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Age-related difference in return rate of Willow Warblers *Phylloscopus trochilus* at two breeding sites in Sweden

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We studied breeding and natal site fidelity of Willow Warblers *Phylloscopus trochilus* in 1983 to 1993 at two ringing sites, Ammarnäs in Swedish Lapland and Kvismaren in South Central Sweden. The yearly trapping effort was rather similar at the two study sites. We used pooled data from all study years in the analyses. The overall recapture rate was almost two times higher at Kvismaren than at Ammarnäs. This difference was caused by an eight times higher recapture rate of Willow Warblers ringed as juveniles at Kvismaren as compared to Ammarnäs, whereas the recapture rate of birds ringed as adults did not differ between study sites. When we restrict the analysis to include mainly local birds, the between year recapture rate of juveniles was still more than 20 times higher at Kvismaren than at Ammarnäs. We discuss two possible explanations for this difference in recapture rate of juveniles between the two study sites. One explanation is that juvenile Willow Warblers at Ammarnäs may suffer higher mortality, either because they have a longer migration route or as a result of adverse weather conditions in the breeding areas in late summer. This is, however, contradicted by the fact that the breeding densities of Willow Warblers in the mountain birch forest are much higher than in other habitats where the subspecies (*P.t. acredula*) occurs in Sweden. Thus a more likely explanation is that natal site fidelity is lower at Ammarnäs, possibly as a result of a homogeneous habitat (mountain birch forest) and because rich food patches (e.g. *Epirrita autumnata*) are unpredictably distributed between years.

1. Introduction

Site fidelity of juvenile birds to their natal area (natal fidelity) and of adult birds to a previous breeding site (breeding site fidelity) are important parameters when studying the dynamics and demography of bird populations (Greenwood 1980, 1989, Greenwood & Harvey 1982, Shields 1983). As a general trend among birds, adults show a stronger fidelity to their previous breeding site than juveniles to their place of birth (Greenwood & Harvey 1982). However, there are some species that have a very low breeding site fidelity, e.g. Redpoll *Carduelis flammea* (Enemar & Nyström 1981) and Brambling *Fringilla montifringilla* (Mikkonen 1983, Hogstad 1985, Lindström 1987). There may also be geographical differences in site fidelity within a species, such as in the Pied Flycatcher *Ficedula hypoleuca* (Tegelström et al. 1990, Lundberg & Alatalo 1992).

Site fidelity has been suggested to have important consequences for birds. For example, territory acquisition (Nolan 1978, Radesäter & Jakobsson 1989), predator avoidance and foraging efficiency (Hinde 1956, Lanyon & Thompson 1986) can be facilitated. Ultimately, site fidelity may affect survival (Pärt & Gustafsson 1989, Part 1990) and reproductive success in birds (van Noordwijk & van Balen 1988, Bensch & Hasselquist 1991, Pärt 1991).

The Willow Warbler *Phylloscopus trochilus* is a common breeder of northern Europe that winters in tropical Africa (Cramp 1992). It is territorial during the breeding season (Radesäter & Jakobsson 1988, Arvidsson & Nergaard 1991) and shows a strong site fidelity to the previous breeding area (Tiainen 1983, Jakobsson 1988, Pratt & Peach 1991) and even to the same territory year after year (Lawn 1983, Jakobsson 1988, Radesäter & Jakobsson 1989).

In this study, we compare between-year recapture rates of Willow Warblers ringed as juveniles and adults, respectively, during the post-breeding period at two ringing sites in Sweden. The distance between the two sites (namely Ammarnäs and Kvismaren) is approximately 1000 km and they differ both in habitat composition and altitude. Willow Warblers inhabiting the two study sites also belong to different subpopulations (*P.t. trochilus* at Kvismaren and *P.t. acredula* at Ammarnäs) with a different wintering area. The aim of the present analysis was to relate possible differences in return rate between subpopulations and age groups which may indicate differences in demographic characteristics (i.e. site fidelity and mortality).

2. Methods

2.1. Ringing sites

Willow Warblers were trapped during standardized mist-netting at two different ringing sites in the summers of 1983–1993.

Ammarnäs (65°58′N, 16°06′E) in Swedish Lapland (altitude 550 m a.s.l.) is a rich subalpine birch forest *Betula pubescens* containing some dense patches of willows *Salix* spp. Nets were in use along the shores of lake Tjulträsk and the stream Tjulån (see Ulfstrand 1968 for a description of the area), 8 km W of Ammarnäs village. Each year we used a total of 22 nets at fixed positions during every rain-free day, from 7.00 am to 13.00–15.00 pm during the period 15 July to 20–25 August. Willow Warblers breed abundantly in the valley where the ringing site is situated at densities from 0.5–1.5 pairs/ha (Arvidsson & Klaesson 1984, Arvidsson & Klaesson 1986).

