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Spring migratory routes of eight trans-Saharan passerines through the central and western Mediterranean; results from a network of insular and coastal ringing sites

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Detailed information on spring migration routes of songbirds across the Mediterranean is still scanty. Results are presented here from a study on the occurrence of eight Palaearctic–African migrants across the western and central Mediterranean based on ringing data collected during the Progetto Piccole Isole, a co-ordinated project based on standardized mist netting at 21 islands and coastal stations. The species were Melodious Warbler *Hippolais polyglotta*, Icterine Warbler *Hippolais icterina*, Bonelli's Warbler *Phylloscopus bonelli*, Wood Warbler *Phylloscopus sibilatrix*, Pied Flycatcher *Ficedula hypoleuca*, Collared Flycatcher *Ficedula albicollis*, Red-backed Shrike *Lanius collurio* and Woodchat Shrike *Lanius senator*. Their capture frequencies were expressed as the frequency of each species relative to the total number of migrants ringed at each station in order to correct for differences in capture effort between stations. For most species, the detailed, quantitative results confirmed the scanty information available so far, whereas in the case of Melodious Warbler and Bonelli's Warbler, evidence of undescribed and unexpected migration routes was found. These results suggest that standardized mist netting provides an important method for studying the migratory routes of small birds, in particular for those species which are not frequently ringed in their breeding and wintering grounds.

Numbers of nocturnal songbird migrants may be particularly difficult to estimate visually at stopover sites, where birds stop for short periods during migration and their presence even during daytime may be hard to quantify (Karr 1976). Visual estimates are heavily influenced by the skill of the observers (see Bibby *et al.* 1992), and caution is needed when comparing the frequencies of different species across localities. This method may therefore be difficult to apply in large-scale studies aimed at collecting information on the relative frequency of a given species and not simply its presence/absence. Because of the difficulty of visually estimating the direction of their movements, as is usually done with large, soaring migrants, the knowledge of songbird migratory routes largely derives from recoveries of ringed birds (Zink 1973).

On the other hand, estimations of the migratory routes of a species based on ringing recoveries are influenced not only by the number of individuals of that species staging in a given area but also by the fraction of individuals that were ringed elsewhere and by the probability of recovery, which may be dependent on factors such as hunting or ringing effort in that area as well as on local reporting rates (Lebreton & North 1993).

A migration route can be completely overlooked if passing migrants belong to populations which are not ringed or when the route involves geographic areas lacking ringing effort. Coordinated ringing activities in southern European countries are relatively recent developments, and data on songbird migration movements within the Mediterranean area, and in particular on those species breeding in this region, are scanty and anecdotal or even absent (Cramp 1992, Cramp & Perrins 1993).

From a more general perspective, spring migration routes of Palaearctic–African songbirds are less well known than their autumn movements (Zink 1973, Dowsett *et al.* 1988); this may be a consequence of the large effort traditionally devoted to ringing during the postnuptial movements, especially in northern Europe. The routes followed by the same birds in autumn and spring may be different ("loop migration"; Zink 1973, Alerstam 1990, Berthold 1993), and for the reasons listed above, such routes are not always easily studied.

Ringing stations distributed over a wide geographic area, where contemporary ringing activities are based on mist netting and standardized methods of data collection, may provide a unique opportunity to get an overview of the mi-

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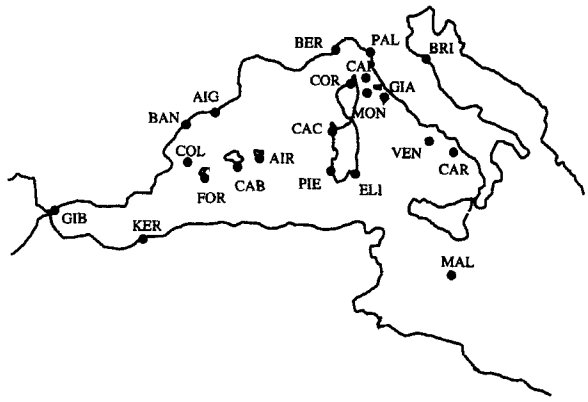

Figure 1. Location of the ringing sites used in this study. Complete site names and their longitude and latitude are given in Table 1.

