

Local survival rates of Pied Flycatchers *Ficedula hypoleuca* depend on their immigration status

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We estimated annual survival rates of adult Pied Flycatchers in a European breeding population and tried to determine factors that influence survival rates. Long-term data (1982–2006) on Pied Flycatchers breeding on the southeastern Baltic coasts (the Courish Spit) were analysed by capture-mark-recapture statistics. Annual variation of survival rate in adult Pied Flycatchers was not related to rainfall parameters and NDVI values from the winter quarters. Local survival rate was significantly related to sex and immigration status: it was the highest (annual mean 46%) in locally hatched males and the lowest in immigrant females during the first winter after immigration (15%). Survival rates of immigrant females in subsequent winters (40%), of immigrant males and locally hatched females (32%) were intermediate. This difference was due to emigration rates, local survival rate of locally hatched males being the closest approximation of the true survival. Survival rate in a local breeding population could appear unrelated to winter conditions at particular localities or averaged across the winter range, even though survival prospects of individual Pied Flycatchers are strongly influenced by local conditions at their wintering sites.

Key words: survival rate, NAO, climate, rainfall, Pied Flycatcher, immigrant status

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1. Introduction

Populations of avian migrants may be limited mainly by the factors acting in their breeding areas, winter quarters (Newton 2004), at stopover sites on migratory routes (Newton 2006) or by a combination of factors. Overwinter survival rates of several long-distance passerine migrants have been shown to be related on rainfall in African wintering areas, especially in species that winter in the Sahel (Peach et al. 1991, Foppen et al. 1999). Abundances of Palaearctic-African migrants were also reported to be related to rainfall in the Sahel (Knape et al. 2009). Droughts that occur there from time to time may have catastrophic consequences for local vegetation development and invertebrate abundance and thus may severely com-

promise survival of small insectivorous birds, Palaearctic winter guests including. Effects of African climatic conditions on survival of Palaearctic migrants have been reported for Sedge Warblers *Acrocephalus schoenobaenus* (Peach et al. 1991, Foppen et al. 1999), Barn Swallows *Hirundo rustica*, House Martins *Delichon urbica* and Sand Martins *Riparia riparia* (Robinson et al. 2008). However, adult survival rate of Reed Warblers *Acrocephalus scirpaceus* in the UK appeared not to be correlated with Sahel rainfall index (Thaxter et al. 2006).

The aim of this study was to estimate adult survival rates in a population of the Pied Flycatcher on the southeastern Baltic coast. Survival rates were estimated separately for males and females, and for birds that were known to have hatched in the study area, and those of unknown origin. To investigate whether survival rates vary in relation to conditions on wintering grounds, local survival rates and adult were compared with climate parameters in West Africa: indices of Sahel and Guinea rainfall, precipitation at selected weather station in the core wintering range, and NDVI values in the same area. We also tested for a relationship with NAO index which is known to influence spring migration of Palaearctic-African passerine migrants (Forchhammer et al. 2002, Sokolov & Kosarev 2003, Both et al. 2006).

2. Material and methods

2.1. Study site, species, and data collection

The Courish Spit is a long and narrow strip of land stretched for 98 km along the southeastern Baltic coast. It is 1–1.5 km wide at most sites, with the maximum of 3.8 km. The spit separates the Courish Lagoon from the Baltic Sea, and is covered by forest which is partly deciduous, partly coniferous (mainly pines). For a more detailed description of the study area see Payevsky (1999).

The study started in 1981 when 231 nest-boxes were provided along the 9-km long part of the Courish Spit. In 2000, 940 more nest-boxes were provided. Thus, the new enlarged study area was 44 km long and included 1340 nest-boxes.

We tried to capture each male and female breeding in nest-boxes in our study area, and to ring all nestlings short before fledging. Nest fate (fledging success) was checked after fledging of the chicks. Capture efficiency of males and females could vary in different plots. Females were usually captured during incubation or feeding their chicks, and males were often captured when they visited empty nest-boxes before the onset of nest construction. The use of this method allowed us to increase the proportion of males captured by 25% (Sokolov et al. 1990). Capture efficiency of males in the core part of the study area reached ca. 85%, in peripheral areas it was lower. Capture efficiency of females breeding in nest-boxes was close to 100%. A fraction of the Pied Flycatcher population (ca. 5–10%) bred in natural cavities, mainly in the peripheral areas covered by mature deciduous forest. These birds were controlled whenever appeared possible. The overall occupancy of nest-boxes by Pied Flycatchers, Great Tits *Parus major*, Blue Tits *P. caeruleus* and other titmice (Coal Tit *P. ater* and Marsh Tit *P. palustris*) did not exceed 30–40%, i.e. nest-boxes were always available in excess.

