our site are mainly stem from the weather conditions that birds encounter *en route* in Europe. Favourable conditions for spring migration must include, among others, temperature regime (Lundberg & Alatalo 1992). Ambient temperatures greatly influence arthropod activity and may to a large extent govern the rate of northward movement of such insectivorous species as the Pied Flycatcher (Sokolov et al. 1998). The data from a long-term monitoring project of arrival timing of Swallows *Hirundo rustica* to Europe showed that arrival dates were earlier during warmer Aprils in Britain and western France, and following a warmer March in Iberia (Huin & Sparks 1998). These authors drew an important conclusion that spring temperatures have an indirect effect on the Swallow by affecting the abundance of its insect prey and the timing of their emergence. They believe that even though the increase in insect abundance starts at the beginning of April (Bryant 1975), but temperature also will have affected their larval development (Huin & Sparks 1998).

Overall spring trapping figures of migrating Pied Flycatchers were not significantly related either to mean April and May temperatures, or to the timing of migration (Tab. 3). However a weak trend towards higher catching totals in years with low mean May temperatures is observed (Tab. 3). The reason for this is probably that in years with cold and late spring, more Pied Flycatchers make stopovers at our study site that in springs with weather conditions favourable for further flight. At the same time, daily trapping dynamics in the first half of migratory period was not infrequently positively correlated with air temperature at noon or with mean daily temperature (Tab. 4, Fig. 2). The first possible explanation is that after a warm-air surge more migrants arrive, stop over and are captured at "Fringilla" trapping station. Secondly, in warmer days birds that stop over near the traps move around more actively and are better captured. The latter suggestion seems unlikely, as, quite to the contrary, in days with low ambient temperature Pied Flycatchers should move around more to find insects that are inactive in such conditions.

Median hatching date suggests that the timing of breeding varied in our study area at a similar level as timing of spring migration (Tab. 1). Like the latter, it was negatively correlated with spring, but not summer, ambient temperatures. Such dependence has been shown in eight out of 11 studied passerine species, long- and medium-distance migrants (Sokolov & Payevsky 1998). High spring temperatures thus facilitate not only early arrival, but also early egg laying and early hatching (Lundberg & Alatalo 1992). Most demonstrative is the year 2000, when the highest mean April temperature (9.7ºC) during the last 43 years was recorded. In that year, earliest ever breeding of Pied Flycatchers was registered: first eggs were laid by some females on 10 May, and first nestlings hatched in late May, not in early June as recorded previously in the earliest years (Sokolov et al. 1990). In 2000, very early breeding was recorded on the Courish Spit in a number of other passerines, e.g. Marsh Tit (*Parus palustris*), Blue Tit (*P. caeruleus*), Chaffinch (*Fringilla coelebs*), Pied Wagtail (*Motacilla alba*). I analysed inter-annual variation in the mean date of starting laying in a northern Pied Flycatcher population (SE Ladoga coast) (Artemiev 1995) and median hatching date on the Courish Spit in 1980-1989. Both parameters were strongly correlated ($r_S = 0.89$; $p<0.001$). Timing of spring migration and breeding of passerines was already reported to vary nearly synchronously in rather distant populations (Sokolov et al. 1998, Sokolov & Payevsky 1998). Artemiev (1995) also concluded that timing of breeding in a northern Pied Flycatcher population are considerably dependent on the course of spring. Between 1970 and 1995, Pied Flycatchers, Great and Blue Tits in northern Germany showed a significant trend towards earlier breeding (Winkel & Hudde 1997). In all three species the fluctuations in annual mean hatching dates were significantly correlated with average spring temperatures (Pied Flycatcher: $r = 0.70$, $p<0.05$ with mean temperatures between 11 April and 10 May).