gratory routes followed by different species. In particular, they can offer a quantitative estimate of the abundance of the various species (Berthold & Querner 1978). One of the problems in comparing the capture frequencies of a species between different ringing stations is that even small habitat differences between stations may greatly influence the species composition of catches (Bairlein 1981). The Progetto Piccole Isole (PPI), initiated and co-ordinated by the Istituto Nazionale per la Fauna Selvatica as the Italian Ringing Scheme, has aimed at investigating spring migration across the Mediterranean Sea through a network of insular and coastal stations stretched across the western and central Mediterranean (Spina *et al.* 1993). These stations were operated during the period of peak migration for trans-Saharan passerine migrants using standardised methods. Some of the stations were run for the first time during this project, whereas others have a very long tradition of ringing activities (e.g. Gibraltar; Finlayson 1992). Since 1994, the PPI has become a part of the wider "European–African Songbird Migration Network" supported by the European Science Foundation (Bairlein 1995). Contemporary ringing activity on such a large geographic scale offered the opportunity to collect information on the relative abundance of many passerine species crossing the Mediterranean Sea area. The location of ringing stations on islands or along the southern coast of Europe should offer a sample of the species composition of migrants less influenced by habitat segregation. The aim of this study was to analyse the frequency of eight bird species, belonging to four genera, of trans-Saharan migrants in different areas of the Mediterranean as a contribution to the description of their migratory routes and strategies.

MATERIALS AND METHODS

Stations, ringing protocols and periods

Mist netting was carried out between 16 April and 15 May on 16 islands and at five coastal sites (Fig. 1, Table 1). Two

Table 1. *Longitude and latitude of ringing stations. On the basis of their geographic location, stations are defined as small island (<250 km²), large island (>250 km²) or mainland coast. Nets were operated between 16 April and 15 May. Data from 1 year and up to 3 years were used*

Capture site	Abbreviation	Year(s)	Country	Latitude	Longitude	Location	Coordinator
Gibraltar	GIB	1992	Spain	36°00'N	5°24'W	Mainland coast	J. Cortes
Kerbacha	KER	1994	Morocco	35°05'N	2°12'W	Mainland coast	G. Gargallo
Punta de la Banya	BAN	1993	Spain	40°37'N	0°35'E	Mainland coast	A. Elliott
Columbrete	COL	1994–1995	Spain	39°53'N	0°41'E	Small island	J. Castany
Formentera	FOR	1993–1994	Spain	38°40'N	1°30'E	Small island	S. Costa
Cabrera	CAB	1993–1994	Spain	39°08'N	2°56'E	Small island	C. Lopez-Jurado
Aiguamolls Empordà	AIG	1993–1995	Spain	42°00'N	3°00'E	Mainland coast	D. Robson, G. Gargallo
Illa de l'Aire	AIR	1993–1994	Spain	39°48'N	4°16'E	Small island	R. Escandell
Capo Caccia	CAC	1993	Italy	40°34'N	8°09'E	Large island	C. Marchetti
San Pietro	PIE	1994	Italy	39°09'N	8°14'E	Small island	C. Marchetti
Bergeggi	BER	1994	Italy	44°15'N	8°26'E	Small island	M. Schiavi
Capo San Elia	ELI	1993–1994	Italy	39°11'N	9°09'E	Large island	S. Nissardi
Capo Corso	COR	1993–1994	France	43°00'N	9°25'E	Large island	J.-P. Cantera
Capraia	CAP	1993–1994	Italy	43°02'N	9°49'E	Small island	A. Roselli
Palmaria	PAL	1993–1994	Italy	44°03'N	9°50'E	Small island	M. Ferro
Montecristo	MON	1992	Italy	42°14'N	10°19'E	Small island	N. Baccetti
Giannutri	GIA	1993–1994	Italy	42°15'N	11°06'E	Small island	A. Massi
Brisighella	BRI	1993–1995	Italy	44°13'N	11°46'E	Mainland coast	U. Giusini
Ventotene	VEN	1993–1994	Italy	40°48'N	13°25'E	Small island	F. Spina
Capri	CAR	1993–1994	Italy	40°33'N	14°15'E	Small island	A. Montemaggiori
Malta	MAL	1993–1994	Malta	35°51'N	14°20'E	Small island	R. Galea