2.2. Data analysis

The data for 1982–2006 were taken for analysis, i.e. we analysed survival rate of Pied Flycatchers in non-breeding seasons 1982/83 until 2005/06. Only birds since their first breeding season were included, i.e. the locally hatched individuals were taken into analyses from their first breeding in the area on rather than from their ringing in the nests. Mark-recapture data were analysed using the computer program MARK 4.3 (Cooch & White 2006). Cormack–Jolly–Seber (CJS) models were developed using the recaptures-only option, which allows general survival and recapture rates to be modelled with respect to time and groups along with individual covariates (Pollock 2002, Cooch & White 2006). The most general model included time-dependent survival and recapture rates, independent for four groups: locally hatched males, males of unknown origin, locally hatched females, females of unknown origin. The number of birds in each of these groups was 368, 302, 730, and 1116, respectively. Model fit was tested by the program RELEASE available within MARK. Akaike's Information Criterion, adjusted for small sample sizes and overdispersion (QAICc) was used to identify the most parsimonious model from each candidate set (Anderson & Burnham 2002). The model with the lowest QAICc and greatest weighting was taken as the best representation of the data. Models were run using the logit link function and all possible combinations of models were tested.

2.3. Rainfall data, NDVI and NAO indices

Various rainfall indices in November – February were included in the analyses after initial models had been investigated; the rainfall effect could then be judged against all other model combinations. Wintering range data were taken from the local bird guide (Borrow & Demey 2001). We included average rainfall in the Sahel (the Sahel rainfall index, taken from the JISAO website, <http://jisao.washington.edu/data/sahel/>), average rainfall in the Guinea savannah (the Guinea index, calculated from individual stations following the template at the JISAO website, the data are from the CISL Research Data Archive, <http://dss.ucar.edu/>), and average rainfall in November – February at individual weather stations in the Guinea zone: Bohicon (Benin, 7°11' N, 2°04' E), Cotonou (Benin, 6°22' N, 2°26' E), Savé (Benin, 8°02' N, 2°29' E), Atakpamé (Togo, 7°32' N, 1°08' E), and Lomé (Togo, 6°08' N, 1°13' E). We also included the NDVI values in the area covering these individual weather stations, and March and April NAO index values in respective years. NAOI is calculated as the difference between the normalized sea-level pressure at the Azores and Iceland (Hurrell et al. 2001) and is a generalised parameter characterising weather in Europe during spring migration of Pied Flycatchers. Monthly NAO indices are archived at the National Oceanic and Atmospheric Administration's Climate Prediction Center website (www.cpc.ncep.noaa.gov/data/teledoc/nao.html). The values were z-transformed for analysis.

3. Results

Goodness-of-fit test generated by the programme RELEASE showed a highly significant test 1 ($\chi^2 = 302.03$, d.f. = 77, $P < 0.001$) indicating a difference between the groups. The other tests were not significant. The model that fitted the data best was the model with time-dependent survival rates of locally hatched males, equal survival rates of males of unknown origin and locally hatched females, and age-dependent survival rate in females of unknown origin. Capture probabilities were constant and equal in both groups of males, but differed in autochthonous and unknown-origin females (Table 1).

It should be noted that several models gained very similar support, as indicated by their small ΔAICc values and significant AICc weights (Table 1). All these models have similar structure: time-dependent survival rates for locally hatched males and constant recapture probabilities with the values for both groups of males constrained to be equal. The second best model differed from the best one by assuming age-dependent survival rate in of males of unknown origin and locally hatched females, as well as in females of unknown origin; the third best one differed from the best one by not assuming equal survival rates of males of unknown origin and locally hatched females (Table 1).

As rainfall data were only available until 2004, we fitted the models with rainfall variables and NDVI as covariates for the partial dataset that did not include the Pied Flycatcher data for 2005 and 2006, i.e. did not estimate survival rates in winters 2004/05 and 2005/06. Only the model including NAO was fitted with the full dataset, as NAO values were available throughout the study period. None of the models including rainfall data or NAO was among the best ones, i.e. climate data did not help explain among-year variation of the survival rate in locally hatched adult Pied Flycatchers (survival rates of the three other groups were not time-dependent; Table 2). In fact, they were among the models gaining least support (e.g. the model with NAO, Table 1).

4. Discussion

4.1. Survival rate estimates of different groups

Different groups of adult Pied Flycatchers showed significantly different local survival rates (Table 3). Local survival rate is a product of the true survival rate and the site fidelity rate, i.e. is the probability that a Pied Flycatcher survives and returns to the study area to breed. We assume that the main source of among-group variation in local survival rate was mainly the difference in site fidelity.

Locally recruited males are probably the most site-faithful group, and their local survival rate estimate seems to be the closest approximation to the true survival rate (even though we certainly cannot claim that contribution of emigration was nil). Our estimate for this group is however below the local survival rate of Pied Flycatchers in winter quarters (return rate in optimal forest habitat up to 67%; Salewski *et al.* 2000) which seems to be close to their physical survival rate.

