SITE FIDELITY, HOME RANGE AND HOMING BEHAVIOUR IN SOME SPECIES OF BIRDS CAPTURED AT THE ORNITHOLOGICAL STATION OF M'BOUR (SENEGAL).

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ABSTRACT

The authors report data on the site fidelity and home range in some species of birds captured and banded at the Ornithological Station of M'bour (Senegal). In addition, the orientational strategies of individuals displaced to sites 13 and 25 km from the home site were studied in two species of doves (the Laughing dove and the Black-billed Wood dove).

The results show that many of the species investigated display a tendency to spend the whole winter (the non-breeding period for most of the birds considered in our study) in a small home plot of very limited size. Other species, on the other hand, apparently range over a much wider area or are found in our study station only during migratory movements. As regards the initial orientation of the displaced doves, the Laughing dove shows a clear tendency to fly in a fixed compass direction with no apparent relationship with the home direction. In the Black-billed Wood dove, on the other hand, this stereotyped directional preference tends to be corrected by a weak but significant homeward orientation.

INTRODUCTION

The attachment of birds to the places where they live is demonstrated not only by the frequent recaptures of individuals in the original ringing area, but also by the marked homing ability usually observed after birds have been experimentally displaced. This site attachment is pertinent not only to the breeding area, but also to the wintering site (see Benvenuti and Ioalè 1980a, b, and Ioalè and Benvenuti 1983) and even to a series of places where birds stop during their migratory flights (see Wiltschko and Wiltschko 1978).

Even if the home fidelity and homing ability of birds have been documented in a variety of species (references for earlier papers are found in Matthews 1968, Able 1980), there has been little recent systematic research on this interesting behaviour, with the exception of longstanding investigations on pigeons (references in Papi, in press), a study on breeding colonies of Sand martins (*Riparia riparia*) (references in Baldaccini et al. 1989), and a series of studies on birds wintering in the USA (Ralph and Mewaldt 1975, 1976) and in the Mediterranean area (Benvenuti and Ioalè 1980a, 1980b, 1983; Ioalè and Benvenuti 1982, 1983; Ioalè et al. 1988).

To make a new contribution to this subject, we performed experiments on the site attachment and homing behaviour of some species of birds wintering or permanently residing in a study area within the Ornithological Station of M'bour in Senegal.

MATERIALS AND METHODS

Study area and capture methods. Our study plot was in the area of the ORSTOM Center (Observatoire geophysique, Station d'Ornithologie et de Mammalogie), 2km SE of M'bour, Senegal. The data given here were mainly collected from November 14th to December 5th, 1988; between these dates only, birds were banded and subjected to passive displacements and to other experimental procedures. Additional captures were performed in the following periods: January 10th-14th and 18th-19th, and February 21th-24th, 1989. During these winter capture-sessions, we recorded data on trapped birds, but neither banding activity nor displacements were carried out. The birds were trapped in mistnets 15 m long and 3 m high, which were in place from sunrise to late afternoon in four "capture stations" (see Fig. 1). Most of the doves and some of the other birds were captured in other sites in the same area where they were sometimes attracted by water and food.

Release experiments. Most of the captured birds, which were banded for individual identification and checked for the wing length and body weight, were released in the immediate vicinity of the capture site. Each of the remaining birds, on the other hand, was placed in a separate cloth bag and carried by car to a release site, usually within a few hours of their capture. We used four different release sites: 5 and 25 km NNW, 5 km SE and 13 km SSE of the capture station (home). The only proof of homing ability was taken to be the recapture of the displaced birds at the trapping site. Some birds were recaptured two or more times, but only the first recapture was considered in our calculations (exceptions will be clearly specified). No displaced birds were recaptured within 24 hrs of the first capture, but several non-displaced birds were; these recaptures were not included in our results. 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. When a bird was trapped twice in the same net, the recapture distance was considered to be zero.

As far as the doves are concerned, we made attempts to study their orientational strategies by releasing them according to the procedures used for the studies on the homing behaviour of pigeons. Releases were accomplished in sunny conditions, with light or moderate wind; the birds were released singly, alternating the two species of doves (the Laughing dove, Streptopelia senegalensis and the Black-billed Wood dove, Turtur abyssinicus) and following them up to vanishing with 10x40 binoculars. Vanishing times and vanishing bearings were recorded according to the standard procedures used in this kind of study.

Statistical methods. Directional data have been treated by vector analysis as in earlier papers on homing pigeons. The distributions of the vanishing bearings were tested for randomness using the Rayleigh and the V test. Comparisons between the bearing distributions of the two species were made using the Watson U2 test and the Mann-Whitney U test adapted to circular distributions (Batschelet 1981); the "adapted U test" estimates potential differences between samples in angular scatter and in angular deviation from the home direction.

