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Site fidelity and recurrence of some migrant bird species in The Gambia

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Regular ringing was carried out over most of five winters at Ginak in The Gambia. We analyse retrap data from 12 species of migrant birds to examine whether they remain for more than one day within a winter, and whether they return to the study area in subsequent winters. We investigate both the rate of recurrence (between-winter retraps within the whole area, approximately 1,000m across) and site fidelity (tendency to be retrapped within 100m of first capture). Some adjustment of recurrence for annual survival is attempted. For individuals trapped at least twice over a winter, we tabulate the interval between first and last capture: in all 12 species this was over six weeks for some individuals; furthermore, site fidelity within a winter is demonstrated in most species retrapped in reasonable numbers, exceptions were Garden Warbler Sylvia borin *and Blackcap* Sylvia atricapilla. *Most species recurred at appreciable rates in successive seasons, and in three species with a sufficient sample size, Subalpine Warbler* Sylvia cantillans, *Whitethroat* Sylvia communis, *and less certainly Olivaceous Warbler* Hippolais pallida, *the evidence was of site fidelity between winters. We compare recurrence rates with data collected at Djoudj in north Senegal.*

A small ringing project was started in The Gambia in late 1994, initially to follow up the Wetland Trust's expeditions to Senegal in 1990-93 (Sauvage *et al.* 1998) and also to act as a station of the European Science Foundation's Songbird Migration Project (Bairlein 1997). One of the objectives was to investigate site fidelity of migrants in their winter quarters, and this paper deals exclusively with these species.

In the Neotropics a number of studies have now established that many wintering landbird migrants are site faithful both within and between winters, and some are also actively territorial (eg Kricher & Davis 1986; several papers in the symposia volumes edited by Keast & Morton 1980 and Hagan & Johnstone 1992; DeGraaf & Rappole 1995, pp 11-12, cite further references). Indeed site fidelity may even be higher in the wintering grounds than when breeding (Holmes & Sherry 1992). However, this need not necessarily lead us to expect high site fidelity in overwintering migrants in Africa, because the habitats used by migrants there are rather different to those used by migrants in the Neotropics (Keast 1980).

In Africa it is also well established that individual migrant landbirds may return to the same general area for wintering (eg Ash 1981, Hanmer 1986, Berthold 1993) but fewer numerical data have been collected. The evidence is most complete for species of *Acrocephalus*, some of which exhibit not only site fidelity between and within winters, but also territorial defence and song (eg De Bont *et al.* 1965, Pearson 1972, Aidley & Wilkinson 1987, Kelsey 1989, Hedenström *et al.* 1993). Recent records from Salewski *et al.* (2000) took the total number of winter migrant species for which between-winter recurrence has been reported in Africa to 60. Further studies from Southern Europe, Israel and India have demonstrated that particular overwintering Palaearctic migrants are also site faithful or territorial there (eg Cuadrado 1995, Cuadrado *et al.* 1995, Rödl 1995, Katti & Price 1996).

Sauvage *et al.* (1998) termed return in subsequent winters to a general area

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"recurrence" and used "site fidelity" to refer to a return to a more circumscribed site. In this paper we have adopted these useful terms and attempt to compare their results to ours because of the comparative proximity of the study areas (about 580km). They analysed the recurrence at Djoudj in north Senegal of 31 species of Palaearctic passerine migrants between 1987 and 1993 and listed seven species for which recurrence had not previously been recorded. They also showed both within- and between-winter fidelity to restricted sites by four species of warbler, although no statistical analysis was made of this because the long distances between their sites and the discontinuous habitat made retraps unlikely away from the initial trapping site.

