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Fidelity to non-breeding site in some species of birds in Senegal

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The authors report the results of observations and experiments on the site fidelity, home range and homing success in some species of birds captured and banded at the ORSTOM Ornithological Station of Mbour (Senegal) during the non-breeding season (November-December 1988 and 1989).

While some bird species range over a wide area or are found in our study area only during migratory movements, most of the species investigated, which include both local birds and palaearctic migrants, display a tendency to spend the winter in a home plot of very limited size.

In addition, homing experiments were carried out by displacing and releasing the birds at sites 5 km from the capture station. Globally, our results are in agreement with the reports on similar investigations in the Mediterranean area: among the species investigated, strong site fidelity, as revealed by high recapture percentages in non-displaced birds, does not necessarily lead to good homing performances after passive displacement. On the whole, the commonest species of small birds which spend the winter in our study plot show different kinds of relationship between individual birds and their habitat with respect to home range, site attachment and homing success.

KEY WORDS: site fidelity, home range, homing, birds, Senegal.

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INTRODUCTION

During the last few decades, evidence has been accumulating that the attachment shown by birds to their native/breeding site (Löhrl 1959, Serventy 1967, Schuz 1971, Bellrose 1972, Berndt & Winkel 1979) is also devoted to their wintering ground. This winter site fidelity has been demonstrated either by the frequent recaptures of wintering individuals in the original ringing area or by the homing ability usually observed after birds have been experimentally displaced from their wintering home site (references in Matthews 1968, Benvenuti & Ioalè 1980a, Ioalè & Benvenuti 1983, Baillon & Benvenuti 1990, Ketterson & Nolan 1990). This site attachment has also been documented in migratory birds which return to the same wintering site year after year, and is apparently pertinent even to their migratory pathway and to a series of places along the way where single individuals stop during their migratory flights (for examples and references see Schuz 1971; Ralph & Mewaldt 1975, 1976; Wiltschko & Wiltschko 1978; Benvenuti & Ioalè 1980b; Ioalè et al. 1988; Ketterson & Nolan 1990).

The literature on this subject is fragmentary and, to make a contribution of a new type, we carried out observations and experiments on the site attachment and homing behaviour of some species of birds captured in the non-breeding season in a study area within the Ornithological Station of Mbour, Senegal. Our investigation, which is an extension of preliminary studies performed by Baillon & Benvenuti (1990) in the same area, is limited by several factors, especially the small sample size. Despite these limits, we wish to make the present contribution available, since very few comparable data have been reported in the literature.

MATERIALS AND METHODS

Study area and capture methods. Our study area was within the ORSTOM Center (Observatoire geophysique, Station d'Ornithologie et de Mammalogie), 2 km SE of Mbour in Senegal (14°23'N, 16°58'W). The vegetation in the capture area, which is not far from the sea coast (Fig. 1), is mainly a savannah with sparse trees and bushes.

Our data were mainly collected in November and December of 2 successive years (from November 14th to December 5th, 1988 and from November 21st to December 14th, 1989). In these periods birds were banded and subjected to passive displacements; additional captures were carried out between January 10th and February 24th, 1989 (11 days of capture) and between January 16th and April 5th, 1990 (22 days). During these additional capture-sessions data on trapped birds only were recorded, while neither banding activity nor other experimental manipulations were performed.

The birds were trapped in mistnets 15 m long and 3 m high, which were set up from sunrise to late afternoon, with a 3 hr interruption around noon, in six «capture stations» (see Fig. 1). In each station there were 7 to 13 preselected sites in which nets were placed (not every day and not all simultaneously). As each mistnet is divided into four horizontal capture shelves, it was possible to estimate the approximate height at which birds were flying when they were trapped. The trapped birds were banded for individual identification with the rings supplied by the Centre de Recherches sur la Biologie des Populations d'Oiseaux (Muséum National d'Histoire Naturelle, Paris, France)