Kvismaren (59°10′N, 15°25′E) in South Central Sweden (altitude 22 m a.s.l.) is two reclaimed lakes. The vegetation surrounding the lakes mainly consists of patches of willows *Salix* spp. and birch *Betula alba.* Most of the lake shore is covered by dense reeds *Phragmites australis.* Willow Warblers were trapped every second or third day, alternatingly at two sites 2 km appart, in the dense vegetation along the lake shore. When trapping birds, a total of 20–25 nets were used from 3.00 am to 12.00 am, during the period 1 July to 31 August. Breeding densities of Willow Warblers around the lake are roughly 0.5-1 pairs/ha (own observ.). However, further from the lake breeding sites are sparsely and patchily distributed, and densities therefore lower.

2.2. Measuring recapture rates

In this study we analysed differences in recapture rate between age groups and ringing sites by χ^2-test using the actual numbers of captured and recaptured birds (Table 1). Since the trapping effort was rather similar at the two sites (Appendix 1), standardizing the number of captured and recaptured birds to account for differences in trapping effort only had a marginal effect on the estimated recapture rates (Table 2). Only birds that were initially ringed and recaptured in a subsequent year at the same site have been considered in the analysis. Hence, this study includes all Willow Warblers that were ringed at the two sites in 1983–1992 and recaptures made in 1984–1993. If an individual was recaptured in more than one year, it was considered as a recapture only once in each analysis. When captured, we classified the age of each individual as 1 y (i.e. in its first summer) or 2 y+ (i.e. in its second summer or later) according to Svensson (1992). In all

analyses, juveniles are birds that were initially ringed during their first summer (as 1 y), and adults are birds initially ringed during their second summer or later (as 2 y+).

3. Results

3.1. Ringing numbers

The trapping effort in 1983–1992 was rather similar at the two ringing sites (Ammarnäs, $\bar{x}$ = 3330 net hours, SD = 731; Kvismaren, $\bar{x}$ = 3711 net hours, SD = 677; $t_{(18)} = 1.21$, $p = 0.24$; see Appendix 1). However, we trapped more Willow Warblers (6945) at Ammarnäs than at Kvismaren (2080; Table 1). At both ringing sites, most of the trapped birds that were unringed were juveniles (Ammarnäs 92.6% and Kvismaren 86.6%).

When comparing the standardized number of ringed Willow Warblers (no.birds/1000 net-hours) pooled for all years, we trapped about three times more Willow Warblers at Ammarnäs (2162 juveniles and 170 adults) than at Kvismaren (596 juveniles and 92 adults; Table 2).

3.2. Recapture rate

The number of birds recaptured in a subsequent breeding season was significantly higher for adults than for juveniles, both at Ammarnäs ($\chi^2_1 = 280$, $p < 0.001$) and Kvismaren ($\chi^2_1 = 48.6$, $p < 0.001$; Table 1).

The overall recapture rate of Willow Warblers (Table 1) was three times higher at Kvismaren (1.4%) than at Ammarnäs (0.45%; $\chi^2_1 = 22.9$, $p < 0.001$). However, this difference was entirely due to an eight times higher recapture rate of juveniles at Kvismaren (0.72%) than at Ammarnäs (0.086%; $\chi^2_1 = 27.8$, $p < 0.001$). The recapture rate of adults did not differ between Kvismaren (5.6%) and Ammarnäs (5.0%; $\chi^2_1 = 0.12$, n.s.).

When looking at the standardized numbers of captured and recaptured birds, the recapture rate was very similar to that calculated from the actual numbers (Table 2). The difference in recapture rate of juveniles was still eight times higher at Kvismaren (0.69%) than at Ammarnäs (0.086%), while there was no difference in recapture rate between adults (Kvismaren 5.5%, Ammarnas 5.5%).

We are aware of two possible biases of our anlysis. First, the probability of capturing Willow Warblers may differ between age groups at the two study sites. To check this first possibility, we looked at the proportion of adults of the total number of captured birds at each of the two sites. The proportion of adult birds captured at Ammarnäs (7.3%) was about half of that at Kvismaren (13%). This suggests either that the capture efficiency of adults was higher or that the capture efficiency of juveniles was lower at Kvismaren than at Ammarnäs. When we take this difference into account the between-year recapture rate of juveniles at Kvismaren was still more than four times higher than at Ammarnäs.

