BACK FROM AFRICA: WHO'S RUNNING AHEAD? ASPECTS OF DIFFERENTIAL MIGRATION OF SEX AND AGE CLASSES IN PALEARCTIC-AFRICAN SPRING MIGRANTS

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SUMMARY

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The differential migration of sex and age classes in 16 species of Palearctic-African migrants during their northward spring journey through the Central Mediterranean has been investigated from a large data set collected on 4 Italian islands during the "Progetto Piccole Isole". Species investigated were: European Nightjar *Caprimulgus europaeus*, Barn Swallow *Hirundo rustica*, Yellow Wagtail *Motacilla flava*, Common Redstart *Phoenicurus phoenicurus*, Whinchat *Saxicola rubetra*, Northern Wheatear *Oenanthe oenanthe*, Black-eared Wheatear *O. hispanica*, Subalpine Warbler *Sylvia cantillans*, Whitethroat *S. communis*, Blackcap *S. atricapilla*, Collared Flycatcher *Ficedula albicollis*, Pied Flycatcher *F. hypoleuca*, Golden Oriole *Oriolus oriolus*, Red-backed Shrike *Lanius collurio*, Woodchat Shrike *L. senator*, Ortolan Bunting *Emberiza hortulana*. The seasonal trapping patterns of males and females have been analysed both from the total samples and on a yearly basis. Males have been found passing earlier than females in 14 out of 16 cases, with differences reaching the level of significance in 13 out of 16 species. In the selected species, although the general trapping patterns may vary significantly among years, a temporal gap between males and females remains a fairly constant feature. In a sub-sample of 13 species, adults are found to migrate earlier than yearlings in 18 of 26 cases (significant differences found in 12 cases), with a slightly higher incidence of earlier movements of adult birds in females than males. This strategy seems to be another feature of spring migration, as confirmed by more detailed analyses referred to samples collected on single years and/or sites.

INTRODUCTION

In several migratory bird species, males reach the breeding grounds earlier than females (Nice 1943; Ketterson & Nolan 1983). Within the Palearctic this seems to be true both for medium- and long-distance migrants (Cramp 1985, 1988, 1992; Cramp & Perrins 1993). An earlier arrival in the breeding areas allows males to establish a territory which will already have well defined boundaries when the females come. For older males, this strategy also increases the chances of re-occupying a territory already known from previous years (Conder 1989); the return to the same site may enhance the possibility of mating with the same partner, which generally improves reproductive success (Coulson 1966).

In some species, like Common Redstart *Phoenicurus phoenicurus* and Pied Flycatcher *Ficedula hypoleuca*, the size of the territory may vary with respect to the density of already settled males, and the number of females a male will be able to attract has been found to be related to the size of this initial territory (Menzel 1971; Dale & Slagsvold 1990; Lundberg & Alatalo 1992). When other males arrive and settle, initial territories which may be contracted to smaller areas are reported for Nightingale *Luscinia megarhynchos*, Common Redstart and Collared Flycatcher *Ficedula albicollis* (Loehrl 1949, 1951; Menzel 1971; Grull 1981).

Both age and experience influence reproductive success in many bird species (Nelson 1966; Brooke 1978; Finney & Cooke 1978; Lundberg & Alatalo 1992). Earlier arriving older male Pied Flycatchers annexe the best territories and, in Scandinavian populations, only early arriving ones may become polygynous (Lundberg & Alatalo 1992); similar indications refer to polyterritorial male Collared Flycatchers (Loehrl 1951). First arriving older males holding the best territories are reported also for the Golden Oriole *Oriolus oriolus* (Reinsch & Warncke 1971). Hill (1989) suggests that the delayed arrival of yearling males may avoid territorial conflicts with older and more experienced ones.

Also among females, more experienced adults are generally the first to reach the breeding grounds (Oring 1982). In Northern America, first-settling female Lark Buntings *Calamospiza melanocorys* fledge more offspring than the later-settling ones (Pleszczynska & Hansell 1980).

An asynchrony in arrival and settlement of females may also have other advantages with respect to reproductive strategies. In Red-winged *Agelaius phoeniceus* and Yellow-headed Blackbirds *Xanthocephalus xanthocephalus*, yearling females arriving 1-2 weeks later than older females created strong asynchrony and increased the environmental potential for polygamy (Crawford 1977).

Though quite detailed information exists on the differences in arrival dates of males and females in the nesting areas, the knowledge of when and how this difference originates is much more scanty. In particular, for several species it is not well known whether males leave the wintering areas earlier than females, as reported for Yellow Wagtails *Motacilla flava* (Wood 1992), or if males fly faster, as suggested for the Willow Warbler *Phylloscopus trochilus* (Hedenstroem & Pettersson 1986).