of these islands (Bergeggi and Palmaria) are less than 2 km from the mainland coast; four other stations (San Pietro, Capo Caccia, Capo San Elia, and Capo Corso) are on or very close to large islands, namely Sardinia and Corsica. The dominant vegetation was various types of Mediterranean matorral (Tomaselli 1981) at all ringing sites except Kerbacha (northern coast of Morocco) and Aiguamolls de l'Empordà (eastern coast of Spain), which were located in reed beds. The study sites were located over an area ranging for approximately 9° of latitude (from 35°N to 44°N, for a total of *c.* 1000 km) and 19° of longitude (from 5°W to 14°E, for a total of *c.* 1800 km). The characteristics of the ringing sites are given in Table 1. Nets were operated from dawn to dusk (for further details on field methods, see Spina *et al.* 1993). When PPI was active (1988–1996), we chose those years when most stations were run for the whole trapping period, and in particular 1993–1995. The species composition of migrants captured at the stations that were active since the beginning of the project did not change substantially between years (Montemaggiori *et al.* 1993, Spina *et al.* 1994). The data set chosen in this study is therefore representative of the typical situation over the whole period.

Analysis of capture frequencies

It is well known that migrants select specific habitats during migration (Bairlein 1981, Brensing 1989); hence, setting nets in different habitats may influence the species composition of catches. When comparing the abundance of migratory species over wide geographic regions, it is necessary to reduce, at a minimum, the bias in capture patterns which might be introduced by even minor habitat differences between ringing stations. The numbers of ringed birds may also be influenced by site features (for instance, other factors being equal, mist nets are less effective at windy sites) and by capture effort (e.g. length and number of nets used). One way to compensate, at least to some extent, is to express the frequency of capture of a migrant species as a frequency relative to the total number of migrants ringed at that station. Species with radically different habitat requirements from those selected for this study (e.g. swallows or chats) were excluded from the total. A subset of eight species was chosen for this study among those ringed during the project (Massi *et al.* 1995): Melodious Warbler *Hippolais polyglotta*, Icterine Warbler *Hippolais icterina*, Bonelli's Warbler *Phylloscopus bonelli*, Wood Warbler *Phylloscopus sibilatrix*, Pied Flycatcher *Ficedula hypoleuca*, Collared Flycatcher *Ficedula albicollis*, Red-backed Shrike *Lanius collurio* and Woodchat Shrike *Lanius senator*. The relative frequency of species *a* at the *i* station (f_{ia}) was calculated as $f_{ia} = n_{ia}/(\text{tot}_i) \times 100$, where n_{ia} was the number of individuals of species *a* captured at station *i* and tot_i was the total number of migrants captured on the same island during the same period (Table 2).

RESULTS

General results

Overall, 24,633 individuals of the eight species were captured at the 21 stations over the period. The total number of migrants captured was 74,448, with an average of 3545 (range 351–20,624) on each island (Table 2). Among the study species, the largest samples refer to Wood Warbler and Pied Flycatcher, which were captured in large numbers at all stations. The Woodchat Shrike, although captured in smaller numbers, was present at all stations but one (Brisighella). The rarest of the eight species was the Collared Flycatcher, with a concentration of captures at the eastern sites. Differences in capture frequencies were generally found between the western, Spanish stations and the stations located in the Thyrrenian Sea. For two species, Bonelli's Warbler and Red-backed Shrike, differences were found between northern and southern stations within the same longitudinal range, suggesting that birds belonging to these species follow, in this part of the study area, west–east and east–west routes, respectively, rather than moving in a south–north direction. Only two species, Pied Flycatcher and Woodchat Shrike, did not show significant geographic variation in their capture pattern and were almost equally frequent at all stations.

Species accounts

Icterine and Melodious Warblers

These warblers showed a clear geographic difference in their capture frequencies (Table 2, Fig. 2A, B). In particular, the Icterine Warbler was abundant in the central Mediterranean (up to 8.5% of the migrants on Capri) but became progressively rarer or absent at the western stations. On average, its capture frequency was 2.3% (s.d. ±2.7) of the total; a similar overall mean capture frequency was found for the Melodious Warbler (mean = 1.8%, s.d. ±2.7). Contrary to what was observed for the Icterine Warbler, the Melodious Warbler was common at the Spanish stations and less common or absent in the central Mediterranean, with the exception of the two northernmost stations (Palmaria, Bergeggi), where this species outnumbered the Icterine Warbler. This pattern may indicate an intense passage of Melodious Warblers from Spain along French Mediterranean and northwestern Italian coasts.