METHODS

Ringing took place on Ginak Island (13°34′ N 16°32′ W), a low-lying coastal island to the north of Barra, in an area of low scrub, mainly *Maytenus senegalensis* and *Tamarix senegalensis* with various acacia species. The Senegal study was at Djoudj (16°10′ N 16°18′ W) about 30 km from the coast where there are large areas of shallow, open water with reed beds (*Phragmites* and *Typha* spp.), patches of scrub (*Salvadora persica, Tamarisk senegalensis*) and a few *Acacia nilotica*, separated by sandy plains.

At Ginak, to conform with the protocols of the European Songbird Migration Project (Bairlein 1997), a "core" site of mist nets was established of a size that could be operated by as few as two ringers (occasionally by only one) who might be dealing with unfamiliar species. This consisted of seven 18m nets within an area 100m across (0.8ha). Throughout the text, use of the word "site" implies an area of this order of size. To avoid the possibility of resident birds becoming net-shy, we did not use the core site every day, so four alternative sites were established. These lay 150-200m to the north and 600-800m to the south of the core site; other sites 1000-3000m away were used occasionally. We refer to all these sites away from the core as "outer" sites.

Coverage was as follows: 1994-95, five days in December and five weeks in February-March; 1995-96, all weeks from early October to the end of March; 1996-97, late September to late April, with a three-week gap from late November to early December; 1997-98, three weeks in October and two weeks in November, then early January until early March; 1998-99, late September to end of October, two weeks in November and from mid-January to mid-March.

RESULTS

Six species of migrant that were rarely retrapped are not analysed further here. These were (numbers in brackets are total number ringed, the number of individuals retrapped in the same winter and the number recurring in two or more winters): Common Sandpiper *Actitis hypoleucos* (20, 1, 1); Tree Pipit *Anthus trivialis* (39, 4, 2); Yellow Wagtail *Motacilla flava* (54, 5, 0); Grasshopper Warbler *Locustella naevia* (19, 4, 0); Reed Warbler *Acrocephalus scirpaceus* (97, 15, 1); and Willow Warbler *Phylloscopus trochilus* (238, 2, 0). The lack of recurrence in Willow Warbler matches the figures from Djoudj in Senegal (of 116 birds, none retrapped in a later year: Sauvage *et al.* 1998); only seven birds were trapped in December and January, so most must be on passage. The analyses described below concern only the other 12 species of migrant.

Recurrence

One estimate of the rate of between-winter recurrence is simply the proportion of individuals ringed (excluding those from only the final trapping winter) that were retrapped in a later winter. In Table 1 we show this statistic for both Ginak and Djoudj, reanalysing the Djoudj data (Sauvage *et al.* 1998) to include only the three winters of the International Expeditions 1990-93, since coverage in previous winters was much less.

One problem with this recurrence statistic is a disproportionate effect of birds trapped in earlier years, because more trapping attempts follow their ringing, so that they have a greater chance to be retrapped at least once. Another problem is that species with a lower survival will appear to have a lower tendency to return to the same area. To avoid both problems we also calculated a "survival-adjusted recurrence". We counted the number of times that birds were caught in two successive winters (ie ignoring recaptures two or more winters after the initial capture

Table 1. Survival-adjusted and unadjusted recurrence at Ginak, The Gambia, and Djoudj, north Senegal. Unadjusted recurrence is here the number of cases of birds being retrapped in consecutive winters, divided by the sum of the numbers of birds caught (ringed or retrapped) in each winter except the last. This is divided by an estimate of annual survival rates (based on Peach *et al.* 2001, or, for those entries marked †, extrapolated from data on similar species) to give the survival-adjusted recurrence. Differences between Ginak and Djoudj are tested statistically (ns implies $P > 0.1$; *P*-values printed are not Bonferroni corrected, but * indicates $P < 0.05$ after correction). Also given is the percentage of individuals ever retrapped in a later winter. Status is a rough estimate of the seasonal pattern of occurrence (for Djoudj based on Sauvage *et al.* 1998 and Rodwell *et al.* 1996): A = common on autumn passage, W = common overwintering, S = common on spring passage; a, w, s = in smaller numbers; rare occurrences are excluded. Figures in brackets include numbers ringed at Djoudj 1985-90, when trapping effort was less.