RESULTS

A. Experiments on site fidelity and home range

Table 1, gives a list of the species of the birds ringed, together with data on recaptures of displaced and non-displaced birds. The numbers of unbanded birds trapped in the winter (January and February) are given too; these numbers can be used to infer which species reside in our area during the whole trapping season and which are only present during migratory movements. Meaningful comparisons between the number of birds banded in autumn (Nov. 14th to Dec. 5th, 1988) and those captured in winter (Jan. 18th to Feb. 24th, 1989) cannot be obtained, on account of the fact that 200 or more Black-headed weavers (Ploceus melanocephalus), several Village weavers (P.

cucullatus) and other birds captured in autumn, were neither banded nor recorded in Table 1. Moreover, the correct number of unbanded birds captured in winter cannot be accurately assessed because of the lack of marks for individual identification, which meant that some birds may have been captured more than once. This problem was particularly relevant to species with high recapture rates (see Table 1). The list of unbanded birds captured in winter can only be used to verify whether a given species was present in our study area during the trapping season.

The recapture percentages of non-displaced birds range between 0.0 (various species) and 100 (Sylvietta brachyura) (but the data in the latter species are based on only two samples); in birds displaced at 5 km from the trapping area the recapture percentages range between 0.0 (Prinia subflava and Ploceus cucullatus) and 25.0 (Lagonostica senegala). Fig. 2 gives the recapture distances for birds belonging to 12 different species. With the exception of Ploceus melanocephalus, for which most recaptures were between 200 and 350 m from the former capture site, the recapture distances are quite small. In fact, 35 out of 50 birds (70.0%) were recaptured within 50 m of the former capture site; as to the palearctic breeders wintering in, or migrating through, our study plot, we have only 9 samples (see Fig. 2), but these too yielded figures consistent with the global result: 6 out of 9 birds (66.7%) were, in fact, recaptured within 50 m of the former capture site.

Data on the recapture interval (time elapsing between the capture and subsequent recapture(s)) are shown in Fig. 3. It turns out that the mean recapture interval is quite long, ranging from 30 to 72 days, the only exception being the Garden warbler (Sylvia borin). Thus, in most of the species considered in our study, it appears that individual birds have a tendency to stay in the area for quite a long time.

B. Homing experiments with Laughing doves and Black-billed Wood doves (Streptopelia senegalensis and Turtur abyssinicus)

Only 26 out of 45 released Laughing (L-) doves (57.8%) and 16 out of 36 Black-billed Wood (BbW-) doves (44.4%) produced useful vanishing bearings; the other birds, in fact, landed soon after the release or were lost behind bushes or trees close to the experimenters. The doves that vanished tended to fly very close to ground level and, due to this behaviour of these birds and to their small body size, vanishing times longer than 1 min. were quite rare.

On the whole, 9 releases (4 at 13 and 5 at 25 km from home; home direction 328° and 157°, respectively) were performed. The orientational data are presented in Table 2 and in Fig. 4. After pooling the vanishing bearings with the home direction set to 0°, the bearing distribution of both the L- and BbW-dove turned out not to differ from random (Rayleigh test: $p>.1$); however, the bearing distribution of the BbW-dove (Fig. 4 C), unlike the L-dove, shows a significant clustering around the home direction (V test: $p<.05$). Neither the U2 test nor the adapted U test reveal any significant difference between the bearing distributions of the two species of birds. After pooling the vanishing data with respect to North set to 0° (Fig. 4, B and D), a tendency to fly Southward (L-dove) or Southwestward (BbW-dove) is revealed (Rayleigh test: $p<.001$ and $.05<p<.1$, respectively).

Only 8 birds were recaptured at the ringing station after the releases: 4 L-doves (3 released at 13 km and 1 at 25 km from home) and 4 BbW-doves (all released at 13 km).

DISCUSSION

A. Experiments on site fidelity and home range

Our experimental design aimed to investigate the home range, site fidelity and homing success of birds outside the breeding season; this topic has not, in fact, received as much attention as that devoted to the study of the breeding territory, on which much empirical information is available in the literature. The results of this study were also intended to provide the base for a comparative analysis drawing on the results of similar experiments performed on birds wintering in the Mediterranean area, i.e. under very different ecological conditions (Benvenuti and Ioalè 1980a, b, 1983; Ioalè and Benvenuti 1982, 1983).