Bonelli's and Wood Warblers

These two species showed a clear east–west clinal pattern very similar to that observed for the two *Hippolais* warblers (Fig. 2C, D). In particular, Bonelli's Warbler was common at the western stations, where it outnumbered the Wood Warbler, to become very rare on the Thyrrenian sites (Table 2). Its overall frequency was low, ranging between 0 and 4.7% (mean = 0.61%, s.d. ±1.24). Bonelli's Warbler was captured at relatively high frequencies on Bergeggi and Pal-

Table 2. *Absolute* (n) *and relative (% of the total number of migrants) frequency of capture of eight passerine migrant species at 21 ringing sites*

Capture site	Icterine Warbler		Melodious Warbler		Bonelli's Warbler		Wood Warbler		Collared Flycatcher		Pied Flycatcher		Red-backed Shrike		Woodchat Shrike		Total no. of migrants[a]
	n	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	
Gibraltar	0	0	185	10.5	83	4.7	12	0.7	0	0	139	7.9	0	0	10	0.6	1771
Kerbacha	10	0.8	102	7.9	5	0.4	24	1.9	0	0	33	2.5	0	0	6	0.5	1298
Punta de la Banya	0	0	54	3.5	14	0.9	2	0.1	0	0	93	6.0	0	0	36	2.3	1556
Columbrete	12	0.3	104	2.8	31	0.8	11	0.3	0	0	76	2.1	0	0	135	3.6	3713
Formentera	2	0.1	31	2.0	12	0.8	42	2.7	0	0	218	14.0	0	0	114	7.3	1556
Cabrera	31	0.7	60	1.4	20	0.5	32	0.7	2	0.1	519	12.0	0	0	129	3.0	4332
Aiguamolls Empordà	1	<0.1	28	1.3	0	0	3	0.1	0	0	40	1.8	0	0	4	0.2	2197
Illa de l'Aire	32	0.9	37	1.0	8	0.2	18	0.5	0	0	81	2.3	1	<0.1	47	1.3	3543
Capo Caccia	4	1.1	1	0.3	0	0	24	6.5	0	0	98	26.4	0	0	5	1.4	371
San Pietro	33	6.8	0	0	0	0	35	7.2	0	0	41	8.4	0	0	7	1.4	487
Bergeggi	2	0.6	12	3.4	13	3.7	34	9.7	0	0	67	19.1	6	1.7	2	0.6	351
Capo San Elia	10	1.2	0	0	2	0.2	54	6.2	0	0	81	9.3	2	0.2	26	3.0	869
Capo Corso	28	1.7	1	0.1	0	0	205	12.5	0	0	74	4.5	3	0.2	8	0.5	1644
Capraia	154	3.3	8	0.2	11	0.2	462	9.8	5	0.1	218	4.6	35	0.7	28	0.6	4717
Palmaria	14	0.8	28	1.7	4	0.2	105	6.3	3	0.2	262	15.7	17	1.0	7	0.4	1674
Montecristo	77	3.1	0	0	1	<0.1	488	19.8	9	0.4	233	9.4	26	1.1	40	1.6	2467
Giannutri	400	4.8	1	<0.1	7	0.1	420	5.0	6	0.1	603	7.2	49	0.6	313	3.7	8370
Brisighella	40	1.6	56	2.2	0	0	127	5.0	4	0.2	172	6.8	97	3.8	0	0	2544
Ventotene	1170	5.7	0	0	13	0.1	2246	10.9	27	0.1	1285	6.2	23	0.1	492	2.4	20,624
Capri	656	8.5	0	0	1	<0.1	1230	15.9	28	0.4	1143	14.8	6	0.1	118	1.5	7728
Malta	184	7.0	0	0	3	0.1	313	11.9	6	0.2	217	8.2	3	0.1	79	3.0	2636
Total	2860		708		228		5887		90		5693		268		1606		74,448

[a] Species considered in the totals, along with the study species, were Nightingale *Luscinia megarhynchos*, Redstart *Phoenicurus phoenicurus*, Spectacled Warbler *Sylvia conspicillata*, Subalpine Warbler *Sylvia cantillans*, Orphean Warbler *Sylvia hortensis*, Lesser Whitethroat *Sylvia curruca*, Whitethroat *Sylvia communis*, Garden Warbler *Sylvia borin*, Blackcap *Sylvia atricapilla*, Chiffchaff *Phylloscopus collybita*, Willow Warbler *Phylloscopus trochilus*, Golden Oriole *Oriolus oriolus* and Ortolan Bunting *Emberiza hortulana*.