Table 1. Modelling annual survival rate (ϕ) and recapture probability (p) in relation to group (g), time (t) and time since marking ('age', a_2). Group 1 are autochthonous males, group 2 – immigrant males, group 3 – autochthonous females, group 4 – immigrant females.

Model	AICc	Δ AICc	AICc weight	Model likelihood	# par	Deviance
Phi(g,1t,2=3,4a2) p(g,1=2)PIM	3851.240	0.00	0.44222	1.0000	30	620.666
Phi(g,1t,[2=3,4]a2) p(g,1=2)PIM	3852.166	0.93	0.27836	0.6295	31	619.553
Phi(g,1t,2,3,4a2) p(g,1=2)PIM	3852.892	1.65	0.19354	0.4377	31	620.279
Phi(g,1t,2=3=4(2),4a2) p(g,1=2)PIM	3854.518	3.28	0.08588	0.1942	29	625.981
Phi(g,1t,2=3) p(g,1=2)PIM	3888.507	37.27	0.00000	0.0000	29	659.970
Phi(g,1t,2=3=4) p(g,1=2)PIM	3890.742	39.50	0.00000	0.0000	28	664.241
Phi(g,1t) p(g)PIM	3892.011	40.77	0.00000	0.0000	31	659.398
Phi(g*t,2=3) p(g,1=2)PIM	3924.069	72.83	0.00000	0.0000	75	600.471
Phi(g*t,2=3) p(g)PIM	3925.184	73.94	0.00000	0.0000	76	599.489
Phi(g*t,2=3) p(t)PIM	3929.104	77.86	0.00000	0.0000	96	561.184
Phi(g,2=3) p(t)PIM	3944.822	93.58	0.00000	0.0000	27	720.356
Phi(g) p(t)PIM	3946.851	95.61	0.00000	0.0000	28	720.351
Phi(g) p(g)PIM	3951.553	100.31	0.00000	0.0000	8	765.514
Phi(g*t) p(t)PIM	3956.833	105.59	0.00000	0.0000	120	537.527
Phi(g,2=3t) p(g,1=2)PIM	3957.956	106.72	0.00000	0.0000	29	729.419
Phi(g*t) p(.)PIM	3964.352	113.11	0.00000	0.0000	97	594.307
Phi(g) p(.)PIM	3967.612	116.37	0.00000	0.0000	5	787.598
Phi(g,2=3,4t) p(g,1=2)PIM	3971.879	120.64	0.00000	0.0000	29	743.342
Phi(g,2=3t) p(g,1=2)PIM	3982.284	131.04	0.00000	0.0000	52	706.560
Phi(t)p(g*t) PIM	3990.339	139.10	0.00000	0.0000	87	641.486
Phi(t) p(g)PIM	3998.045	146.81	0.00000	0.0000	28	771.545
Phi(g) p(g*t)PIM	4008.632	157.39	0.00000	0.0000	100	632.203
Phi(.) p(g)PIM	4009.234	157.99	0.00000	0.0000	5	829.221
Phi(g,1NAO,2=3,4a2) p(g,1=2)PIM	4013.146	161.91	0.00000	0.0000	7	829.116
Phi(.) p(g*t)PIM	4018.208	166.97	0.00000	0.0000	72	700.894
Phi(g*t) p(g*t)PIM	4043.125	191.89	0.00000	0.0000	192	464.808
Phi(t) p(t)PIM	4093.645	242.41	0.00000	0.0000	48	826.176
Phi(.) p(t)PIM	4095.369	244.13	0.00000	0.0000	24	877.001
Phi(.) p(.)PIM	4101.885	250.65	0.00000	0.0000	2	927.887
Phi(t) p(.)PIM	4103.665	252.43	0.00000	0.0000	25	883.266

Table 2. Time-dependent annual survival rate estimates, standard deviation, lower and upper limits of 95% confidence interval for locally hatched Pied Flycatcher males derived from the best CMR model (see Table 1).

Winter	Survival rate	SD	Lower limit	Upper limit
1982/83	0.475	115.055	0	1.000
1983/84	0	0.0001	0	0.999
1984/85	1	0	1	1
1985/86	0.893	0.085	0.594	0.980
1986/87	0.757	0.101	0.516	0.901
1987/88	0.380	0.075	0.248	0.534
1988/89	0.363	0.100	0.196	0.571
1989/90	0.337	0.125	0.145	0.604
1990/91	0.358	0.119	0.168	0.606
1991/92	0.569	0.156	0.275	0.821
1992/93	0.190	0.091	0.068	0.428
1993/94	0.407	0.263	0.075	0.853
1994/95	0.420	0.363	0.038	0.931
1995/96	1	0	1	1
1996/97	0.631	0.240	0.185	0.928
1997/98	0.200	0.107	0.063	0.482
1998/99	0.713	0.162	0.344	0.922
1999/2000	0.619	0.128	0.360	0.824
2000/01	0.482	0.116	0.272	0.698
2001/02	0.627	0.105	0.411	0.802
2002/03	0.343	0.074	0.214	0.500
2003/04	0.473	0.093	0.301	0.652
2004/05	0.361	0.104	0.189	0.578
2005/06	0.153	0.085	0.047	0.395