The present contribution to this subject, however, is limited by several factors, including the difficulty of defining the limits between the breeding and non-breeding season in our area. The period in which our data were collected was outside the main breeding time of the species taken into consideration. However, we cannot exclude the possibility that some of the birds used in our tests were in breeding conditions; Laughing doves, in fact, breed all through the year in this region, and Black-billed Wood doves may still be active around the nest in November (see Urban et al. (eds.) 1986). On the other hand, most small passerine birds - and 17 out of 20 species listed in Table 1 are passerines - are not involved in widespread breeding activity in the period in which our experiments were performed (most birds were recaptured in January or February; see Fig. 3). Of course, this problem only affects tropical species, certainly not the palearctic breeders wintering in tropical regions (7 out of 20 species; numbers 2, 7, 10, 11, 14, 18 and 19 in the list in Table 1).

Another problem arises from the fact that we made no attempt to determine the age of the banded birds, due to the lack of reliable methods in the season where our experiments were performed. The degree of skull ossification may cause mistakes in November and December, because at this time many young birds born in spring or early summer may resemble adult ones in this respect.

To come now to our findings, it turns out that few data are available for most of the species listed in Table 1; this prevents us from drawing firm conclusions or producing a solid base for comparative studies. Our findings must be considered a preliminary study allowing the selection of a number bird species on which attention should be focused in future.

Bearing in mind these limits, we may try to analyze the relationship between the birds considered in our investigation and the study area. In our study site fidelity is testified and measured by the percentage of the banded birds which have subsequently been retrapped in the area. This recapture percentage varies greatly among the species. The small sample size certainly contributes to this variability, which may also reflect different degrees of site attachment in different species. If we consider the recapture rate of non-displaced birds, the species listed in Table 1 may be distributed in 3 categories which correspond to 3 different kinds of relationship between individual birds and their habitat.

I). This category includes species of birds attached to a home site of limited extent; as regards the empirical findings, in these species we expect high recapture percentages, small recapture distances and long mean recapture intervals, indicating that the birds reside in the area permanently or for a long time. Several species of local birds (Prinia subflava, Camaroptera brachyura, Pycnonotus barbatus, Pogoniulus chrysoconus) and of palearctic breeders (Phoenicurus phoenicurus and Luscinia megarhynchos) fit this pattern of features. It is worth noting once again that the home site in the latter two species is the wintering site, which is temporally and spatially distant from the breeding territory; on the other hand, it is not so easy to define the home site of local residents, which may be attached to the breeding territory even in non-breeding periods.

II). We have included in this category those species in which the members of the population are not attached to a small home site but range over a large area, which may be much wider than our study plot. In species adopting this strategy we expect long recapture intervals (the population is present in the area, at least during the winter) and low recapture percentages (individual birds range over a wide area and the probability of trapping them twice is rather small). The presence of the species in the area, in spite of the low recapture rates, should be confirmed by frequent captures of non-banded individuals during the trapping season. A local bird (Ploceus melanocephalus) and a palearctic breeder (Hippolais pallida) fit this set of features.

III). This category includes birds migrating through our study plot to reach their winter quarters in other areas. These birds are, therefore, only present for short periods during migrations and we expect no recaptures during the winter (but recaptures may occur during the subsequent migratory trip in the opposite direction); recaptures can only occur within a time-span of a few days, giving short recapture intervals. Captures of unbanded individuals during the trapping season should not occur, or should, at least, be extremely rare. Two species of palearctic breeders can be included in this category: Sylvia borin and Hippolais polyglotta. For the latter species, the small sample size calls for further investigation, but our data find support in Moreau (1972), according to whom these birds winter at lower latitudes. The same Author reports that the Blackcap (Sylvia atricapilla) winters at the latitude of our study plot, but we have no recapture data for this species. This result, in conjunction with the fact that we have no captures of unbanded individuals during the winter, indicates that the Blackcap may well winter at our latitude, but our study plot is apparently not included in the habitat of this species outside the migratory periods.

In addition, the field data for Serinus mozambicus, an African species for which we have no recapture records either in banded or in unbanded individuals, fit this category of birds.

As regards the species which have not been included in any of the 3 categories, the small sample sizes connected with unclear results call for further collection of empirical data.

It is interesting to note that, unlike Ploceus melanocephalus, many other species show a global tendency to occupy a small home site, as witnessed by the fact that most of the recaptures were within 50 m of the former capture site (see Fig. 2).

As shown by Benvenuti and Ioalè (1980a) and by Ioalè and Benvenuti (1983), strong home fidelity is not necessarily related to good homing performances after passive displacement. In fact, several species of wintering passerine birds show high recapture percentages in non-displaced birds, i.e. they are faithful to their home site, but show quite poor homing success after a displacement of 4-8 km. Besides this, there are lower recapture percentages in non-displaced birds than in displaced ones in the data reported here; this aspect of our study, however, is at a very preliminary stage and cannot yet be discussed in detail.