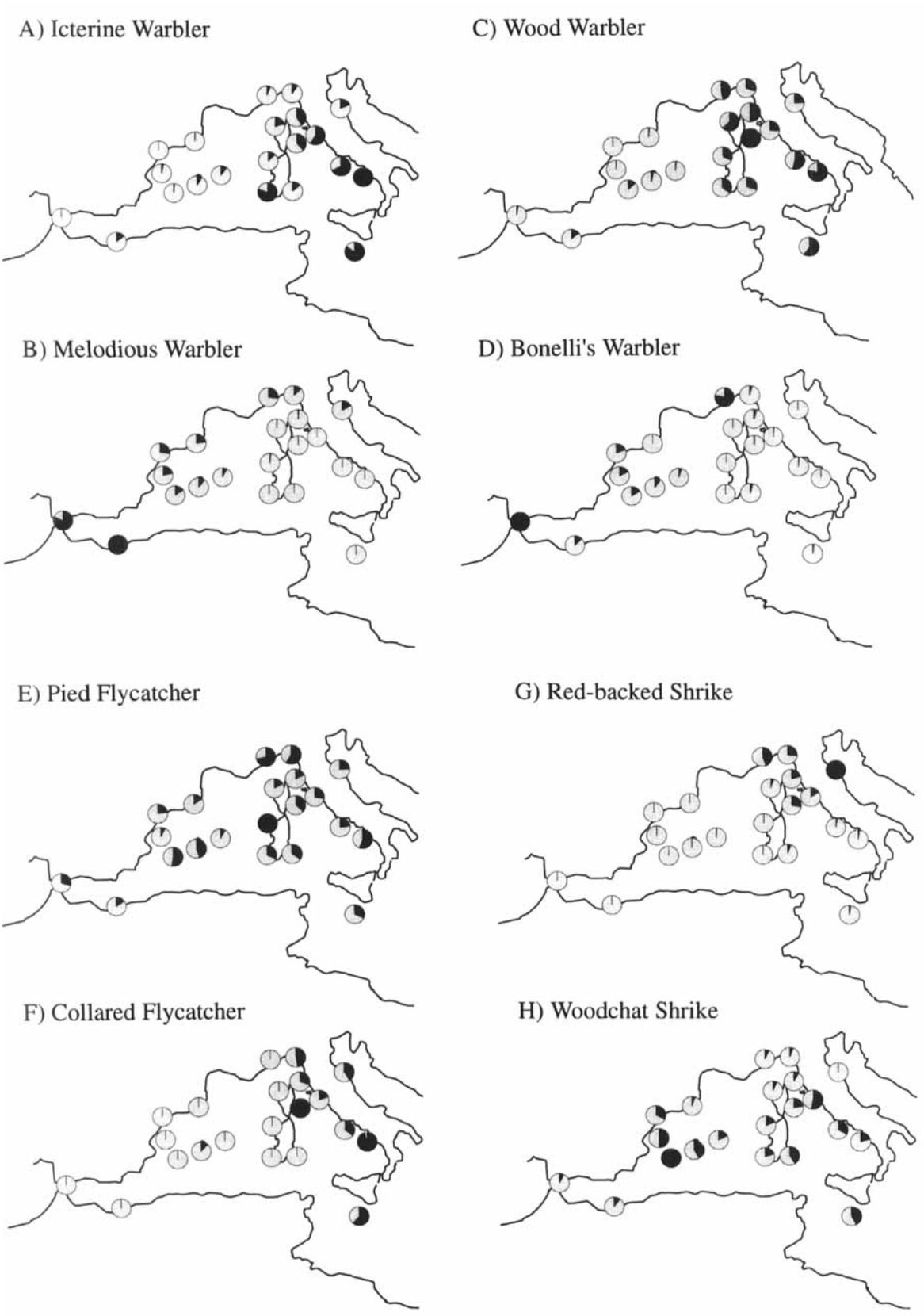

Figure 2. Capture frequency of eight passerine migrant species on the 21 PPI stations. For each species, frequencies were standardized in order to vary between 1 for the station with the highest relative capture frequency (black) and 0 for the station where the migrant was never captured (grey).

maria, whereas it was very rare in the central Thyrrenian. Although present at all 21 stations, the Wood Warbler was ringed only in small numbers at the Spanish stations, while it was captured at very high frequencies in the central Mediterranean where it was one of the commonest migrants, its frequency ranging between 5% and 20% (mean = 6.4%, s.d. ±5.6) of the total number of migrants considered for this study (Fig. 2D, Table 2).

