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## Latitudinal Variation in Female Local Return Rate in the Philopatric Pied Flycatcher (*Ficedula hypoleuca*)

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**ABSTRACT.**—Philopatry and dispersal distances of female Pied Flycatcher (*Ficedula hypoleuca*) are presented for European populations using data from 25 breeding areas from 40 to 70°N. Female annual survival probabilities according to capture–recapture models were similar in two study areas in central Spain (45 and 52%). The present study shows that survival is underestimated by using annual local return rate in one of the two breeding populations under study in central Spain. In southern and central Europe, females were found to return equally regularly to their breeding areas, whereas in northern Europe (latitude >60°N) females returned at lower rates. I did not find that median dispersal distance varied among sites, nor was breeding distance related to local survival rate. Therefore, the present study suggests that the decline in between-year local return rate of female Pied Flycatchers with increasing latitude over Europe may be more probably caused by differences in mortality than by geographical differences in site fidelity.

In many species of birds, adults show high breeding-site fidelity (Greenwood and Harvey 1982). A typical passerine that shows a high level of fidelity to the breeding territory in successive breeding seasons is the Pied Flycatcher (*Ficedula hypoleuca*) (Lundberg and Alatalo 1992). Because of this, female and male local return rates have repeatedly been used in analyzing annual survival rates (Askenmo 1979, Røskaft et al. 1986, Järvi et al. 1987, Slagsvold and Lifjeld 1988, Alatalo and Lundberg 1989, Potti and Montalvo 1991a, Sanz 1997a, Siikamäki and Hovi 1997, Eeva and Lehikoinen 1998, Hemborg and Lundberg 1998, Hemborg 1999). In those studies, local return rate was often estimated as the proportion of marked individuals realized in one year that were recaptured in the next year. However, local return rate includes both the probability of survival and the probability of recapturing on the next year (Martin et al. 1995), and is affected by dispersal distances. These confounding factors might limit the interpretation of those studies, and it is questionable whether local return rate could be used as a survival estimate (Martin et al. 1995).

In a previous review of female local return rates and breeding dispersal distances from different Eu-

ropean populations of Pied Flycatchers (Lundberg and Alatalo 1992), a relatively small number of studies was used ( $n = 14$  areas) from a narrow latitudinal range studied (50 to 66°N). Because of the large number of studies published on the Pied Flycatcher near the peripheral parts of its range in the Palearctic (Sanz 1997b), it is now possible to analyze geographical variation in those parameters using a relatively large data set ( $n = 25$  areas) from a more extensive geographic range (40 to 70°N). Most studies of breeding dispersal have concentrated on identifying the factors associated with the movement of birds from previously occupied territory (Pärt and Gustafsson 1989, Potti and Montalvo 1991b). Here, I test (1) whether annual survival rate of female Pied Flycatcher can be estimated from the local return rates on small-scale study plots, and (2) whether female local return rate and breeding dispersal in this species vary with latitude.

**Methods.**—The Pied Flycatcher is a small, migratory, philopatric, and hole-nesting passerine bird of European woodlands. It leaves Europe for the wintering grounds in west Africa around mid-August (Lundberg and Alatalo 1992), and it returns to the breeding areas during May (Sanz 1997b).

The data presented were collected in two breeding populations in central Spain (Sanz 1995) that were separated by distance of ~20 km: (a) a montane coniferous forest of *Pinus sylvestris* (hereafter called Siete Picos) at 1,900–2,000 m a.s.l. near Navacerrada pass, Madrid (40°48'N, 4°01'W). That study plot is on steep northern slopes close to the tree-limit with a severe climate (Sanz 1995). From 1989 to 1994, 250 nestboxes were checked for occupation by Pied Flycatchers; (b) a deciduous forest of *Quercus pyrenaica* (hereafter called Valsain) at 1,200 m a.s.l. near the vicinity of La Granja, Segovia (40°54'N, 4°01'W). Climate in this area is less harsh (Sanz 1995), and from 1991 to 1999 I checked 150–350 nestboxes for occupation by Pied Flycatchers.

Nestboxes were erected in a grid with 25 m between adjacent boxes. The nestboxes occupied by Pied Flycatchers were protected to prevent predation and were cleaned every year after the breeding season. Most of the breeding females (92.4% in Siete Picos and 91.7% in Valsain) were caught and identified (or banded if they had not been encountered previously) during incubation or when they were feeding

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TABLE 1. Annual return rate, survival and recapture probabilities (mean  $\pm$  SE) of the female Pied Flycatchers breeding in Siete Picos and Valsain (central Spain). Data are presented per study year.