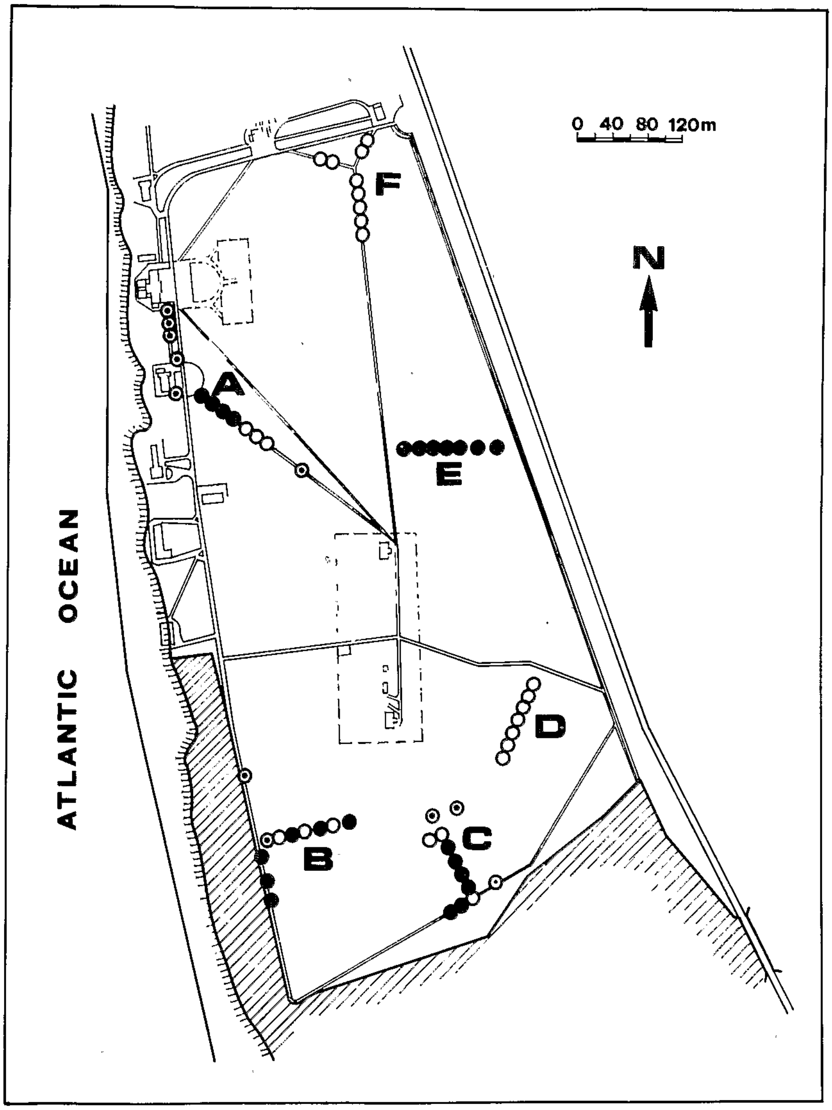

Fig. 1. — Map of the study area, 2 km SE of Mbour in Senegal. The buildings are offices, laboratories and staff residences of the ORSTOM Observatoire geophysique, Station d'Ornithologie et de Mammalogie. The areas A, B, C, D, E, and F indicate the six capture stations where mistnets (7 to 9, 15 m long and 3 m high) were placed. The nets were not operating every day and no more than two stations were used simultaneously. Symbols show the site where mistnets were routinely set up in the six capture stations: dotted, open and solid circles refer to nets used in 1988, 1989 and in both years, respectively.

and checked for wing length and body weight. We recorded the sex of birds in species with conspicuous sexual dimorphism, but we made no attempt to distinguish between young and adult individuals.

Release experiments. Some of the banded birds were released at the capture site. Each of the remaining birds was placed in a separate cloth bag and carried by car, within a few hours of their capture, to one of the two release sites at 5 km NNW and SE. We did not record the vanishing bearings of the released birds because nearly all of them landed on nearby trees or bushes soon after being tossed. The only two bird species which produced useful vanishing bearings at release were the Black-billed Wood dove (*Turtur abyssinicus*) and the Laughing dove (*Streptopelia senegalensis*); the orientational performances of these birds are the topic of a separate paper (BENVENUTI et al. 1991), so they have not been reported here. Homing ability was taken to be demonstrated by the recapture of displaced birds in the original trapping area. As regards the recapture distance, we have considered the distance between the median points of the two nets in which each single bird was captured and subsequently recaptured (for birds trapped twice in the same net, the recapture distance was considered to be zero). These methods are much the same as those used in previous similar experiments in the same area (BAILLON & BENVENUTI 1990) and in the Mediterranean region (BENVENUTI & IOALÈ 1980a, 1980b, 1983; IOALÈ & BENVENUTI 1982, 1983).