Second, the probability of capturing local resident Willow Warblers (either adult breeders or fledglings local to the ringing site) may differ at the two study sites. We tested this possibility by performing the same ringing and recovery analysis for juveniles (pullus class 1 and 2, i.e. 17–28 days after hatching; Bensch & Lindström 1992) and adult breeders (trapped before 1 August at Ammarnäs and 16 July at Kvismaren). By doing so, we exclude most of the non-local birds that had dispersed from their previous breeding site and were present at the ringing site during stopover or when moulting. This analysis shows an even larger difference between sites with a more than 20 times higher probability of recapturing juveniles at Kvismaren (2.6%) than at Ammarnäs (0.12%, Table 3).

4. Discussion

4.1. Recapture rate of adults

The overall recapture rate of adult Willow Warblers was rather similar at the two ringing sites (Table 1 and 3). These figures (5–8%) are low compared to return rates of Willow Warblers to their previous year's breeding site found in intensive studies of colour ringed breeding populations in England (36% of males and 23% of females, Lawn 1983), southern Sweden (24–44% of males, Jakobsson 1988) and southern Finland

(35% of males and 17% of females, Tiainen 1983). At our study sites, ringing was carried out in a rather restricted area covering roughly 10–15 territories. However, both sites also attracted moulting adults and juveniles during the post-breeding period (e.g. Bensch & Grahn 1993). Thus, our data on recapture rates are not absolute measures of breeding or natal site fidelity. However, we can use our data to compare demographic parameters, such as site fidelity and mortality between the two studied populations.

4.2. Recapture rate of juveniles

For juveniles we found a much higher recapture rate at Kvismaren than at Ammarnäs. There are two possible explanations for this large difference; juveniles from Ammarnäs may (1) show lower natal site fidelity, or (2) suffer higher mortality.

(1) Lower natal site fidelity for the northern than the southern population of Willow Warblers may be caused by the predictability and distribu-

Table 1. Number (%) of captured (1983–1992) and recaptured (1984–1993) Willow Warblers at Ammarnäs (North West Sweden) and Kvismaren (South Central Sweden). Data for adults and juveniles are presented separately.

	Ammarnäs			Kvismaren		
	No. ringed	Recaptured (%)		No. ringed	Recaptured (%)	
Adults	556	28	(5.0)	323	18	(5.6)
Juveniles	6945	6	(0.086)	2080	15	(0.72)
Total	7501	34	(0.45)	2403	33	(1.4)

Table 2. Standardized number (%) of captured (1983–1992) and recaptured (1984–1993) Willow Warblers at Ammarnäs (North West Sweden) and Kvismaren (South Central Sweden). Data for adults and juveniles are presented separately. We standardized the number of captured and recaptured birds each year as (no. birds/1000 net hours). These standardized numbers were then summed for all study years to obtain the total number of captured and recaptured birds per 1000 net hours for each age group and study site.

	Ammarnäs			Kvismaren		
	No. ringed	Recaptured (%)		No. ringed	Recaptured (%)	
Adults	170	9.4	(5.5)	92	5.1	(5.5)
Juveniles	2162	1.9	(0.086)	596	4.1	(0.69)
Total	2332	11.3	(0.48)	688	9.2	(1.3)

Table 3. Number (%) of captured (1983–1992) and recaptured (1984–1993) Willow Warblers at Ammarnäs and Kvismaren that presumably are local birds. To ensure this, only juveniles (pullus class 1 and 2 (Bensch & Lindström 1992) and adults trapped before 1 August at Ammarnäs and 16 July at Kvismaren, have been included in the analysis, see results for more details.

	Ammarnäs			Kvismaren		
	No. ringed	Recaptured (%)		No. ringed	Recaptured (%)	
Adults	393	19	(4.8)	167	14	(8.4)
Juveniles	3246	4	(0.12)	189	5	(2.6)
Total	3639	23	(0.63)	356	19	(5.3)