B. Homing experiments with doves

Considering that homing pigeons use a map based on olfactory information (see Papi, in press; Wallraff 1986a), it is interesting to test other species of birds belonging to the same Family (Columbidae) for comparative analysis. Laughing doves and Black-billed Wood doves appear to be particularly suitable for this kind of investigation because they are quite common as resident birds in our study area, can be trapped in good number and can be easily manipulated and subjected to homing experiments.

Compared to pigeons, the orientational behaviour of the doves was quite poor, and a barely significant homeward tendency is only revealed in BbW-doves. Longer mean vectors, however, especially in the case of L-doves, are obtained by pooling the orientational data with respect to North; in this case the birds show a tendency to fly toward the South-Southwestern sector of the horizon. The meaning of this orientational strategy is not clear: both wild birds and homing pigeons often reveal a stereotyped tendency to fly in a compass direction with no apparent relationship to the home direction ("nonsense orientation" according to Mathhews 1968, or "preferred compass direction" according to Wallraff, 1986b).

It is worth noting, however, that the doves used in our experiments were captured in an area along the sea, where the coast approximately runs from NNW to SSE. Thus, a compass orientation in directions included in this sector, such as that exhibited by our birds (especially by BbW-doves), is the best one for a bird to reach the coastal area from inland regions (the release sites were 2 and 10 km from the sea). A similar orientational strategy is shown by several littoral and river-bank inhabiting arthropods and other animals which exhibit stereotyped oriented movements toward the water direction when they are displaced to dry environments (references in Wehner and Wehner 1986); this mechanism, however, would be surprising in birds, which do not simply need to reach an area characterized by optimal ecological conditions, but a specific small fraction of the proper habitat (i.e. their individual territory).

Firm conclusions cannot be drawn from our experiments, which are a preliminary study whose aim is to verify the feasibility of using L- and BbW-doves for homing experiments. Our tests have shown that these two species of birds can produce oriented vanishing bearings and that the BbW-dove appeared to show superior homeward orientation to that of the L-dove, which exhibited stereotyped Southward orientation; further research, with a greater number of samples, is now needed to verify our results and to investigate the orientational strategy of displaced doves. This latter aspect should be taken into consideration by choosing another trapping area far from the sea cost, so as to allow release experiments at 4 different localities symmetrically arranged around the home site; this experimental design is the most favourable for the investigation of the initial orientation of displaced animals (see Wallraff 1983).

A preliminary study on the actual home range of young and adult birds is also required in order to define what and where home really is with respect to the release site.

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Tab. 1. List of ringed birds and recapture data. We only give details for the species in which a minimum of 7 individuals were banded, or a minimum of 2 recaptures were recorded.

	Species	N	Rh	Hh	%	Rd	Hd	%	n
1	Ploceus melanocephalus	195	104	11	10.6	91	3	3.3	450
2	Sylvia borin	50	30	2	6.7	20	0	-	0
3	Streptopelia senegalensis	45	2	0	-	45*	4	8.9	7
4	Turtur abyssinicus	38	2	0	-	36	4	11.1	9
5	Prinia subflava	32	19	8	42.1	13	0	-	17
6	Estrilda bengala	29	15	1	6.7	14	0	-	9
7	Phoenicurus phoenicurus	21	21	4	19.0	0	-	-	7
8	Camaroptera brachyura	17	17	8	47.1	0	-	-	5
9	Pycnonotus barbatus	17	17	5	29.4	0	-	-	10
10	Sylvia atricapilla	15	15	0	-	0	-	-	0
11	Hippolais pallida	14	14	1	7.1	0	-	-	6
12	Serinus mozambicus	13	13	0	-	0	-	-	0
13	Ploceus cucullatus	11	8	0	-	3	0	-	113
14	Luscinia megarhynchos	10	10	3	30.0	0	-	-	0
15	Lagonostica senegala	8	4	0	-	4	1	25.0	4
16	Laniarius barbarus	8	8	1	11.1	0	-	-	5
17	Pogoniulus chrysoconus	8	8	5	62.5	0	-	-	12
18	Hippolais polyglotta	7	7	0	-	0	-	-	0
19	Phylloscopus collybita	7	7	0	-	0	-	-	2
20	Sylvietta brachyura	2	2	2	100.0	0	-	-	3
21	17 other species	32	32	4	12.5	0	-	-	35
22	26 other species	-	-	-	-	-	-	-	69
	T O T A L	579	355	56	15.8	226*	12	5.3	763

N = number of ringed individual birds for each given species. n = number of unbanded birds trapped in January and February. Rh and Rd = birds released at the capture site (home) and at 5km 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. * Two L-doves (Streptopelia senegalensis) homed after release have been used again in subsequent release experiments; so, in this case (marked by an asterisk), the total number of banded birds (45) is less than the total number of data (2 Rh + 45 Rd).