Collared and Pied Flycatchers

The Collared Flycatcher was almost completely absent from most of the western Mediterranean stations (Table 2, Fig. 2E). Only one individual, out of 4332 migrants, was captured on Cabrera, whereas it never occurred at the other Spanish stations, Kerbacha, Sardinia and Corsica. Its overall capture frequency ranged between 0 and 0.4% (mean = 0.1%, s.d. ±0.1). Stations where this species occurred most frequently were Montecristo, Capri and Malta. In contrast, the Pied Flycatcher was the most common migrant of the species studied and was uniformly distributed in the study area (Table 2, Fig. 2F). Its overall frequency was 9.0% (s.d. ±6.2).

Red-backed and Woodchat Shrikes

Red-backed Shrikes were ringed in large numbers only on the northern Thyrrenian stations and in the single Adriatic site (Brisighella), while the species was only occasionally recorded on Malta, Ventotene, Capri and Capo S. Elia; just one bird was ringed in the Spanish stations (Table 2, Fig. 2G). Its frequency over the total number of migrants was 0.5% (s.d. ±0.9). In contrast, the Woodchat Shrike was captured at all stations with the exception of Brisighella (Fig. 2H). Its frequency of the total number of migrants was 1.9% (s.d. ±1.7).

DISCUSSION

Icterine and Melodious Warblers

The breeding and wintering ranges of Icterine and Melodious Warblers are completely separated (Cramp 1992). The breeding range of the Icterine Warbler spreads from central Europe (Germany) eastwards, whereas that of the Melodious Warbler is restricted to North Africa, Spain, France and Italy. The former species winters south of the equator and the latter near the equator in western Africa (Cramp 1992). It is not surprising that the Icterine Warbler was absent from the westernmost stations; it is reported to be very common during spring migration in North Africa, widespread in Libya, Tunisia and eastern Algeria, while it is only occasionally recorded in Morocco (Cramp 1992) and at Gibraltar (Finlayson 1992). The Icterine Warbler was particularly abundant in the central Thyrrenian stations and on Malta.

In contrast, the finding that the Melodious Warbler was virtually absent from the central Mediterranean stations, despite being a common breeder along the whole Italian peninsula (Meschini & Frugis 1993), was surprising. In spring, the species is common at Gibraltar, rare in Tunisia (Cap Bon), Libya and Malta and regular in Algeria (Cramp 1992, Finlayson 1992), and the main spring route is thought to cross the western Mediterranean. The fact that the Melodious Warbler was absent or nearly so at some of the stations where the Icterine Warbler was very abundant (e.g. Ventotene) and vice versa at other stations (e.g. Gibraltar) suggests that this pattern of occurrence was not determined by a bias caused by habitat differences since the two species are ecologically very similar to each other (Cramp 1992). Hence, our results strongly suggest that the eastern breeding populations of the Melodious Warbler, and in particular the Italian ones, arrive in Europe through Morocco, following a southwest–northeast direction via Spain and France before changing to a more eastern direction or to a nearly southern direction for the birds breeding along the Italian peninsula. An important route along the coasts of Spain and France is also suggested by the relatively high frequency of this species on Palmaria and Bergeggi. If this is true, the southern Italian population, which is separated from those breeding in eastern Algeria and Tunisia by a few hundred kilometres, would cover a migratory route at least 3000 km longer to reach their breeding grounds from North Africa.