Numbers of Pied Flycatchers breeding in the study area, estimated by the number of nests with broods, depends not only on nest-box availability, but on spring temperatures as well (Tab. 3). In years with warm spring we find more nests with eggs and with nestlings. It is not improbable that in early springs more new unmarked birds remain in our area for breeding. Another possibility is that in such springs arriving Pied Flycatchers survive the pre-breeding period better, thus more pairs start breeding. Possible effects of the weather on spring survival were reported elsewhere (Payevsky 1985, Sokolov & Payevsky 1998, Sokolov 1999). Numbers of nests found in different years on the SE Ladoga coast (Artemiev 1995) and on the Courish Spit near Fringilla were significantly correlated ($r_S = 0.90$; $p<0.001$). This shows that even in distant populations (distance between Courish Spit and Ladoga study sites ca. 1000 km) year-to-year fluctuations of numbers may be rather synchronised. Total number of nestlings survived to ringing (i.e. to the age of 6-10 days) at our study site was higher in years with warm springs and early migration of Pied Flycatchers (Tab. 3). In such years more pairs breed in the study area. Further, in years with early breeding mean brood size is frequently higher than in late cold years when a substantial part of a brood may perish of inadequate warming and insufficient food supply (Payevsky 1982, 1999, Lundberg & Alatalo 1992, Sokolov 1999). In a study of impact of the weather on breeding success of Pied Flycatchers and Siberian Tits (*Parus cinctus*) in high latitudes in Finland it was shown that under low ambient temperatures Pied Flycatchers alter their foraging niche and diet (Veistola et al. 1997). In such conditions, the majority of birds start to collect food on the ground and catch less flying insects. These changes in foraging behaviour were however not able to compensate for poor feeding conditions; under low temperatures nestling feeding rates decreased. Inadequate feeding of nestlings in cold and rainy days generally resulted in lower growth rate and fledging success. In northern Germany in Pied Flycatchers, Great and Blue Tits clutch size and number of fledged juvenilis increased significantly from 1970 to 1995 (Winkel & Hudde 1997). These authors believe that the increased clutch size and fledging success of Pied Flycatchers agree with the fact that breeding dates show a significant advancement during the study period, because in this species a strong correlation exists between breeding date and clutch size (the earlier in the season Pied Flycatcher lays eggs, the larger the clutch, e.g. Berndt & Winkel 1967).

After fledglings gain independence, juvenile Pied Flycatchers usually start post-fledging dispersal (Sokolov 1997). Since then, they are captured in Rybachy-type traps. The timing of post-fledging dispersal considerably varies between years, as shown by first captures and median capture dates of birds ringed as pulli (Tab. 1, 2). It is generally dependent on the timing of hatching: more early the young hatch, earlier in the season juvenile dispersal starts (Fig. 7C). Spring temperatures influence the timing of post-fledging dispersal indirectly, through the timing of breeding. A similar dependence was found in the majority of passerines breeding on the Courish Spit (Sokolov & Payevsky 1998). Summer temperatures (June, July) have practically no impact on the timing of post-fledging dispersal of Pied Flycatchers in our study area (Tab. 3).

Mean age of leaving the immediate natal site (with a radius ca. 1 km) does not vary much between years (Tab. 1, 2). It is also practically independent from the timing of breeding or post-fledging dispersal. It may be suggested that in different years juvenile Pied Flycatchers leave their natal sites in roughly the same age, ca. 35 days. This happens even though Pied Flycatchers hatched late in the season are first captured in stationary traps in an earlier age than those hatched early (Sokolov et al. 1990). It cannot be excluded that our material is yet insufficient to reveal that in years with late breeding young flycatchers leave their natal site in an earlier age.

Breeding success in a particular year can be estimated not only by the number of fledglings, but by the recapture rate in post-fledging period as well. Besides, the overall number of juveniles in the study area in this period is also an estimate of the population's breeding success. The highest recapture rate of juveniles ringed as pulli is reached in years with early and warm spring and early breeding (Tab. 2, Fig. 8A, B). The most probable reason for this is that in such years, mortality of juveniles after fledging until recapture in stationary traps is considerably lower than in years with late breeding. This period is known to be most important for survival of juveniles during their first year (Payevsky 1985, 1999, Sokolov et al. 1990, Sokolov 1991, Naef-Daenzer et al. 1999).