Species	*Study area*	*Status*	*Sum of no caught each winter*	*No consecutive -winter retraps*	*Ginak-Djoudj comparison P-value*	*Unadjusted recurrence (%)*	*% birds retrapped in later winters*	*Survival rate assumed (%)*	*Survival -adjusted recurrence (%)*
Wryneck	Ginak	A w S	14	3		21	18		31
	Djoudj	W	32	0	0.037	0	0	69†	0
Nightingale	Ginak	A W S	31	4		13	20		31
	Djoudj	a s	(9)	0	ns	0	0	42	0
Redstart	Ginak	W	223	19		9	8		17
	Djoudj	A w S	(140)	0	0.0007*	0	0	49	0
Melodious Warbler	Ginak	A w	205	14		7	5		14
	Djoudj	a s	0	—	—	—	—	51	—
Olivaceous Warbler	Ginak	A W S	294	35		12	11		24
	Djoudj	W	269	35	ns	13	11	50†	26
Subalpine Warbler	Ginak	A W S	706	64		9	10		18
	Djoudj	W	1,673	117	ns	7	7	50†	14
Garden Warbler	Ginak	A	338	5		2	2		3
	Djoudj	a s	99	0	ns	0	0	54	0
Blackcap	Ginak	a W S	528	0		0	0		0
	Djoudj	a s	0	—	—	—	—	44	—
Whitethroat	Ginak	w S	623	37		6	6		13
	Djoudj	w S	195	4	0.037	2	2	44	5
Orphean Warbler	Ginak	a W S	101	14		14	16		28
	Djoudj	w S	120	1	0.0004*	1	2	50†	2
Chiffchaff	Ginak	a W s	193	1		1	1		1
	Djoudj	a W s	5,921	360	0.0018*	6	6	48	13
Western Bonelli's Warbler	Ginak	Ws	106	4		4	4		9
	Djoudj	ws	21	1	ns	5	10	42†	11

unless the individual has also been recaptured in an intermediate winter). This total was divided by the sum of the numbers caught in each winter, except the last, that we expect to survive to the next winter: expected survival is taken from Peach *et al.* (2001), using mean values for congeners where necessary (but with the Wryneck estimated from figures from non-social non-migratory woodpeckers, given in Virkkala (1993) and by U. Wiktander (pers comm). Table 1 presents these results, along with the results of our equivalent reanalysis of the 1990-93 data from Djoudj (Sauvage *et al.* 1998). We were interested to know whether the recurrence rates were consistent between these two locations and if not to propose possible reasons. Recurrence rates were compared between Djoudj and Ginak by analysing the 2x2 table of frequencies of captures and next-winter retraps, using χ^2 or Fisher's exact tests. There were ten species in which the comparison was possible, which inflates the chance of getting a significant *P*-value just by chance. Accordingly, we corrected for this using the sequential Bonferroni procedure (Rice 1989), which tends to be conservative.

A lower trapping effort will retrap a lower proportion of the recurring individuals. Djoudj might thus be expected to show higher recurrences than Ginak, owing to the larger number of netting sites, which were more frequently manned and covered a larger area.

Site fidelity

Recurrence is based on retrapping a bird anywhere within the whole study area (over 1km across). By site fidelity we mean an individual bird remaining in a smaller area than this, as we are familiar with when birds are on their summer breeding territories. It is possible that birds are site faithful within a winter, but choose a different site the next winter. Accordingly site fidelity was analysed separately for retrappings within winters and for those between winters.