Bonelli's and Wood Warblers

As in the case of the Melodious Warbler, there is an indication of an important southwest–northeast route followed by Bonelli's Warbler along the eastern Spanish coast, southern France and the northwestern Italian coast to reach the European breeding areas. Like the Melodious Warbler, the Italian birds seem to reach their breeding grounds (Meschini & Frugis 1993) from the north rather than from the south by crossing the central Mediterranean. The western subspecies of Bonelli's Warbler *Phylloscopus bonelli bonelli* winters in a narrow belt along the southern edge of the Sahara, from Sénégal and southern Mauritania east to lake Chad and northern Cameroon, and it is fairly common in the extreme north of Nigeria (Cramp 1992). Spring passage is reported to be heavy in Morocco but only weak in Algeria. It becomes common again in eastern Libya and Egypt; probably all birds there belong to the eastern population (Cramp 1992). The pattern observed at the PPI stations confirms that the western population migrates through the western African countries and Gibraltar (Finlayson 1992) and is most likely to be confronted with only a limited desert and sea crossing. On the other side, the eastern subspecies is confined to the eastern Mediterranean, where it is one of the commonest small migrants (Cramp 1992).

The Wood Warbler is a common winter visitor in several central African countries, and the core of its wintering range lies due south of Italy (Moreau 1972). The species is much less numerous in western Africa. Its wide breeding range spreads from France and the British Isles to central Siberia. The migration pattern shown here suggests an im-

portant south–north movement through the central Mediterranean, as confirmed also by the lack of records from Mauritania and the western Sahara and the large numbers recorded in spring from the wooded areas of eastern Morocco, Algeria, Tunisia and northern Libya (Cramp 1992). Its abundance at the central Thyrrenian stations is probably due to the fact that those birds breeding in central and eastern Europe pass through these stations and are much more numerous that those breeding in western Europe (Cramp 1992).

Collared and Pied Flycatchers

The presence of the much less numerous Collared Flycatcher only at the more eastern stations is a further indication of the clearly eastern Mediterranean route followed by the species in spring (Cramp & Perrins 1993) on return from winter quarters distributed in east-central Africa, mainly south of the Equator (Zink 1973, Cramp & Perrins 1993). In contrast, the Pied Flycatcher is known to follow a south southwest to west southwest route in autumn, with a concentrated passage in northwestern Africa, while spring movements indicate a loop migration, with the return movements much farther east. Most spring recoveries of Scandinavian and central European birds are from North Africa, Morocco, Algeria and eastern Tunisia (Zink 1973), which is in agreement with our results.

Red-backed and Woodchat Shrikes

A presence of Red-backed Shrike limited to the northern Thyrrenian sea was expected because of the very eastern migratory route followed by this migrant in spring returning from the winter quarters of tropical and southern Africa (Cramp & Perrins 1993). Our data confirm that the European birds follow an east southeast to west northwest route from the Balkans, and the very high frequency of Red-backed Shrikes on Brisighella suggests an intense passage across the northern Adriatic from the former Yugoslavia. The complete lack of records from the Balearics and the coast of Catalunya suggests that the Spanish breeding birds reach their breeding grounds via the Pyrenees, along an east–west, continental route.

The Woodchat Shrike was present at the majority of stations, as expected from its winter and summer distributions (Cramp & Perrins 1993). Nonetheless, it showed a variable capture frequency. In particular, a high frequency was observed at stations located on small islands in the open sea (Fig. 2H), which are concentrated in the Balearics archipelago and in the central Thyrrenian, whereas coastal stations and those located in Corsica showed lower capture frequencies.

The data presented here are the first example of the use of the results from a large-scale project, based on standardized ringing stations active during the same period and over a wide geographic range, to obtain information on the abundance of different passerine species during migration and to track their migratory routes. In particular, capture frequencies have shown an insight into movements that can be usefully integrated with the information derived from recoveries of birds ringed on the breeding grounds. When a number of stations are involved, this approach allows a detailed description of routes and can detect unexpected migratory movements, as in the case of the Melodious Warbler. In this study, the capture frequencies were nearly constant between years, particularly in the case of trans-Saharan migrants (Montemaggiori *et al.* 1993). Thus, in the future, our results may be integrated with other ringing stations using the same methodology in other Mediterranean areas. The use of coastal and island capture sites seems to be particularly appropriate for studies on spring migration because of the high concentrations of migrants found in these areas and the consequent large samples of migrant species which can be collected in a few years (Pilastro & Spina 1998). The difficulty of telling apart habitat and geographic effects on capture frequency can be overcome, at least in part, through comparison with the capture frequencies of species with similar ecological requirements.

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