Year	Siete Picos			Valsain		
	Return rate	Survival	Recapture	Return rate	Survival	Recapture
1989	0.2857	0.2857 $\pm$ 0.1207	1.00 $\pm$ 0.00			
1990	0.5152	1.0000 $\pm$ 0.0000	0.39 $\pm$ 0.08			
1991	0.4242	0.4531 $\pm$ 0.1420	0.56 $\pm$ 0.17	0.5000	0.5000 $\pm$ 0.0945	1.00 $\pm$ 0.00
1992	0.2174	0.1354 $\pm$ 0.0417	0.86 $\pm$ 0.13	0.3721	0.5037 $\pm$ 0.1289	0.47 $\pm$ 0.12
1993	0.3500	0.3889 $\pm$ 0.1905	0.46 $\pm$ 0.16	0.4737	0.5316 $\pm$ 0.0970	0.69 $\pm$ 0.09
1994				0.4667	0.4777 $\pm$ 0.0669	0.96 $\pm$ 0.04
1995				0.4267	0.4454 $\pm$ 0.0605	0.86 $\pm$ 0.06
1996				0.5577	0.5894 $\pm$ 0.0766	0.92 $\pm$ 0.06
1997				0.3474	0.3963 $\pm$ 0.0607	0.78 $\pm$ 0.08
1998				0.3913	0.7233 $\pm$ 0.2631	0.54 $\pm$ 0.17
Mean	0.3585	0.4526	0.65	0.4420	0.5209	0.78

the nestlings. The subsequent annual local return rate of females was observed through recapture in the following breeding season. Female annual survival rate was calculated according to the Cormack–Jolly–Seber capture-recapture model (Lebreton et al. 1992) as presented in the program SURGE (Cooch et al. 1997). The capture–recapture model considered was cohort–time dependent for survival and simple time dependent for recaptures (Cooch et al. 1997). The total number of capture histories was 219 females for Siete Picos and 437 females for Valsain. Breeding dispersal of females in Valsain was determined as the distance (to the nearest 5 m) between the occupied nestboxes in successive breeding seasons on a detailed map of the study area. To avoid dependence among observations, only the first distance moved by an individual female was used ( $n = 166$ ).

I used the data from my two study sites and 23 others from across Europe (see Appendix) to exam-

ine geographic variation in return rate and dispersal distance. The parameters included in the analyses were “annual local return rates” and “breeding dispersal distances” of females. If data for several years were available, the mean values for each study area were used in the analyses. For all areas, the latitude in decimal degrees was determined. I included only latitude in the analyses because the distribution of that species shows a southwest to northeast trend in Europe (Sanz 1997b). Proportions were analyzed after arcsine square root transformation. Values are presented as means  $\pm$  SD.

**Results.**—In Siete Picos, the local female return rate (35.8%) did not differ significantly (Wilcoxon test,  $Z = 0.76$ ,  $df = 5$ ,  $P = 0.46$ ) from the calculated female survival rate (45.3%; Table 1). In Valsain, the local return rate and survival rate of the females in successive breeding seasons were 44.2 and 52.1%, respectively (Table 1). In Valsain, female local return rates in successive breeding seasons was significantly lower than the calculated survival rates (Wilcoxon test,  $Z = 2.37$ ,  $df = 8$ ,  $P = 0.018$ ). Mean female annual local return rate of all study sites in western Europe was 23.6% ( $n = 25$  studies). When female local return rates were compared among study sites, there was a significant negative relationship with latitude of the study areas (Fig. 1).

During the study period, female emigration from one population to the other was never observed. Median female breeding dispersal distance in Valsain was 145 m (range 0–1,215 m,  $n = 166$ ). Mean nearest neighbor distance between nestboxes was 25 m. Only 7.2% of females nested in the same nestbox in consecutive years, and the median number of nestboxes moved between breeding seasons was six. Female breeding dispersal distances did not vary with the latitude for the seven studies that reported dispersal data ( $r = 0.12$ ,  $df = 7$ ,  $P = 0.75$ ), and no relationship was found between local female return rate and dispersal distance ( $r = -0.15$ ,  $df = 7$ ,  $P = 0.72$ ).

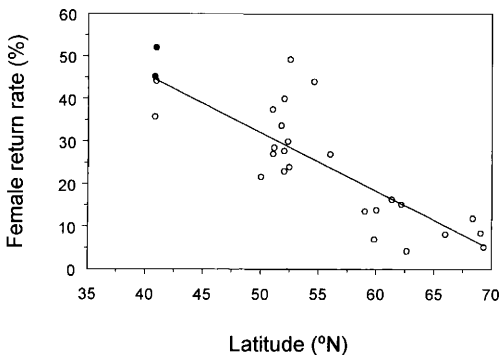


FIG. 1. The relation for the Pied Flycatcher between female annual local return rate and latitude of the study areas ( $Y = 1.444 - 0.017 X$ ,  $r = -0.80$ ,  $df = 24$ ,  $P < 0.001$ ). Black dots represent annual survival rate according to the Cormack–Jolly–Seber capture-recapture model (Lebreton et al. 1992).

*Discussion.*—Some investigators working on nest-box studies claim that it is legitimate to ignore capture probability because all nestboxes are checked during the breeding season. If interior zeros in capture histories are noted in such studies (e.g. capture histories such as 1011), then the capture probability parameter may reflect temporary emigration (non-breeding or nesting in natural cavities). Therefore, capture probability is needed in modeling capture history data regardless of the events it represents (Lebreton et al. 1992). Some unknown number of zeros following final captures reflect birds still alive and in the "superpopulation" of interest (Kendall et al. 1997). If capture probability is not included in the capture probability modeling, annual survival will be underestimated by methods that assume that all birds die in the interval following their final capture.