Statistical methods. The χ^2 or the Fisher exact test, depending on the sample size, has been used to compare the number of recaptures, in different sets of two species, with respect to the total number of released birds. Differences between species in the vertical distribution of capture pattern have been tested using the Mann-Whitney U test (SIEGEL 1956).

RESULTS

General trapping patterns. Apparently, the capture season in autumn 1988 was more successful than in 1989 (Fig. 2); if we consider the number of birds trapped in 1000 m of mistnets per hour, the outcome is that in 1989 we have lower figures in 10 species out of 12 (excluding *Pogoniulus chrysoconus* because the 1988 data are equal to those for 1989); this result differs from random: Binomial test, $P<0.02$. The extremely poor trapping rate in 1989 forced us to double the efficiency of our capture methods in terms of number of capture stations and mistnets set up in the time unit.

As regards data on the height at which birds were trapped, Fig. 3 shows the pattern of vertical distribution. It can be observed that the results relative to *Sylvia borin* and *Uraeginthus bengalus* differ drastically from each other (Mann-Whitney U test: $P<0.0001$), the former being trapped at a higher mean level than the latter. The vertical distributions of these two species, moreover, differ significantly from all the others ($P<0.0001$ or $P<0.001$ in most comparisons). As regards the patterns of the other species, they look quite similar to each other: the Mann-Whitney U test reveals that significant results, often at marginal levels ($P<0.05$), are obtained in a minority of the available comparisons.

Site fidelity and homing ability. Table 1 gives a list of the species used in our experiments, and the recapture data of displaced and non-displaced birds (1988 and 1989 data have been pooled): species with less than 10 banded individuals were not considered. The recapture percentages of non-displaced birds, taken here as a measure of attachment to the home site, range between 0.0 (various species) and 61.5 (*Pogoniulus chrysoconus*). For the latter species and for *Prinia subflava* and *Camaroptera brachyura*, we recorded the highest values for recapture percentages (over 40%); the

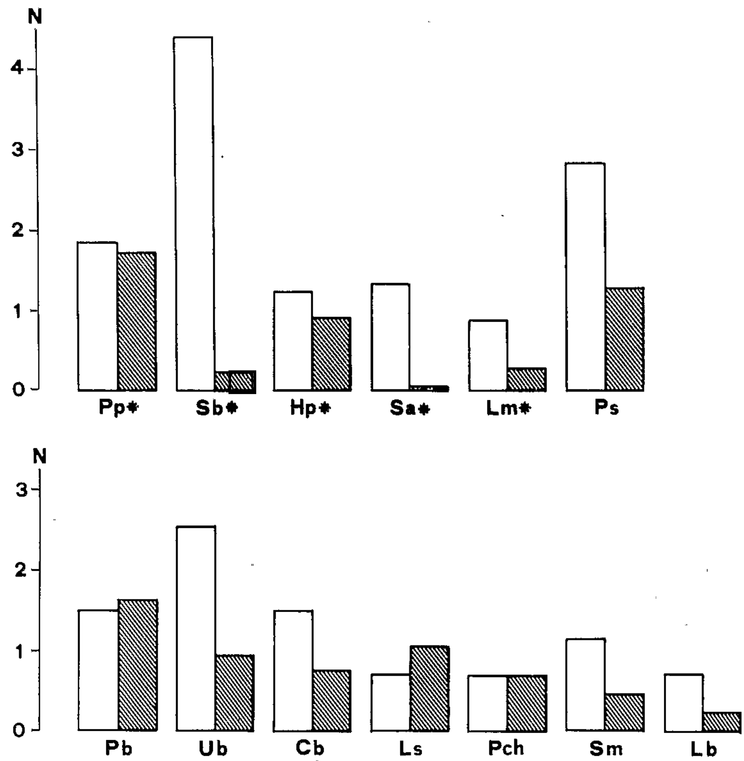

Fig. 2. — For each species the height of each bar is proportional to the mean number of birds captured in 1000 m of mistnets per hour. Open and shaded bars refer to the 1988 and 1989 data. The names of the species are abbreviated as follows: Pp = *Phoenicurus phoenicurus*, Sb = *Sylvia borin*, Hp = *Hippolais pallida*, Sa = *Sylvia atricapilla*, Lm = *Luscinia megarhynchos*, Ps = *Prinia subflava*, Pb = *Pycnonotus barbatus*, Ub = *Uraeginthus bengalus*, Cb = *Camaroptera brachyura*, Ls = *Lagonostica senegala*, Pch = *Pogoniulus chrysoconus*, Sm = *Serinus mozambicus*, Lb = *Laniarius barbarus*. *Ploceus cucullatus* and *P. melanocephalus* (abbreviated as Pcu and Pm in Table 2 and Fig. 5) have not been included because we banded these species in 1988 but not in 1989. Palaearctic migrants are marked by asterisks.

comparison between each of these species and all of the others leads to statistical significance in many cases (see Table 2A).