Repeatedly trapping an individual bird at the same site is not necessarily convincing evidence of site fidelity. If enough birds are retrapped, we expect some to be retrapped at the same site just by chance. This is particularly the case if that site is attractive habitat for the species, or if nets are more often set there than elsewhere. In an extreme case, if only one site in the study area is suitable habitat, all retraps will occur at it, but this would indicate nothing about how site faithful individuals would be if adjacent sites were equally suitable. The latter is what is interesting to know, and such information on a species' behaviour can be applied whatever the variation in habitat quality. Accordingly, we have constructed a null hypothesis that incorporates different capture rates at the different sites, and then statistically compared the observed number of site-faithful retraps against the numbers predicted by the null hypothesis.

Our null hypothesis is that where an individual is recaptured depends only on the rates of capture of the species in the core or outer sites, and not on whether it has been caught earlier in one site rather than another. From the rates of initial captures each winter in the outer and core sites, and the total number of retraps each winter, we can calculate the expected number of movements within and between the core and outer sites if the null hypothesis holds. Further details of the calculation of these expectations are given in the Appendix.

We used a one-tailed binomial test to examine whether the observed number of movements between the core and the outer sites were a significantly smaller proportion of the total number of retraps than expected. One capture within the core site and another in an outer site imply movement of over 100m, whereas two captures within the core site do not. Two captures both in the outer sites may, or may not, entail a movement over 100m. Since we wanted to test for a tendency not to move over 100m (rather than merely to stay within the outer sites), the few observed movements within the outer sites of over 100m were counted as between sites. This procedure makes the test for site fidelity at this scale conservative.

For this analysis data from outer sites over 1km from the core site were excluded. If an individual was caught twice on the same day or on the next day we ignored the second capture (so as to ignore very short-term site fidelity and in case trapping disrupted subsequent behaviour). If an individual was recaptured at more than one site within one winter, we counted only the further of these sites from the site of original capture. In the between-winter analysis, if an individual was caught in more than two

Table 2. Site fidelity within and between winters at Ginak, The Gambia. Details of the analysis are given in the text. ns indicates $P > 0.1$. The last column gives the P-value adjusted to correct for the number of tests performed (ignoring cases based on < 16 retraps in total). Index of site fidelity is not calculated if the expected number of within-site retraps was less than 9.

Species	*Initial captures at*		*Within or between winters*	*Observed retraps*		*Expected retraps within sites*	*Index of site fidelity*	*1-tailed P-value*	*P-value Bonferroni adjusted*
	core	*outer*		*total*	*within sites*				
Wryneck			within	5	2	3.1	—	ns	—
	7	5	between	2	0	1.0	—	ns	—
Nightingale			within	10	9	5.7	—	0.029	—
	12	16	between	5	2	2.3	—	ns	—
Redstart			within	45	38	26.0	1.4	0.0001	0.001
	153	106	between	17	10	9.0	1.1	ns	ns
Melodious			within	18	18	11.4	1.6	0.0003	0.003
Warbler	158	79	between	10	7	5.0	—	ns	—
Olivaceous			within	93	75	52	1.4	<0.0001	0.0001
Warbler	165	182	between	33	22	16	1.4	0.025	ns
Subalpine			within	130	111	68.9	1.6	<0.0001	<0.0001
Warbler	449	348	between	66	49	32.6	1.5	<0.0001	0.0004
Garden			within	28	23	22.5	1.0	ns	ns
Warbler	373	68	between	6	4	3.6	—	ns	—
Blackcap			within	66	42	41.0	1.0	ns	ns
	322	206	between	0	0	—	—	—	—
Whitethroat			within	200	157	104.0	1.5	<0.0001	<0.0001
	344	364	between	34	26	16.6	1.6	0.001	0.007
Orphean			within	39	31	20.8	1.5	0.0006	0.005
Warbler	49	51	between	14	10	6.8	—	0.074	—
Chiffchaff			within	18	13	10.2	1.3	ns	ns
	125	82	between	2	2	1.0	—	ns	—
Western		within	16	13	9.7	1.3	0.072	ns	
Bonelli's	49	51	between	4	0	1.7	—	ns	—
Warbler									

winters we discarded the information for all but the first two winters to avoid pseudoreplication. Likewise in the within-winter analysis, if an individual was recaptured within a winter in two different winters, we counted only the first winter. The analysis resulted in 23 P-values (Table 2), so there was a good chance that at least one P-value would show up as significant even with no site fidelity. Accordingly the sequential Bonferroni procedure was applied to the 14 P-

values which are based on a reasonable number of retraps (arbitrarily taken as > 16).