In years with early and warm spring and early breeding, more young Pied Flycatchers are trapped during post-fledging period, both previously ringed in nest and unringed. It is important that this is typical not only of birds ringed as pulli in nest-boxes, but also of unringed individuals hatched in natural cavities outside the study plot. This shows that in years with early and warm spring, numbers of breeding Pied Flycatchers and of their offspring increases not only in nest-boxes, but in natural cavities as well.

A clear dependence between spring ambient temperatures, timing of breeding and return rate in subsequent years is revealed (Tab. 3, Fig. 9A, B). Highest return rate in subsequent years is observed in birds that are hatched in years with a warm and early spring and early breeding. This is probably explained by their better post-fledging survival in such years. It is however not excluded that in early years birds imprint their future breeding sites at a smaller distance from the natal site than in late years, and thus show a higher return rate to the study plot (Sokolov et al. 1990, Sokolov 1997).

The number of autumn migrants appeared to be most strongly related to numbers of juveniles, both marked and unmarked, captured in stationary traps in the post-fledging period (Tab. 3, Fig. 11C). A similar relationship has been shown elsewhere in 11 passerines breeding on the Courish Spit (Sokolov et al. 2000). This suggests that in years with a warm and early spring, Pied Flycatchers as a rule breed successfully not only on the Courish Spit, but also in large areas to the north from our study site.

Timing of autumn migration of Pied Flycatchers through the Courish Spit appeared to be significantly related only to the mean April temperature and to the timing of breeding and post-fledging dispersal (Tab. 3). Warm spring and early breeding cause early autumn migration of juveniles. Similar results were obtained on the Courish Spit for some other passerines (Sokolov et al. 1999). A similar dependence of the timing of migratory departure from hatching dates was reported by Ryzhanovsky (1997) for the Willow Warbler (*Phylloscopus trochilus*), Arctic Warbler (*Ph. borealis*), Bluethroat (*Luscinia svecica*) and Little Bunting (*Emberiza pusilla*) from the sub-Arctic (lower Ob river). The author concluded that the development of the migratory disposition is rather rigidly connected with a certain age of a juvenile and comparatively independent from the environment. I agree with Ryzhanovsky (1997) that in principle, weather situation influences the schedule of autumn migration since spring. Beginning of spring and the rate of temperature increase primarily influence timing of arrival, breeding, and moult, and indirectly also departure schedule. In years with a warm and prolonged autumn departure of insectivorous birds may be slightly delayed, but the bulk of the population leave sub-Arctic areas rather early due to endogenous control of the onset of migration (Ryzhanovsky 1997).

On the basis of all these data I conclude that in Pied Flycatchers, the timing of such important annual events as spring migration, breeding, post-fledging dispersal and autumn migration is largely dependent on spring ambient temperatures. High temperature in spring as a rule shift these events to an earlier season. This leads to a higher breeding success of the local population and higher numbers of juveniles in this population. Besides, in years with an early and warm spring high numbers of autumn migrants are usually recorded. The reason for this is probably the increased number of first-autumn birds in northern breeding populations, due to high breeding success in these populations. The impact of spring ambient temperature on these annual events in the Pied Flycatcher, as in many other passerines, is indirect. Spring air temperature influences such phenological events as soil temperature, development of vegetation, emergence and activity of insects etc., and on survival of both adults and juveniles.

Acknowledgements

I am most grateful to Vadim G. Vysotsky (Zoological Institute, St.Petersburg) for a long and fruitful cooperation in the study of Pied Flycatcher's breeding biology on the Courish Spit. My thanks are also due to all colleagues, especially to Mikhail Yu. Markovets, who participated in collecting and storing the data and in data analysis.