In birds displaced at 5 km from our study plot, the recapture percentages range between 0.0 (*Sylvia borin*) and 54.5 (*Pogoniulus chrysoconus*). The latter species show remarkable homing success, significantly better than that recorded in all the others, with the exception of *Phoenicurus phoenicurus* (Table 2B). In all the species investigated the recapture percentage of displaced birds is lower than that of birds which have been released at the capture site; this difference, however, reaches the level of statistical significance in two cases only: *Prinia subflava*, $\chi^2 = 8.72$, $P<0.01$, and *Camaroptera brachyura*, Fisher exact test, $P<0.02$. Homing success does not seem to

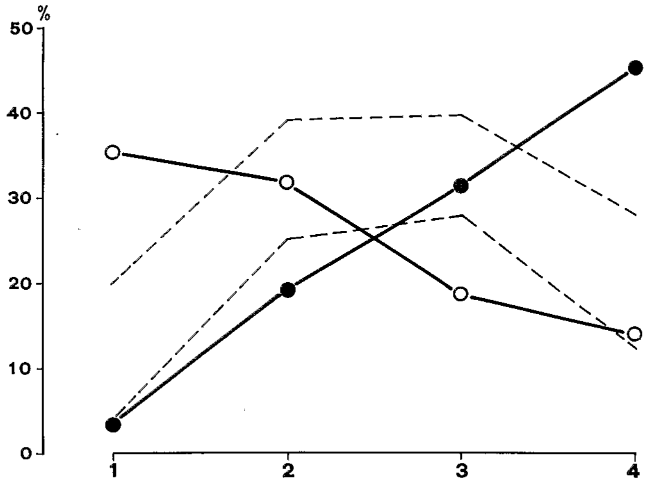

Fig. 3. — Vertical distribution of the trapped birds. Only those species for which 50 or more data (including winter captures) were available, have been considered. The figure shows the percentage (ordinates) of birds trapped in the four capture shelves (abscissae) at different height above the ground level: 1 to 4 = 50, 125, 200 and 275 cm (height of the centres of the four shelves), respectively. Solid and open symbols refer to *Sylvia borin* and *Uraeginthus bengalus*, respectively. All the other species (*Phoenicurus phoenicurus*, *Hippolais pallida*, *Ploceus cucullatus*, *P. melanocephalus*, *Camaroptera brachyura*, *Prinia subflava*, *Pogoniulus chrysoconus*, *Pycnonotus barbatus*), exhibit similar patterns of vertical distribution, which are included in the area between the two dashed lines.

Table 1.
Number of released birds and recapture data.

m/l	Species	N	Rh	Hh	(%)	Rd	Hd	(%)
1 m	*Phoenicurus phoenicurus* (Linnaeus 1758)	60	32	10	(31.3)	28	5	(17.9)
2 m	*Sylvia borin* (Boddaert 1783)	55	35	2	(5.7)	20	0	(0.0)
3 m	*Hippolais pallida* (Hemprick & Ehrenberg 1833)	34	18	3	(16.7)	16	1	(6.3)
4 m	*Sylvia atricapilla* (Linnaeus 1758)	16	16	0	(0.0)	—	—	—
5 m	*Luscinia megarhynchos* (Brehem 1831)	14	14	4	(28.6)	—	—	—
6 l	*Ploceus melanocephalus* (Linnaeus 1758)	195	104	11	(10.6)	91	3	(3.3)
7 l	*Prinia subflava* (Gmelin 1789)	55	29	12	(41.4)	26	1	(3.8)
8 l	*Pycnonotus barbatus* (Desfontaine 1789)	54	34	10	(29.4)	20	1	(5.0)
9 l	*Uraeginthus bengalus* (Linnaeus 1776)	50	24	4	(16.7)	26	1	(3.8)
10 l	*Camaroptera brachyura* (Vieillot 1820)	39	24	11	(45.8)	15	1	(6.7)
11 l	*Lagonostica senegala* (Linnaeus 1776)	28	28	0	(0.0)	0	—	—
12 l	*Pogoniulus chrysoconus* (Temminck 1832)	24	13	8	(61.5)	11	6	(54.5)
13 l	*Serinus mozambicus* (Müller 1776)	23	23	0	(0.0)	0	—	—
14 l	*Laniarius barbarus* (Linnaeus 1776)	13	13	2	(15.4)	0	—	—
15 l	*Ploceus cucullatus* (Müller 1776)	11	11	0	(0.0)	0	—	—