Tab. 2. Ori entational behaviour of doves: pooled results with the home direction set to 0.

			- Home vector -				- Compass vector -			
Sp	n	N	a	r	Dh	Hc	a	r	Dh	Hc
L	26	(45)	325	.16	-35	.127	187	.60***	-173	-.59
BbW	16	(38)	354	.32	- 6	.316*	232	.42	-129	-.26

Sp = species of the released birds (L: *Streptopelia senegalensis*; BbW: *Turtur abyssinicus*). n and N = number of recorded bearings and of birds actually released. For each species, the direction (a) and the length (r)of the mean vector is given. Dh and Hc = deviation from the home direction and homeward component, respectively. Significance by the Rayleigh (r) and the V test (Hc) is indicated by asterisks: * = p<.05, *** = p<.001.

CAPTIONS TO THE FIGURES

Fig. 1. Map of the study area, 2 km SE of M'bour in Senegal. The buildings are offices, laboratories and staff residences of the ORSTOM Observatoire geophysique, Station d'o rnithologie et de Mammalogie. In the four capture stations A, B, C and D, the solid circles represent the sites where mistnets were routinely set up. The nets were not operating every day, and not all four sim ultaneously. Most of the doves and some birds of the other species were trapped at sites oütside the usual capture stations.

Fig. 2. Recapture distance in 12 species of birds. For each species and for each individual bird the symbols indicate the distance between the capture and the recapture site. Dotted symbols refer to the birds which have been retrapped twice, and indicate the second recapture . The distance has been approximated to the nearest 50 meters (e.g.: between 0 and 50 m, between 50 and 100 m, and so on). The names of the species have been abbreviated in the following way: Pm: Ploceus melanocephalus; Cb: Camaroptera brachyura; Ps: Prinia subflava; Pc: Pogoniulus chrysoconus; Pb: Pycnonotus barbatus; Pp: Phoenicurus phoenicurus; St: Streptopelia turtur; Ta: Turtur abyssinicus; Lm: Luscinia megarhynchos; Eb: Estrilda bengala; Sb: Sylvia borin; Sbr: Sylvietta brachyura. Species in which only one recapture occurred have not been considered.

Fig. 3. Recapture intervals in 12 species of birds, the same species and the same birds included in Fig. 2. The horizontal lines connect two short vertical marks indicating the capture and the recapture dates for each single bird during the whole capture season (November 14th, 1988, to February 24th, 1989). In the cases in which there were two subsequent recaptures of the same individual, the first recapture is indicated by a vertical mark at an intermediate point somewhere along the horizontal line at the appropriate date. In the right margin, the mean recapture interval is indicated for each species. The arrows indicate the dates on which mistnets were operating. The abbreviations in the left margin indicate the species according to the explanations given in Fig. 2.

Fig. 4. Initial orientation of Laughing doves (A and B) and Black-billed Wood doves (C and D). In these diagrams, releases performed on several days and at two different release sites have been pooled with the home direction set to 0 (A and C) and with the north set to 0 (B and D). Each symbol refers to the vanishing bearing of a single bird; open symbols: birds released at 13 km SSE; dotted symbols: birds released at 25 km NNW. The arrows represent the mean vectors, whose length can be read using the scale in the A (top left) diagram. Dashed arrows are used when the bearing distributions do not differ from random according to the Rayleigh test.