tion of the food in the breeding area (e.g. Wiens 1974, Järvinen 1983). The mountain birch forest is a highly homogeneous habitat which may decrease the disadvantage of dispersal; Willow Warblers that disperse are likely to find good breeding sites since there are vast areas with habitats suitable for breeding. In fact, it might even be advantageous for the Willow Warblers inhabiting the mountain birch forest to disperse. An important food resource for subalpine birch forest birds, including the Willow Warbler, is the mountain birch moth *Epirrita autumnata* (Enemar et al. 1984). The mountain birch moth has a very patchy distribution with large between-year differences in the distribution of rich patches (Tenow 1975, Haukioja 1991). When a food resource is patchily distributed and the distribution of rich patches changes between years, as in the present case, theoretically the best an individual can do is to track the rich food resources and this would lead to low site fidelity between years. This has been suggested in some other passerine species inhabiting birch forests in northern Scandinavia (Enemar & Nyström 1981, Mikkonen 1983, Hogstad 1985, Lindström 1987). This tendency towards low site fidelity is expected to be more pronounced for juveniles because adults that are site faithful can benefit from more efficient territory acquisition and maintenance (Ydenberg et al. 1988, Jakobsson 1988, Radesäter & Jakobsson 1989, Godard 1991) and also experience higher breeding success (e.g. van Noordwijk & van Balen 1988, Bensch & Hasselquist 1991, Pärt 1991). An argument against the strategy of tracking abundant food resources in mountain birch forest birds is that it may be hard to estimate the abundance of *Epirrita* at the time of the birds' arrival to the breeding area.

(2) There are some data suggesting that mortality may differ between different populations of Willow Warblers in Scandinavia. The southern Swedish populations (*P. t. trochilus*), including birds from Kvismaren, migrate a relatively short distance to their winter quarters north of the equator in West and Central Africa. The northern Swedish populations (*P. t. acredula*), including birds from Ammarnäs, start their autumn migration later (Hedenström & Pettersson 1984) and migrate longer distances to winter quarters well south of the equator in South Central to South Africa (Zink 1973, Hedenström & Pettersson 1987). Thus, the northern population of Willow Warblers may suffer higher mortality during migration due to the longer distance travelled and the later start of the migratory journey. This is likely to be more pronounced in juveniles than in adults since the juveniles have no experience of migration.

Another reason for higher mortality among juveniles of the northern population may be the risk of starvation on the breeding grounds during unfavourable weather in the post-breeding period (Lindström et al. 1985, Järvinen 1987, Lindström et al. 1990). This is supported by the observation that juveniles of the northern population leave their natal areas at a relatively earlier age than birds from the southern population (Gwinner et al. 1972, but see also Högstedt & Persson 1982).

The explanation that a higher juvenile mortality can explain the observed differences in return rate between the study sites is contradicted by data on density of breeding Willow Warblers. In mountain birch forests, the density of Willow Warblers is the highest reported from Sweden (125 pair/km^2; Ulfstrand & Högstedt 1976), while in other habitats the densities are lower (about 50 pairs/km^2; Ulfstrand & Högstedt 1976). Thus, these data suggest that the mountain birch forest act as a 'source' population. Keeping this in mind, it seems unlikely that there is a relatively much higher juvenile mortality of Willow Warblers inhabiting the mountain birch forests.

In conclusion, we found no difference in between-year recapture rate of adult Willow Warblers from the two studied populations in Sweden, while there was a much higher between-year recapture rate of juveniles from the southern population. This difference may be caused by differences in mortality or site fidelity that affect juveniles more than adults. Juveniles from the northern population may suffer higher mortality because they leave their breeding grounds later in the season and have a longer migratory journey. However, it seems more likely that the main explanation is that juveniles from the northern population show lower natal site fidelity because they inhabit a more homogeneous breeding habitat where rich food patches are spatially unpredictable between years.

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Appendix 1. Yearly numbers of juvenile and adult Willow Warblers ringed (1983–1992) and recaptured in subsequent years (1984–1993) at Ammarnäs and Kvismaren, respectively. Total catching effort (net hours) per year is given for the two study sites.

	Ammarnäs					Kvismaren				
		Juveniles		Adults			Juveniles		Adults	
Year	Nethrs	Ringed	Recapt.	Ringed	Recapt.	Nethrs	Ringed	Recapt.	Ringed	Recapt.
1983	3072	478		27		4053	100		16	
1984	3350	778	0	41	1	3631	91	0	20	0
1985	2032	711	0	40	5	3846	231	1	20	0
1986	3983	1171	2	75	3	3027	260	2	39	0
1987	3458	522	0	106	5	2306	308	1	45	4
1988	4288	677	0	44	1	4495	363	1	50	1
1989	3504	759	0	82	6	4670	181	3	39	1
1990	2707	565	0	39	5	3741	302	2	39	2
1991	4242	617	1	45	1	3650	70	0	25	3
1992	2660	667	3	57	0	3693	174	1	30	3
1993	2650		0		1	5634		4		4
Total	35946	6945	6	556	28	42746	2080	15	323	18