m/l = palaearctic migrant or local (tropical) species, respectively. N = number of birds released for each given species. Rh and Rd = birds released at the capture site (home) and 5 km from home, respectively; Hh(%) = recaptured birds among those released at home and related recapture percentage; Hd(%) = recaptured birds among those released 5 km from the home site and related recapture percentage.

Table 2.
Site fidelity (A) and homing ability (B): levels of statistical significance.

A: Site fidelity

	Pp	Sb	Hp	Sa	Lm	Pm	Ps	Pb	Ub	Cb	Ls	Pch	Sm	Lb
Sb	.02													
Hp	—	—												
Sa	.05	—	—											
Lm	—	—	—	.05										
Pm	.02	—	—	—	—									
Ps	—	.01	—	.01	—	.001								
Pb	—	.05	—	.05	—	.02	—							
Ub	—	—	—	—	—	—	—	—						
Cb	—	.001	—	.01	—	.001	—	—	—					
Ls	.01	—	—	—	.02	—	.001	.01	—	.001				
Pch	—	.001	—	.001	—	.001	—	—	.02	—	.001			
Sm	.01	—	—	—	.05	—	.01	.02	—	.001	—	.001		
Lb	—	—	—	—	—	—	—	—	—	—	—	.05	—	
Pcu	—	—	—	—	—	—	.05	—	—	.01	—	.01	—	—

B: Homing ability

	Pp	Sb	Hp	Pm	Ps	Pb	Ub	Cb
Sb	—							
Hp	—	—						
Pm	.05	—	—					
Ps	—	—	—	—				
Pb	—	—	—	—	—			
Ub	—	—	—	—	—	—		
Cb	—	—	—	—	—	—	—	
Pch	—	.01	.01	.001	.01	.01	.01	.02

A. Site fidelity, expressed by the number of recaptures with respect to the total number of non-displaced birds, has been compared between species using the χ^2 or the Fisher exact test (depending on the sample size), whose level of statistical significance is given (— = not significant). Abbreviations as in Fig. 2. B. Analogous values are given in B for homing success, expressed by the number of recaptures with respect to the total number of displaced individuals.

be related to site fidelity: it is worth noting, for example, that while *Camaroptera brachyura* and *Pogoniulus crysoconus* exhibit a similar strength of attachment to their home site, indicated by a comparable level of recapture percentages both in non-displaced birds and in birds retrapped 1 year after the first capture, there is a noticeable difference between these species in the homing performance of displaced birds (Fisher exact test, $P<0.02$) (Fig. 4).

In most species considered in our study, individuals show a tendency to stay in the area for quite a long time, as indicated by the recapture intervals reported in Fig. 5. Some species, however, are present in our study plot for a short period during the autumn, whereas they are absent or very rarely found during the winter (*Sylvia borin*, *S. atricapilla*, *Serinus mozambicus*).

Table 3 gives data on birds which were retrapped 1 year after their first capture; the recapture percentage varies between 0.0 (five species) and 37.5 (*Pogoniulus chrysoconus*).