The present study shows that survival is underestimated by using annual local return rate in one of the two breeding populations under study in central Spain. In central Spain, the annual survival estimates of female Pied Flycatchers were similar in both study areas. Moreover, in southern and central Europe, females were found to return equally regularly to their breeding areas, whereas in northern Europe (latitude  $>60^{\circ}\text{N}$ ), females returned at lower rates. The lower return rates in northern Europe might be related to either lower breeding-site fidelity and long distance dispersal, or to higher female mortality. Von Haartman (1960) suggested that the breeding site fidelity of Pied Flycatchers declined towards the north in Europe, but the available evidence (Appendix) does not support that suggestion. I did not find that median dispersal distance varied among sites, nor was breeding distance related to locate survival rate. If the latitudinal trend in return rate was solely a product of differences in philopatry, then dispersal rate would have had to have been 400% higher in the north, and the data suggest no such difference.

Survival plays a strong role in the evolution of life-history tactics through its relationship with fecundity (Roff 1992, Stearns 1992). At an interspecific level, annual survival and clutch size are inversely related (Sæther 1988, Martin 1995). Northern populations of Pied Flycatchers tend to produce larger clutches and raise larger broods (Sanz 1997b), and females may therefore experience higher mortality. The generalization that adult survival and clutch size are inversely related within species is widely accepted (Högstedt 1981, Sæther 1988, Karr et al. 1990, Martin 1995), and intraspecific costs of reproduction might account for the inverse relationship between latitude and return rate in Pied Flycatchers. However, other components of fecundity such as nest success and juvenile survival are also important and must be examined in greater detail to fully evaluate this hypothesis (Bennett and Harvey 1988). Clearly, the latitudinal gradient in return rate that exists in female Pied Flycatchers can only be explained after

experimental studies of the cost of reproduction have been conducted at different latitudes. Given my results, survivorship should be measured with mark-and-recapture statistics that account for dispersal and attempt to separate it from mortality (e.g. Lebreton et al. 1992).

The general idea from previous studies (Lundberg and Alatalo 1992) is that if a Pied Flycatcher has started to breed at a certain site she, if having survived, is very likely to return to the same area in the next breeding season. In Valsain, the present study shows that a few females (7.2%) reoccupied their previous nestbox, whereas most of them occupied nestboxes in  $<100\text{ m}$  (44% of females). This low degree of nestbox fidelity has been suggested to be a result of a high frequency of forced movements due to breeding tits (*Parus* spp.) or to earlier arrived conspecifics (Harvey et al. 1984). Another factor causing a low degree of nestbox fidelity may be the high density of nestboxes (Pärt and Gustafsson 1989). Female Pied Flycatchers are more selective at high than at low nestbox density (Alatalo et al. 1988).

The present study shows a decline in between-year local return rate of female Pied Flycatchers with increasing latitude over Europe. This may be more probably caused by differences in mortality than by geographical differences in site fidelity. Hopefully this study will stimulate more research to solve the problem of latitudinal variation in survival.

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APPENDIX. Annual local return rates (percentage) and median dispersal distance (meters) between successive breedings of female Pied Flycatchers in different parts of Europe. Sample sizes are in parentheses.

Latitude	Female return rate	Female dispersal	Reference
69° 20' N	5.2 (115)		Järvinen (1993)
69° 03' N	8.49 (271)		Järvinen (1983, 1993)
68° 21' N	11.96 (92)		Hemborg (1999)
65° 58' N	8.2 (1260)	200–300	Nyholm and Myhrberg (1983); Nyholm (1986)
62° 37' N	4.3 (92)	175	Siikamäki and Hovi (1997)
62° 10' N	15.22 (46)		Haartman (1960)
61° 20' N	16.4 (832)		Eeva and Lehtikoinen (1998)
60° 00' N	13.9 (576)		Haartman (1960)
59° 50' N	7.0 (393)		Lundberg and Alatalo (1992)
59° 00' N	13.6 (154)		Enemar (1948)
56° 00' N	27.0 (363)		Haartman (1960); Curio (1959)
54° 35' N	44.0 (176)		Lundberg and Alatalo (1992)
52° 31' N	49.23 (1298)	100–200	Berndt and Sternberg (1969); Sternberg (1989)
52° 27' N	24.0	400–500	Winkel (1982)
52° 00' N	23.0 (646)	c. 115	Campbell (1959)
52° 00' N	27.78 (198)		Haartman (1960)
51° 45' N	33.74 (763)	127	Harvey et al. (1984, 1988)
51° 30' N	27.1 (340)	c. 150	Creutz (1955)
51° 13' N	28.57 (14)		Dhondt et al. (1987)
51° 00' N	37.5 (40)		Trettau (1952)
50° 00' N	21.7 (115)		Trettau and Merkel (1943)
41° 42' N		159	Potti and Montalvo (1991a, 1991b)
40° 54' N	44.2 (437)	145	This study
40° 48' N	35.85 (219)		This study