Site fidelity is not an all-or-nothing phenomenon. We have calculated an index of site fidelity as an estimate of the tendency for that species to remain within 100m. This is simply the observed number of birds recaptured within 100m divided by the expected number of within-site retraps generated by the null hypothesis. The conservative procedures described above will tend to lead to this index being an underestimate. Note that a high index need not be significantly different from 1 (random movement within the whole study area) if the sample size is low; so this index must be interpreted in conjunction with the *P*-values. For the same reason we have not calculated the index at all if the sample size was very small.

Length of stay

The above analysis of site fidelity within winters ignores how long a bird stays, as long as it stays for more than a day. But birds might feed up for only a few days and then move on. To examine this, Table 3 shows the distribution of intervals between an individual's first and last capture in a winter, including the longest such interval for each species (and when this commenced). Also shown is the proportion of birds caught that were retrapped more than a day after capture in that winter, and the proportion of these retrapped birds that were retrapped 14 or more days later.

One might hypothesise that the birds which remain at the site for a long time are those that have established a home range or territory, and thus that retraps of these individuals are more likely to be within 100m of first capture than are retraps of individuals present for a shorter period which might be exploring more widely. Table 3 shows the proportion of birds caught more than 100m from the site of first capture in a winter, calculated separately for birds retrapped over ≥14 days, and for those potentially present only more briefly. These proportions are compared statistically.

SPECIES DISCUSSIONS

Wryneck *Jynx torquilla*

Recurrence at Ginak was just significantly greater than the zero recurrence at Djoudj, although there were three recurrent birds at Djoudj from the earlier years excluded from our analysis. Retraps were too few to judge site fidelity within 100m, either between or within winters. Scebba & Lövei (1985) found considerable recurrence in winter in south Italy but some birds appeared not to spend the whole winter in their study area.

Nightingale *Luscinia megarhynchos*

Despite relatively small numbers caught, there are indications of site fidelity within a winter and a good proportion of birds stayed for over a month. The recurrence rate also seems quite high. Two individuals were ringed and retrapped only in a later spring, which could indicate passage birds.

Redstart *Phoenicurus phoenicurus*

Site fidelity was highly significant within each winter, but not between winters. The recurrence rate was moderate at Ginak but zero at Djoudj. Four of the 17 recurrent birds were ringed and retrapped only in spring, suggesting passage visits only. A good proportion of other individuals were, however, present over long periods within a winter.

Melodious Warbler *Hippolais polyglotta*

Judging from when most birds were ringed, this species was primarily an autumn passage migrant at Ginak, so it is unsurprising that only a small proportion of the total catch was ever retrapped again. However, some birds stayed for longer, and for birds retrapped within a winter the site fidelity was high and significant. Recurrence at Ginak was moderate; none were caught at Djoudj. In the Ivory Coast four out of 69 individuals were retrapped in a later winter (6%: Salewski *et al.* 2000).

Table 3. Length of stay and site fidelity. For birds caught twice or more within a winter, we have calculated the time interval between first and last catches that winter, and show the numbers of birds in each category. Shown separately are the longest interval between first and last captures of an individual within a winter (with date of its first capture in brackets), the percentage of birds trapped in a winter that were retrapped in the same winter, and the percentage of these staying ≥14 days. The last three columns test the hypothesis that the proportion of birds retrapped >100m apart is less in birds staying ≥14 days than in others: *P*-values are from a 1-tailed Fisher's exact test, and not Bonferroni corrected. Individuals retrapped only the same day or the day following the first capture, are not counted as retrapped. Individuals caught in more than one winter contribute to the figures more than once.