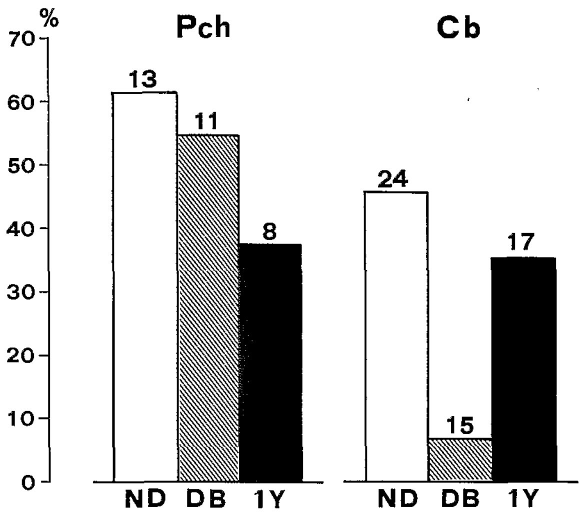

Fig. 4. — The height of the bars is proportional to the recapture percentages in non-displaced birds (ND), in birds displaced at 5 km from the capture site (DB), and in birds banded in 1988 and retrapped 1 year later (1Y). The numbers on top of each bar indicate the sample size. The left-hand set of bars refers to *Pogoniulus chrysoconus* (Pch), and the right-hand set of bars to *Camaroptera brachyura* (Cb).

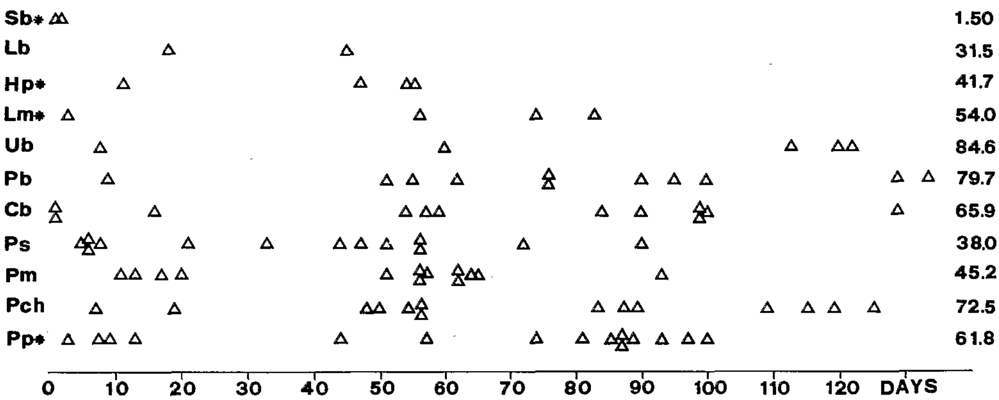

Fig. 5. — Recapture intervals in 11 species of birds. Birds banded in the 1988 capture season and retrapped 1 year later have not been included. Each symbol, for each species, indicates the length of the interval between the first and the last capture of a single bird. In the right margin, the mean recapture interval is indicated for each species. The names of the species have been abbreviated (left margin) as in Fig. 2.

Table 3.
Data on birds banded in autumn 1988 and retrapped in autumn/winter 1989.

m/l	Species	N	n	%
1 m	*Sylvia borin*	50	0	0.0
2 m	*Phoenicurus phoenicurus*	21	1	4.8
3 m	*Sylvia atricapilla*	15	0	0.0
4 m	*Hippolais pallida*	14	1	7.1
5 m	*Luscinia megarhynchos*	10	1	10.0
6 l	*Ploceus melanocephalus*	195	15	7.7
7 l	*Prinia subflava*	32	4	12.5
8 l	*Uraeginthus bengalus*	29	1	3.4
9 l	*Camaroptera brachyura*	17	6	35.3
10 l	*Pycnonotus barbatus*	17	3	17.6
11 l	*Serinus mozambicus*	13	1	7.7
12 l	*Ploceus cucullatus*	11	0	0.0
13 l	*Laniarius barbarus*	8	0	0.0
14 l	*Lagonostica senegala*	8	0	0.0
15 l	*Pogoniulus chrysoconus*	8	3	37.5

N and n = number of birds banded in autumn 1988 and retrapped in the following wintering season; the related recapture percentage (%) is also given. Only species in which a minimum of seven individuals were banded have been taken into account. Other explanations as in Table 1.