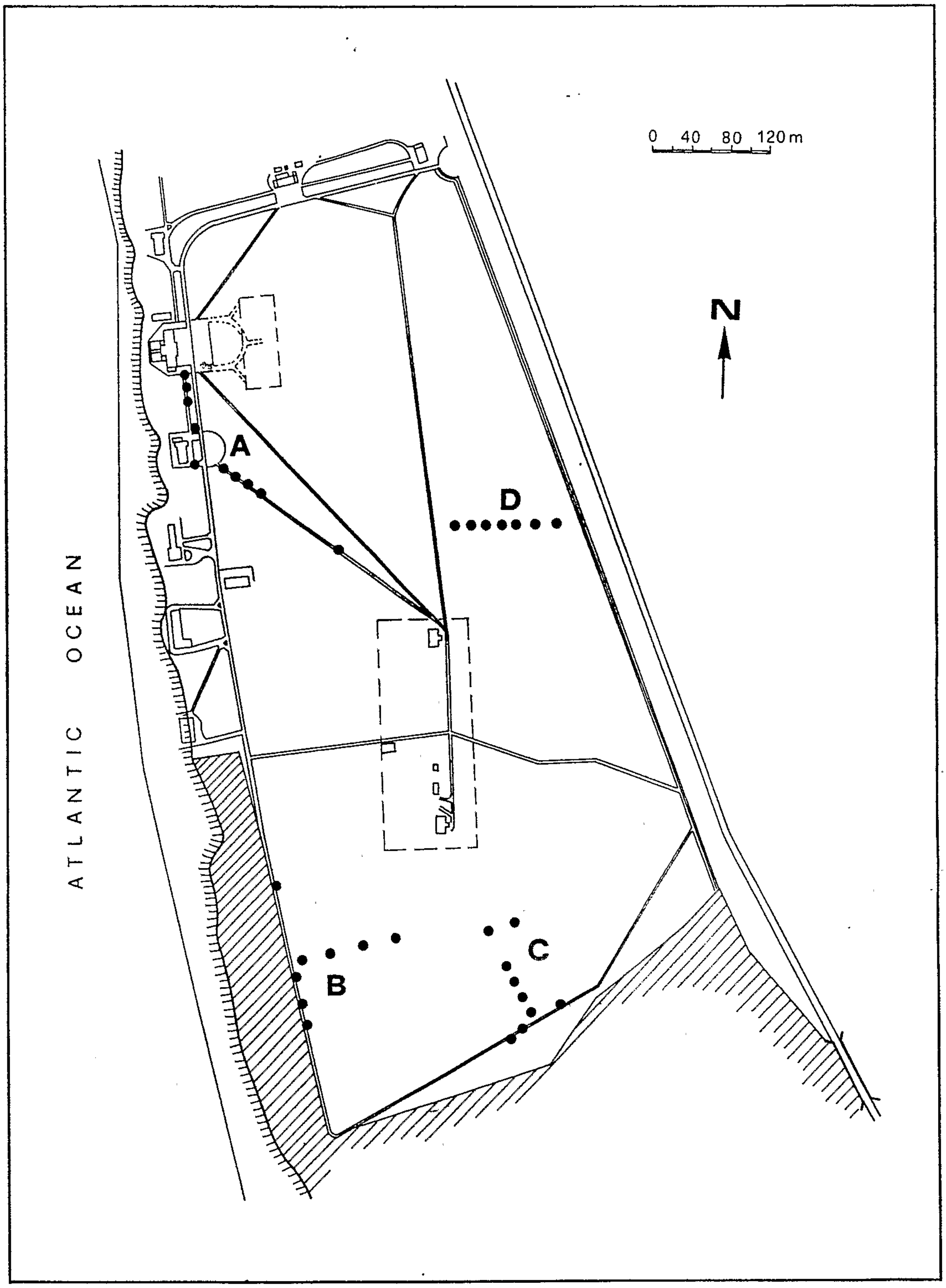

FIG 1

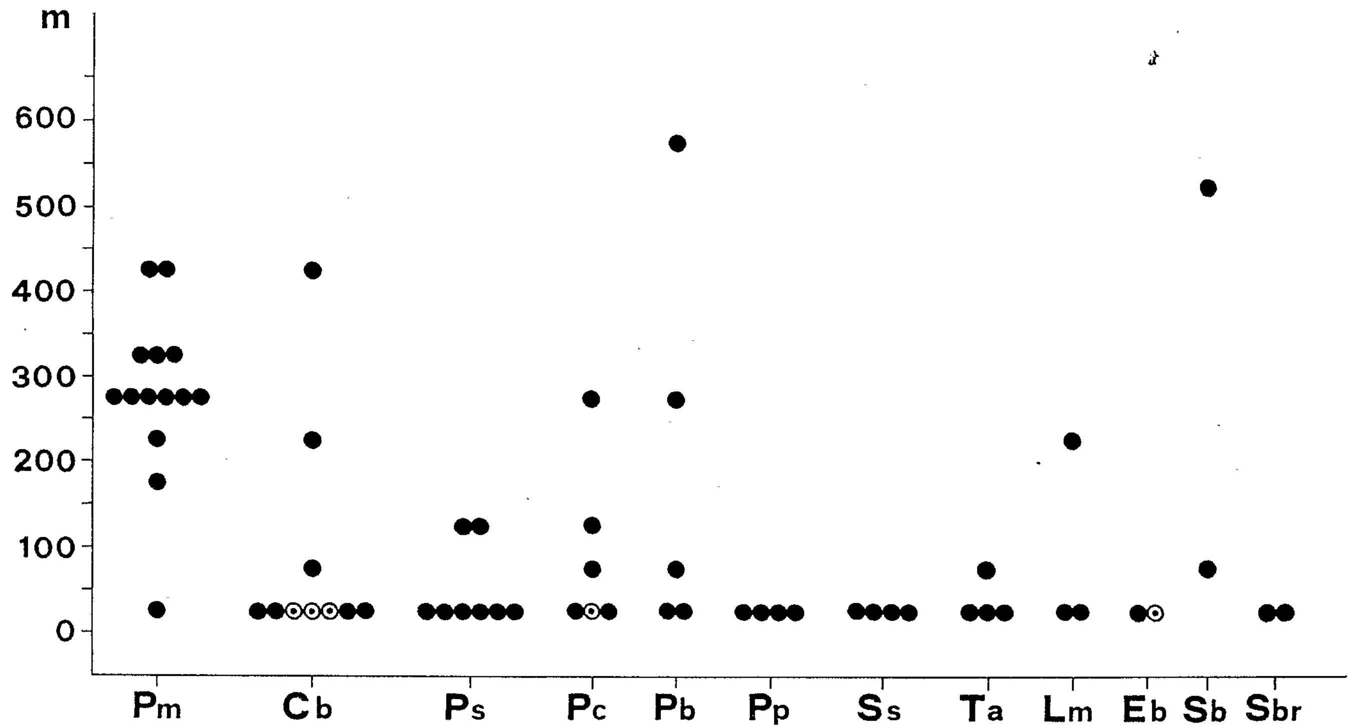

FIG 2