	Duration (days)					*Longest residence (days) and start date*	*% of trapped birds retrapped in same winter*	*% of retraps trapped ≥14 days*	*% of retraps moving > 100m*		*1-tailed P-value*
	2-13	*14-27*	*28-41*	*42-83*	*≥84*				*<14 days*	*≥14 days*	
Wryneck	2	1	1	1	0	72(20/11)	33	60	0	100	ns
Nightingale	4	0	1	3	2	118(20/11)	29	60	0	20	ns
Redstart	16	10	3	8	8	131(23/10)	16	64	6	21	ns
Melodious Warbler	10	2	1	5	3	103 (22/10)	8	52	0	0	ns
Olivaceous Warbler	27	10	11	27	25	149 (02/11)	26	73	19	23	ns
Subalpine Warbler	39	24	18	30	26	156(08/10)	16	72	26	9	0.034
Blackcap	37	11	6	10	2	96(24/11)	13	44	24	52	ns
Garden Warbler	20	6	2	1	0	52(14/10)	4	31	25	11	ns
Whitethroat	85	52	26	27	12	134(21/10)	45	58	19	32	ns
Orphean Warbler	15	5	5	12	4	108(04/12)	35	63	20	42	ns
Chiffchaff	8	6	2	2	0	65(20/11)	9	56	25	30	ns
Western Bonelli's Warbler	9	0	1	5	1	120(30/11)	14	44	11	29	ns

Olivaceous Warbler *Hippolais pallida*

A high proportion of retrapped birds stayed much of the winter, and site fidelity was highly significant within winters, but only marginally so between winters. Nevertheless the recurrence rate was high at both Ginak and Djoudj. A sizeable minority of birds (≥16%) were of the subspecies *reiseri*.

Subalpine Warbler *Sylvia cantillans*

At Djoudj during one season there was no interchange between two sites only 400m apart, admittedly separated by almost bare desert. At Ginak the habitat between the ringing sites is continuous, yet site fidelity was still high and highly significant both within and between winters. There was a fairly high recurrence rate at Ginak, as at Djoudj. One bird at Djoudj was recorded at the same site for five winters, and at Ginak two birds were retrapped at the same sites for four successive winters.

Garden Warbler *Sylvia borin*

Site fidelity was not well tested in this species because a low proportion of catches were away from the core site. At Ginak there was a large autumn movement with only very small numbers in spring and almost none in winter. Thus only 4% of birds caught were retrapped in the same winter and few of these had stayed for long (although three for over four weeks). In 1994-95, when coverage in October and November was lacking, only nine birds were caught. Furthermore, all six recurring birds were ringed and retrapped in autumn. So we suggest that Garden Warblers return by a different route in spring. Recurrence rate was very low at Ginak and zero at Djoudj. In a study in Uganda, there was evidence of some birds remaining in the same area over winter, but the proportion of birds retrapped over 20 days or more only became high when the many birds on autumn passage were excluded (Pearson 1972). In a study in Zaire the recurrence of three individuals suggested a higher recurrence rate there (De Bont *et al.* 1965), and recurrence was also high in Malawi (9%: Peach *et al.* 2001).

Blackcap *Sylvia atricapilla*

This species is a special case. Very few were captured in most winters and, of the 528 birds ringed, the bulk occurred in 1995-96 when there seemed to be an "invasion". Most of these were caught in December at one site 800m to the east that was selected because Blackcaps were there feeding around fruiting fig trees. They seemed to remain all winter but wandered around, some moving 1.5km (the furthest distance between trapping sites). Some birds were retrapped a considerable time apart in the same winter, but site fidelity within a season was not significant, and recurrence was zero. In Spain, Cuadrado *et al.* (1995) conclude that Blackcaps show fidelity but that this fidelity may be to "the same great core area" within which they search out ephemeral food sources. This is compatible with our results. Furthermore, Blackcap numbers in West Africa generally fluctuate (Cramp 1992). No Blackcaps were caught at Djoudj.