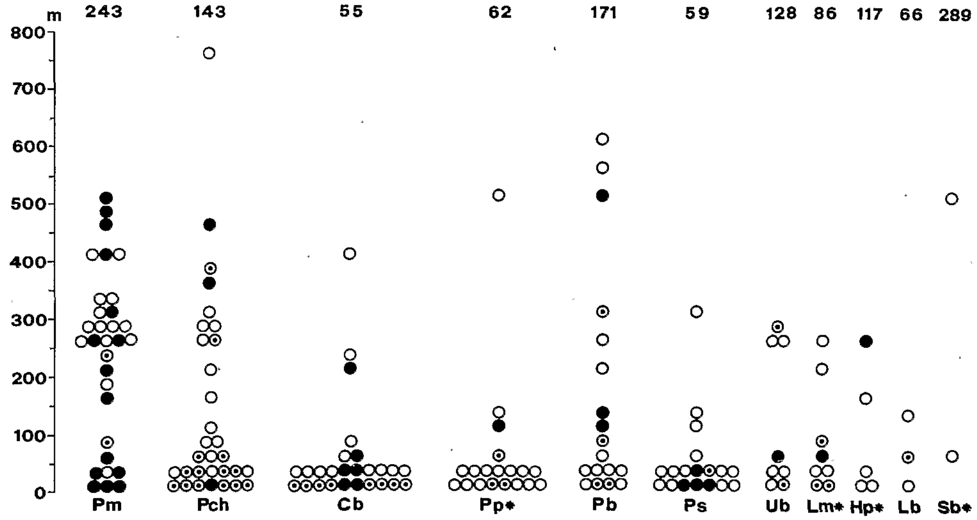

Fig. 6. — Recapture distance in 11 species of birds, the same included in Fig. 5. For each species and for each individual bird the symbols indicate the distance between the capture and recapture sites. Open symbols refer to birds which have been retrapped only once within each wintering season, dotted symbols to birds which have been retrapped twice or more times, so indicating the second or subsequent recapture; solid symbols refer to birds banded in autumn 1988 and retrapped during the wintering season of the subsequent year. For each species the mean capture distance is given. The abbreviations indicate the species according to the explanations given in Fig. 2.

Home range. Recapture distances, which are certainly related to the home range, are given in Fig. 6. With the exception of *Ploceus melanocephalus*, for which most recaptures were carried out at distances greater than 200 m from the former capture site, the recapture distances are quite small. In fact, 83 out of 138 birds (60.1%) were recaptured within 50 m of the former capture site. Palaearctic migrants yielded figures consistent with the global result: 22 birds out of 34 (64.7%) were retrapped within 50 m of their former capture site. Many birds, both local and migrant species, show a year-to-year attachment to the same winter home, as testified by the fact that many recaptures 1 year after the former capture occur within a limited area: excluding *Ploceus melanocephalus*, 9 out 20 birds (45%) were retrapped within 50 m from their former capture site [12 out of 20 (60%) within 100 m].

DISCUSSION

The site attachment of birds to the non-breeding home ground has not received as much attention as that devoted to the study of the breeding site. Our experimental plan aimed to contribute to the knowledge of home range and site fidelity in non-breeding birds. Five out of the 15 species considered in our study are palaearctic migrants wintering in tropical areas; in these cases, therefore, the wintering site is spatially distant from the breeding ground. The tropical resident birds, on the other hand, may be attached to the breeding territory even in non-breeding periods. For these species, moreover, it is not easy to define the limits between the breeding and non-breeding season; our observations, however, indicate that the tropical species included in Table 1 are not involved in widespread breeding activities in the period in which our experiments were carried out.

It is not clear why the trapping rate was higher in 1988 than in 1989. It is true that we started 1 week later in 1989 than in the previous year and this delay may have influenced the capture rate of migratory birds, if we suppose that migration peaks in our area earlier than either of the two starting dates. A delay of 1 week, however, cannot influence the capture rate of local birds, which should have been affected by other factors, including the possibility that in 1989 food availability was poorer than in 1988; this consideration derives from the impression that in 1988 insects were more plentiful than in 1989. Anyhow, the ecological features of our study area seems to be favourable not only to several species of local birds, but also to palaearctic breeders; the extensive literature on African-Palaearctic migrants indicates that birds are almost exclusively confined to savannah and scrub habitats during their overwintering in the tropics (Moreau 1972, Leisler 1990).

As regards data on the vertical distribution of the trapped birds, the significant presence of *Uraeginthus bengalus* in the lower capture shelves can easily be explained by this species' preference for spots of ground free of vegetation (like those we have used for setting the nets), where these birds have often been observed to feed. Conversely, the Garden warbler (*Sylvia borin*) reveals a strong preference for higher levels. As our study aimed to compare site fidelity and homing ability among the various species of birds, our experimental plan was certainly not appropriate to the investigation of foraging strategies and vertical segregation; we therefore consider this as a marginal aspect of our results, which does not require further exploration.