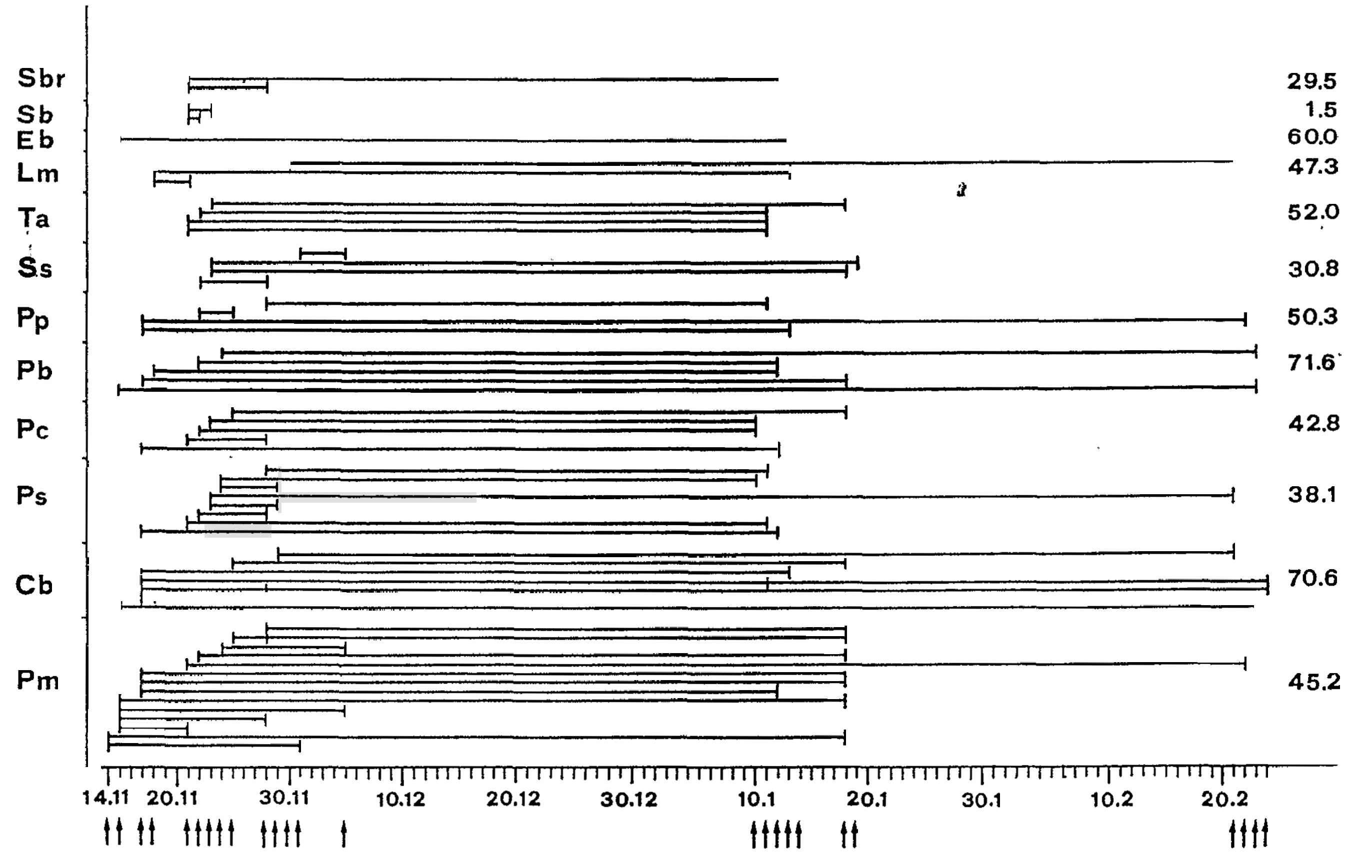
Sbr
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FIG 3