Whitethroat *Sylvia communis*

Site fidelity was highly significant within each winter and marginally significant between winters. A relatively high proportion of birds caught in January was retrapped in the same winter, many a considerable time later, and a few even overwintered from November. These are somewhat surprising results since the great majority of Whitethroats at Ginak appeared in spring, presumably on passage. Recurrence at Ginak was moderate and higher than at Djoudj. Some individuals returned to Ginak after two years or even three. In late spring, five of the eastern subspecies *icterops* were caught; one was retrapped two days later at the same site, and one two years later, also at its original site.

Orphean Warbler *Sylvia hortensis*

Site fidelity was significant within each winter but non-significant between winters. A relatively high proportion of birds caught were retrapped in the same winter, often a considerable time later. Recurrence was high at Ginak but very low at Djoudj. They were certainly wintering at Ginak but probably not at Djoudj.

Chiffchaff *Phylloscopus collybita*

The rate of within-winter retrapping was rather low at Ginak, and site fidelity was not significant within or between winters. Only two birds recurred in a later winter, making recurrence very low at Ginak, and significantly lower than the moderate level at Djoudj. At Djoudj on two pools 400m apart, the large majority of subsequent-winter retraps were at the same site, a few moved between the pools, and some were retrapped up to 2.2km away. Nomadism was also shown there by records of colour-ringed birds (Sauvage *et al.* 1998). The lower retrap rate at Ginak could be attributable to the habitat: most sites at Djoudj were in relatively low bushes with few trees, whereas there are considerable numbers of tall acacias at Ginak which Chiffchaffs favoured, especially in the dry season when these were in leaf. It was difficult to net at a suitable height, so at Ginak a lower proportion of recurring birds might have been retrapped.

Western Bonelli's Warbler *Phylloscopus bonelli*

The remarks about Chiffchaffs feeding in acacias apply equally to Western Bonelli's Warblers, and may again have led to low numbers retrapped. Site fidelity was not significant either within or between winters. There was a low recurrence rate at Ginak but numbers at Djoudj were too low to estimate this there.

GENERAL DISCUSSION

For 10 species we have data on more than 16 retraps within a season (Table 2). In all of these 10 species the within-season index of site fidelity is above 1 (suggesting some site fidelity), and in six of these cases this is statistically significant (even after the Bonferroni adjustment). In 11 species, over 44% of retrapped individuals remained for 14 days or longer, and some individuals were retrapped at the same site at least two months apart (Table 3). Within-winter site fidelity would thus seem to be not unusual. Sinclair (1978) suggested that, since in West Africa migrants overlap with residents during the dry season and must therefore be competing, perhaps the migrants are nomadic. Our results contradict this theory.

Most of the species treated here also recurred regularly at Ginak, implying that they were faithful at least to the larger area between winters (Table 1). The prominent exceptions were Blackcap, Garden Warbler, Chiffchaff and Willow Warbler. For only four species did we have data on more than 16 between-winter retraps at Ginak. In three of these species there was significant site fidelity at a more local scale also, and in two cases this remained significant even after Bonferroni adjustment (Table 2). Between-winter site fidelity to a small area may well occur in a wider range of species, but more data needs to be gathered to decide this. One striking pattern not considered by the preceding statistics is that individuals that were retrapped in a second winter only within 100m of the original capture, were also always trapped within 100m if retrapped again in a subsequent winter (26 individuals).

Opposite to our expectation from trapping effort, the rate of recurrence was significantly higher at Ginak than at Djoudj in four species (two after Bonferroni correction), probably owing to a higher proportion of passage birds at Djoudj. This is compatible with it lying further north. The opposite pattern was significant in Chiffchaff but we discuss above why this might have been caused by the height of the vegetation making mist netting inefficient at Ginak.