References

Alerstam, T. 1990. Bird Migration. Cambridge Univ. Press.

Artemiev, A.V. 1995. Individual variations in summer events in the Pied Flycatcher (*Ficedula hypoleuca*) near Ladoga Lake. Ornitologia 26: 33-44 (in Russian with English summary).

Berndt, R. & Winkel, W. 1967. Die Gelegegröße des Trauerschnäppers (*Ficedula hypoleuca)* in Beziehung zu Ort, Zeit, Biotop und Alter. Vogelwelt 88: 97-136.

Berthold, P. 1996. Control of Bird Migration. Chapman & Hall, London.

Bryant, D.M. 1975. Breeding biology of House Martin *Delichon urbica* in relation to insect abundance. Ibis 117:180-216.

Cramp, S. (ed.). 1992. The Birds of the Western Palearctic. Vol. VI. Oxford Univ. Press, Oxford, New York.

Cramp, S. & Perrins, C.M. (eds.). 1994. The Birds of the Western Palearctic. Vol. VII. Crows to Finches. Oxford Univ. Press.

Crick, H.P.Q. & Sparks, T.H. 1999. Climate change related to egg-laying trends. Nature 399: 423-424.

Crick, H.P.Q., Dudley, C., Glue, D.E. & Thomson, D.L. 1997. UK birds are laying eggs earlier. Nature 388: 526.

Dolnik, V.R. 1975. Migratory Disposition of Birds. Nauka Press, Moscow (in Russian).

Ellegren, H. 1990. Timing of autumn migration in Bluethroats *Luscinia s. svecica* depends on timing of breeding. Ornis Fenn. 67:13-17.

Gauthreaux, S.A., Jr. 1982. The ecology and evolution of avian migration systems. In: Farner, D.S. & King, J.R. (eds) Avian Biology. Vol. 6. Academic Press, London: 93-168.

Gwinner, E. 1996. Circadian and circannual programmes in avian migration. J. Experim. Biol., 199: 39-48.

Huin, N. & Sparks, T.H. 1998. Arrival and progression of the Swallow *Hirundo rustica* through Britain. Bird Study 45: 361-370.

Jarvinen, A. 1996. Correlation between egg size and clutch size in the Pied *Flycatcher Ficedula hypoleuca* in cold and warm summers. Ibis 138: 620-623.

Kok, O.B., Van Ee, C.A. & Nel D.G. 1991. Daylength determines departure date of the Spotted Flycatcher *Muscicapa striata* from its winter quarters. Ardea 79: 63-66.

Lunberg, A. & Alatalo, R.V. 1992. The Pied Flycatcher. T & A D Poyser, London.

Mikhantiev, A.L. & Selivanova, M.A. 1996. The breeding terms of the Mallard *Anas platyrhynchos* in the Northern Kulunda and their dependence from environmental factors. Siberian Journal of Ecology 3: 285-293 (in Russian).

Moss, S. 1998. Predictions of the effects of global climate change on Britain's birds. British Birds 91: 307-325.

Morton, M.L. 1992. Effects of sex and birth date on premigration biology, migration schedules, return rates and natal dispersal in the Mountain White-crowned Sparrow. Condor 94: 117-133.

Nager, R.G. & van Noordwijk, A.J. 1995. Proximate and ultimate aspects of phenotypic plasticity in timing of Great Tit breeding in a heterogeneous environment. Am. Natur. 146: 454-474.

Naef-Daenzer, B., Widmer, F. & Nuber, M. 1999. The range use of Great and Coal Tits during the post-fledging period. The Ring 21: 20.

Payevsky, V.A. 1982. Reproduction and demography of the chaffinches at the Kurische Nehrung according to twenty-years data. In: Dolnik, V.R. (ed.). Population Ecology of the Chaffinch (*Fringilla coelebs*): 165-190 Nauka Press, Leningrad (in Russian with English summary).