Proceeding now to our main results, it should be noted that not all the species investigated by us winter in our study plot. The Garden warbler, for example, winters at lower latitudes and is present in our area for short periods only during migratory movements (MOREAU 1972). In fact, we did not trap Garden warblers during the winter but only in November-December, recording a very low recapture percentage and short recapture intervals. MOREAU (1972) reports that the Blackcap (*Sylvia atricapilla*) winters at the latidude of our area, but we have no recaptures for this species and this result, in conjunction with the fact that the captures of unbanded individuals are quite rare in winter (one individual), indicates that our study plot is not a favourable area for wintering blackcaps. This conclusion also seems to fit the field data recorded for *Serinus mozambicus*, an African species for which captures and recaptures parallel those recorded in the Blackcap.

A second group of investigated species is actually resident in our area, but individual birds are not attached to a small home site and range over a wide area. In species adopting this strategy we expect low recapture percentages (individual birds range over a wide area and there is a small probability of trapping them twice), long recapture intervals (the population is present in the area during the whole trapping season) and long recapture distances. *Ploceus melanocephalus* fits this set of features. We may suppose that *Ploceus cucullatus* and *Lagonostica senegala* have similar strategies, but the small sample sizes call for further collection of field data. This result is consistent with those obtained by BENVENUTI et al. (1990) in similar investigations carried out on some species of granivorous Passerines wintering in the Mediterranean area.

A third group of species, which includes both palaearctic migrants (*Phoenicurus phoenicurus*, *Hippolais pallida* and *Luscinia megarhynchos*) and local birds (*Prinia subflava*, *Pycnonotus barbatus*, *Uraeginthus bengalus*, *Camaroptera brachyura*, *Pogoniulus chrysoconus* and *Laniarius barbarus*), proves to be attached to a home site of limited extent, as shown by relatively high recapture percentages, small recapture distances and long mean intervals between the first and last capture, indicating that birds of these species reside in the area permanently or for a long time during the winter. The recapture percentages in species belonging to this group range between 15.4 (*Laniarius barbarus*) and 61.5 (*Pogoniulus chrysoconus*), and it is questionable whether this variability really matches differences in strength of site fidelity between species. This variability may in fact be due to small sample sizes and to other factors, including the possibility that it reflects different proportions of adults and sub-adults in different species: young birds may have not yet fully developed an attachment to a home site (see BENVENUTI & IOALÈ 1983, IOALÈ & BENVENUTI 1983). Moreover, we have to consider that we are dealing with both migratory and resident species and an unknown proportion of banded birds may have been trapped during a short stay in our area in the course of migration or dispersal movements, so influencing the variability in the recapture percentages among the species.

Moving on to the homing success of birds subjected to displacement experiments, it is not surprising that no Garden warblers, which do not winter in the study area, were retrapped after passive displacement. As regards the other species, we obtained variable results, and this variability can be explained by the same factors considered in the discussion of the recapture percentages of non-displaced birds. In addition, different species may differ with respect to levels of navigational ability and/or motivation to reach home; these factors could account for the significant difference in homing performance between *Pogoniulus chrysoconus* and most of the other species, in spite of the fact that in some of the latter we recorded comparable levels of attachment to their home ground. This result is in agreement with that reported by BENVENUTI & IOALÈ (1980a, 1980b) and by IOALÈ and BENVENUTI (1983) in similar investigations in the Mediterranean area: strong home fidelity (revealed by high recapture percentages in non-displaced birds) does not necessarily lead to good homing performances after an experimental displacement.

Lastly, it may be no coincidence that in *Camaroptera brachyura* and *Prinia subflava*, the two species in which we observed the highest reduction of the recapture percentage after displacement compared with non-displaced birds, are both local species which range in a small home site (the smallest sites among the species considered in our study). We suppose that the homing success of birds which are familiar with a plot of very limited area is more likely to be affected by a short-distance displacement.

In most of the investigated species individual birds show a tendency to spend the non-breeding season in a small home site, as testified by higher recapture percentages, small recapture distances and long mean intervals between the first and last capture. The home site may be the same year after year, as indicated by the fact that recapture distances within the season do not differ significantly from those recorded in birds captured 1 year later.

In conclusion, our results show that the commonest species of birds which can be trapped in our study area (15 species, mostly Passerines, which include both local birds and palaearctic migrants) exhibit different kinds of relationship between individual birds and their habitat, with reference to their home range, site fidelity and homing success outside the breeding season.

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