However, some circumspection is due in interpreting these differences between study areas, because there was significant variation in recurrence between winters at Ginak ($F_{3,30} = 3.91$, $P = 0.018$, based on log-transformed recurrences for each species for each winter). Numbers are too small to show this in individual species, but in nine out of 11 species recurrence was highest in 1995-96. The probable reason is that in the preceding winter ringing was carried out over a shorter period. This is likely to have resulted in a lower proportion of birds being caught that were just passing through compared with those that were site faithful within the winter, and it is the latter that seem likely to recur the following winter. Variation in survival between winters is also a possible explanation. There was no indication of variation in recurrence between winters at Djoudj (only the three winters with high effort were analysed).

We hypothesised that birds that stayed for longer during a winter might be those that have set up territories and thus consist of a higher proportion of site-faithful birds (ie trapped only within 100m) than those present more briefly. In only one species was the predicted effect statistically significant (Table 3), and this no more so than one would expect by chance given the number of species considered. In fact most species showed the opposite trend. Maybe birds present for a long time shift their home ranges. But the effect could just be the result of longer staying birds being caught more often, with a higher chance therefore of being caught at least once away from their usual home range.

This study has added to a number of ringing projects across sub-Saharan Africa that have established that a range of Palaearctic migrants remain in a local patch for much of the winter and recur there in subsequent winters (see our introduction). Much remains to be discovered even about species where such fidelity has been demonstrated, because site fidelity may vary from place to place. Even within a locality it may often be the case that only a proportion of the population is site faithful, whereas the rest is nomadic or on passage, with these proportions changing with time of year. Which strategy a bird follows may depend on its age, sex or summer breeding area. To fully elucidate these patterns will require colour ringing studies, where the higher rate of resighting gives better information on the duration of stay and the extent of movement (eg Staicer 1992). These will also answer whether these overwintering migrants ever attempt to defend exclusive territories.

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APPENDIX

We wish to calculate the number of retraps expected at the same site (core or outer) and at different sites. Each species is analysed separately. Consider first the within-winter analysis, and suppose that in Winter 1 a_1 birds were caught first at the core site, b_1 birds caught first at the outer sites, and that the total number of same-winter retraps was r_{11}. Under the null hypothesis we expect that the probability of being retrapped at one site rather than another is the same as that of being trapped there initially, and that it is independent of where that particular individual was first trapped. The probability that a trapping will be at the core site that winter is therefore taken as $a_1/(a_1+b_1)$ and at the outer sites $b_1/(a_1+b_1)$. For an individual caught twice, the probability of being caught both times at the core site is therefore $(a_1/(a_1+b_1))^2$, and of being caught both times at the outer site $(b_1/(a_1+b_1))^2$. Therefore the expected number of retraps at the same site is $r_{11}(a_1^2+b_1^2)/(a_1+b_1)^2$; the expected number of retraps at different sites is r_{11} minus this figure. These expected totals of within-winter retraps were calculated for all five winters individually and then summed. From this sum we calculated the overall proportion of within-winter retraps expected to occur at the same site. This proportion was used in a one-tailed binomial test which calculated the probability of the observed total number of same-site within-winter retraps, or more, occurring by chance if the null hypothesis were true.

For the between-winter analysis, suppose that in Winter 2 a_2 birds were caught the first time that winter at the core site, b_2 birds caught the first time that winter at the outer sites, and r_{12} birds retrapped that had first been caught in Winter 1. Of these r_{12} retraps we expect $r_{12}(a_1a_2+b_1b_2)/((a_1+b_1)(a_2+b_2))$ to have been caught in both winters at the same site. The same calculation has to be made for all possible pairs of winters and these expected numbers summed. The overall proportion calculated from the sums is used in a binomial test in the same way as before.