Payevsky, V.A. 1985. Demography of Birds. Nauka Press, Leningrad (in Russian).

Payevsky, V.A. 1999 Breeding biology, morphometrics, and population dynamics of *Sylvia* warblers in the Eastern Baltic. Avian Ecol. Behav. 2: 19-50.

Ravussin, P.-A. & Neet, C. 1995. Facteurs affectant la ponte l'une population de Gobemouche noir *Ficedula hypoleuca* dans l'ouest de la Suisse. Nos oiseaux 43: 163-178.

Perrins, C.M. 1996. Eggs, egg formation and the timing of breeding. Ibis 138: 2-15.

Richardson, W. J. 1990. Timing of bird migration in relation to weather: updated review. In: Gwinner, E. (ed.). Bird Migration. Springer, Berlin-Heidelberg-New York: 78-101.

Rytkönen, S., Koivula, K. & Lindgren, E. 1993. The population size and breeding biology of the Rook *Corvus frugilegus* in northern Finland. Ornis Fenn. 70: 202-212.

Ryzhanovsky, V.N. 1997. The Ecology of Postbreeding Period of Passerines in subarctic. Urals Univ. Press, Yekaterinburg (in Russian).

Sema, A.M. 1989. The Phenology of Bird Migration in Kazakhstan. Nauka Press, Alma-Ata (in Russian).

Sokolov, L.V. 1997. Philopatry of Migratory Birds. In: Phys. Gen. Biol. Reviews. Vol. 11: 1-58. Harwood Acad. Publ., The Netherlands.

Sokolov, L.V. 1999. Population dynamics in 20 sedentary and migratory passerine species of the Courish Spit on the Baltic Sea. Avian Ecol. Behav. 3: 23-50.

Sokolov, L.V. & Payevsky, V.A. 1998. Spring temperatures influence on year-to-year variations in the breeding phenology of passerines on the Courish Spit, eastern Baltic. Avian Ecol. Behav. 1: 22-36.

Sokolov, L.V., Vysotsky, V.G. & Bardin, A.V. 1990. Philopatry and natal dispersal of the Pied Flycatcher (*Ficedula hypoleuca*) at the Courish Spit of the Baltic sea. Ornitologia 24: 5-19 (in Russian).

Sokolov, L.V., Markovets, M.Yu., Shapoval, A.P. & Morozov, Yu.G. 1998. Long-term trends in the timing of spring migration of passerines on the Courish Spit of the Baltic Sea. Avian Ecol. Behav. 1: 1-21.

Sokolov, L.V., Yefremov, V.D., Markovets, M.Yu., Shapoval, A.P. & Shumakov, M.E. 2000. Monitoring of numbers of passage populations of passerines over 42 years (1958-1999) on the Courish Spit of Baltic Sea. Avian Ecol. Behav. 4: 31-53.

Thingstand, G. 1997. Annual and local reproductive variations of a Pied Flycatcher *Ficedula hypoleuca* population near a subalpine lake in Central Norway. Ornis Fenn. 74: 39-49.

Veistola, S., Lehikoinen, E. & Eeva, T. 1997. Weather and breeding success at high latitudes – the Pied Flycacher *Ficedula hypoleuca* and the Siberian Tit *Parus cinctus*. Ornis Fenn. 74: 89-98.

Winkel, W. & Hudde, H. 1997. Long-term trends in reproductive traits of tits (*Parus major, P. caeruleus*) and Pied Flycatchers *Ficedula hypoleuca*. J. of Avian Biol. 28: 187-190.

Zajac, T. 1995. Selection on laying date in Blue Tit *Parus caeruleus* and the Great Tit *Parus major* caused by weather conditions. Acta ornithol. 30: 145-151.

Žalakevicius, M. 1997. Bird migration and climate change. Acta Zool. Lithuanica 6: 20-30.