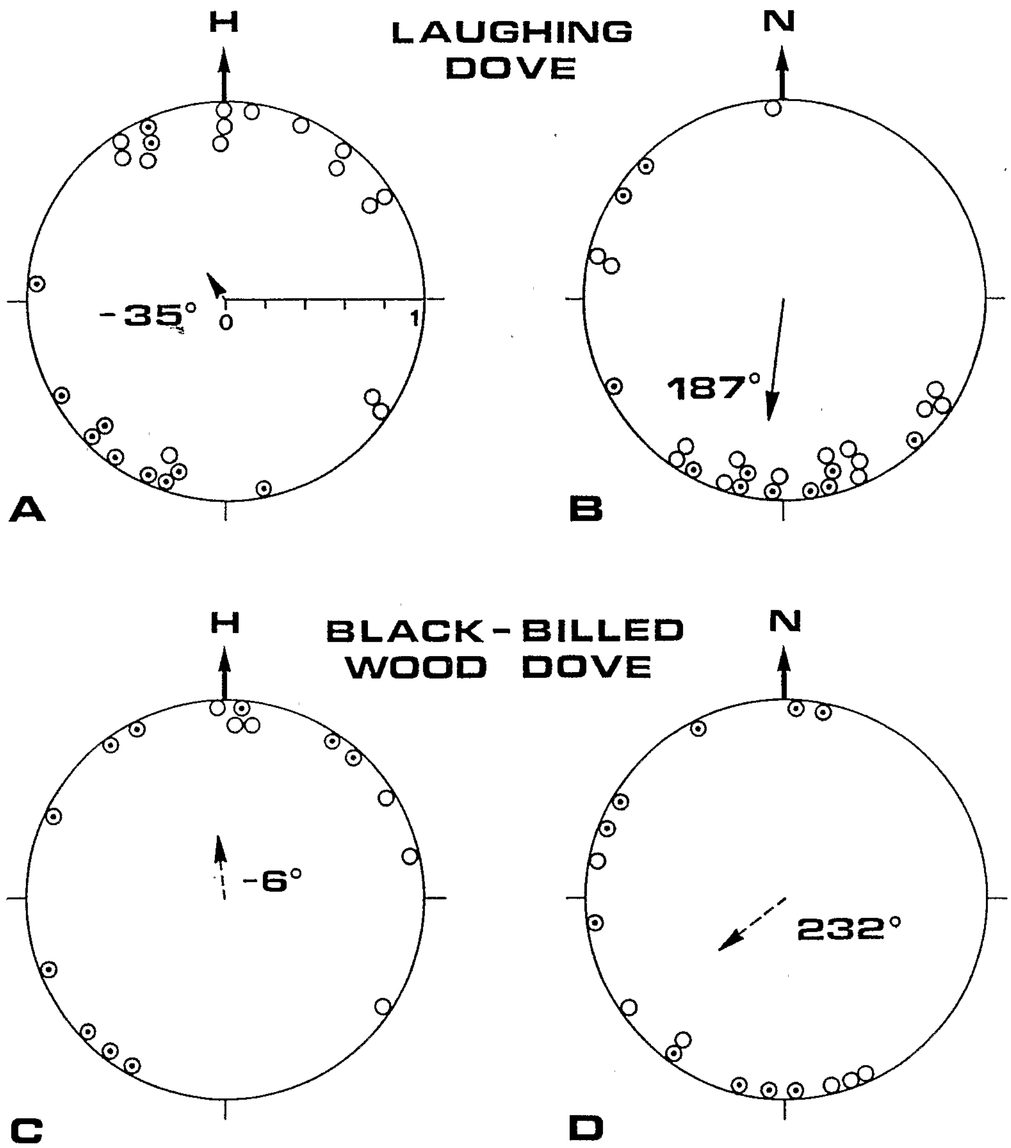
H
LAUGHING
DOVE
N
-35°
0
1
187°
A
B
H
BLACK-BILLED
WOOD DOVE
N
-6°
232°
C
D

FIG 4