Males of unknown origin and locally recruited females had a significantly lower local survival rate (Table 3). Even though we cannot rule out that the birds of these groups survive less well than locally hatched males, we assume that the difference was mainly due to the higher emigration rate of males of unknown origin and of locally hatched females. One reason that allows us to assume this is the longer average breeding dispersal distance of female Pied Flycatchers (Winkel 1982, Sokolov 1991) resulting in significantly lower return rate of females, at least in the northern part of the breeding range (Haartman 1960; Nyholm & Myhrberg 1983; Leivits & Vilbaste 1990; Lundberg & Alatalo 1992; Sokolov 1991, 1997; Artemyev 2008a). We believe that fewer adult males than females permanently emigrate and breed outside our study plot.

Table 3. Survival rate estimates of Pied Flycatchers belonging to different groups.

Group of birds	Survival rate estimate	Standard error	95% confidence interval
Locally hatched males (annual average)	0.4643	0.0419	0.3822–0.5464
Males of unknown origin	0.3152	0.0149	0.2867–0.3452
Locally hatched females	0.3152	0.0149	0.2867–0.3452
Females of unknown origin, winter 1	0.1481	0.0149	0.1212–0.1798
Females of unknown origin, subsequent winters	0.3986	0.0337	0.3347–0.4661

As for males of unknown origin, they have a significantly lower local survival rate than local males. Some of these birds may in fact be local birds that hatched in natural cavities and thus had not been ringed by us as nestlings. However, others are probably immigrants from outside the study plot. Immigrant Pied Flycatchers are known to often show lower return rate to the site of their former breeding (Sokolov 1991, 1997; Artemyev 1994, 2008b; but see Gashkov 2003) than autochthonous birds. Females of unknown origin had a time-since-marking-dependent local survival probability (Table 3): it was *ca.* 15% during the winter following marking, and *ca.* 40% in subsequent winters. The first winter refers to the winter after marking as a breeder in the study area, i.e. it is at least the second winter in their life, thus this difference unlikely originates from age-dependent survival rate, but rather is a result of varying site fidelity. Birds that immigrated from elsewhere and for the first time bred on the Courish Spit (in many if not most birds this was probably their first breeding attempt in their second calendar year) were likely to emigrate from the area, but those few that remained showed a high return rate, even slightly higher than locally recruited females. We do not know where the immigrant females emigrate to, but can speculate that a proportion of them may return to their natal areas. A significant proportion of Pied Flycatchers hatched on the Courish Spit are first recaptured at the age greater than 1 year, suggesting that as yearlings they may have attempted to breed elsewhere (Chernetsov et al. 2006). The proportion of such females (41%) is higher than males (23%), suggesting that this behaviour may be female-biased.

To summarise, our data suggest that males that return to breed to their natal area are the most site faithful group of Pied Flycatchers; immigrant males and locally recruited females are more prone to undergo breeding dispersal; and immigrant females are quite likely to leave the area after the first breeding season, may be returning to their natal area. However, those that remain are even slightly more site faithful than local females.

4.2. Lack of influence of African conditions

We failed to find any relationship between annual survival rate of Pied Flycatchers on the Courish Spit and NAO, NDVI values in their presumed wintering range, or precipitation values expressed either as Sahel or Guinea rainfall index

or as average rainfall in November – February at individual weather stations in the Guinea zone. However, we do not conclude that condition in winter quarters, including rainfall, did not influence Pied Flycatcher survival rates. A more likely explanation for the lack of relationship is that Pied Flycatchers from the same local breeding population spend their winter at different sites across the species' wintering range, as known for e.g. Siskins *Carduelis spinus* (Payevsky 1994), several thrush species *Turdus spp.* (Payevsky et al. 2005), Oriental Honey Buzzards *Pernis ptilorhyncus* (Yamaguchi et al. 2008) etc. Average winter rainfall values at different individual weather stations included in our analysis were not correlated (Chernetsov, Sokolov, Kosarev, unpubl.), suggesting that local conditions in different part of the Pied Flycatcher's winter range could vary broadly. Survival rate in a local breeding population could then appear unrelated to winter conditions at particular localities or to the value averaged across the winter range, even though survival prospects of individual Pied Flycatchers are strongly influenced by local conditions at their wintering sites.

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