In order to collect further information on spring migration, the Istituto Nazionale per la Fauna Selvatica, Italian Ringing Scheme, started a coordinated project in 1988 with the aim of analysing the strategies used by Palearctic-African migrants during their flight across the Mediterranean in spring. This project, named Progetto Piccole

Isole, is based on continuous and standardized mist-netting on several Central- and Western-Mediterranean islands. The project has more recently been fully endorsed by EURING (The European Union for Bird Ringing). For further details, see Spina *et al.* (1991, 1993) and Montemaggiori *et al.* (1993).

The aim of this paper is to present a brief overview of data on the differential migration of sex and age classes in a group of medium and long-distance Palearctic-African migrants.

MATERIALS AND METHODS

Mist netting was carried on between March 17th and April 15th in 1989 (pentads 16-21, see below), and between April 16th and May 15th in 1988 and 1990-1993 (pentads 22-27), on a series of small- to medium-sized islands within the Western and Central Mediterranean (Montemaggiori *et al.* 1993). If not otherwise specified, reference will generally be made here to the second series of study periods (mid-April to mid-May). For this paper, data collected in 5 years (1988-1992) on 4 islands (Montecristo 42.19N - 10.17E, Giannutri 42.15N - 11.06E, Ventotene 40.48N - 13.25E and Capri 40.33N - 14.15E, Fig. 1) were analysed; for further details on the study sites, see Spina *et al.* (1993).

Age classes have been expressed following the EURING codes. In each year, an average of 300 m mist-nets were continuously operated from dawn to dusk; the nets were occasionally closed only in the case of severe weather conditions. Qualified ringers have been directly responsible for ringing and data gathering on each station, where all birds were usually measured and aged by the same person. For further details on methods see Spina *et al.* (1993). A sample of 16 species (Table 1) has been chosen, in which the sexes could be separated on the basis of plumage patterns, and for which a reasonable sample had been collected. Within this sample, long-distance migrants are strongly represented, with species wintering both north and south of the Equator, and one case (Blackcap *Sylvia atricapilla*) referred to a species with winter quarters mostly within the Mediterranean basin (Berthold *et al.* 1990).

To analyse the migratory patterns of the different age classes, a sub-sample of 13 species was chosen, excluding those characterized by a complete winter moult for both adults and first-year birds.

PRESENTATION OF RESULTS

The seasonal trapping patterns will be shown on the basis of standardized 5-day periods (Berthold 1973); a Harvard Graphics package has been used to produce the graphs. Since our ringing activity was targeted to study the peak spring migratory period, we did not fully cover the whole migratory season for any of the species. Only "relative" median dates could therefore be calculated, with reference to our trapping period; these will simply be used to quantify the observed time gap between

TABLE 1
MAIN WINTER QUARTERS OF THE SELECTED SPECIES; ENGLISH NAMES FROM HOWARD & MOORE (1991)

Species	North of Sahara	South of Sahara North of Equator	South of Equator
European Nightjar *Caprimulgus europaeus*		X	X
Barn Swallow *Hirundo rustica*			X
Yellow Wagtail *Motacilla flava*		X	X
Common Redstart *Phoenicurus phoenicurus*		X	
Whinchat *Saxicola rubetra*		X	
Northern Wheatear *Oenanthe oenanthe*		X	
Black-eared Wheatear *Oenanthe hispanica*		X	
Subalpine Warbler *Sylvia cantillans*		X	
Whitethroat *Sylvia communis*		X	
Blackcap *Sylvia atricapilla*	X	X	
Collared Flycatcher *Ficedula albicollis*			X
Pied Flycatcher *Ficedula hypoleuca*		X	
Golden Oriole *Oriolus oriolus*			X
Red-backed Shrike *Lanius collurio*			X
Woodchat Shrike *Lanius senator*		X	
Ortolan Bunting *Emberiza hortulana*		X	

sex/age classes within our temporal sample, and are not meant to indicate the median dates of the spring migration of the different species. Non-parametric tests have been chosen for the statistical analyses following Siegel (1956). For all tests the SPSS-PC package has been used.

RESULTS

General aspects

In previous analyses referred to the first two years of the project, Spina *et al.* (1993) could show a general similarity of trapping patterns in a same season on the 4 islands for several species, with passage peaking on a single pentad on all sites. This seems to be the case also when taking into account this larger sample from 4 years (1988, 1990-1992), as exemplified in Fig. 2 for the Whinchat *Saxicola rubetra*. On the basis of these indications, we decided to clump together data collected on all islands in the same period in order to obtain a general description and perform a pooled analysis of the seasonal patterns of sexes.

Annual variability in trapping patterns

General trapping patterns for a given species (males and females together) may vary among years; when testing for example the seasonal trapping patterns of Whinchat across years, we always found significant differences (6 tests, each year vs. the others, all cases with $p < 0,05$, Mann-Whitney U-test). Nevertheless, although the timing of the

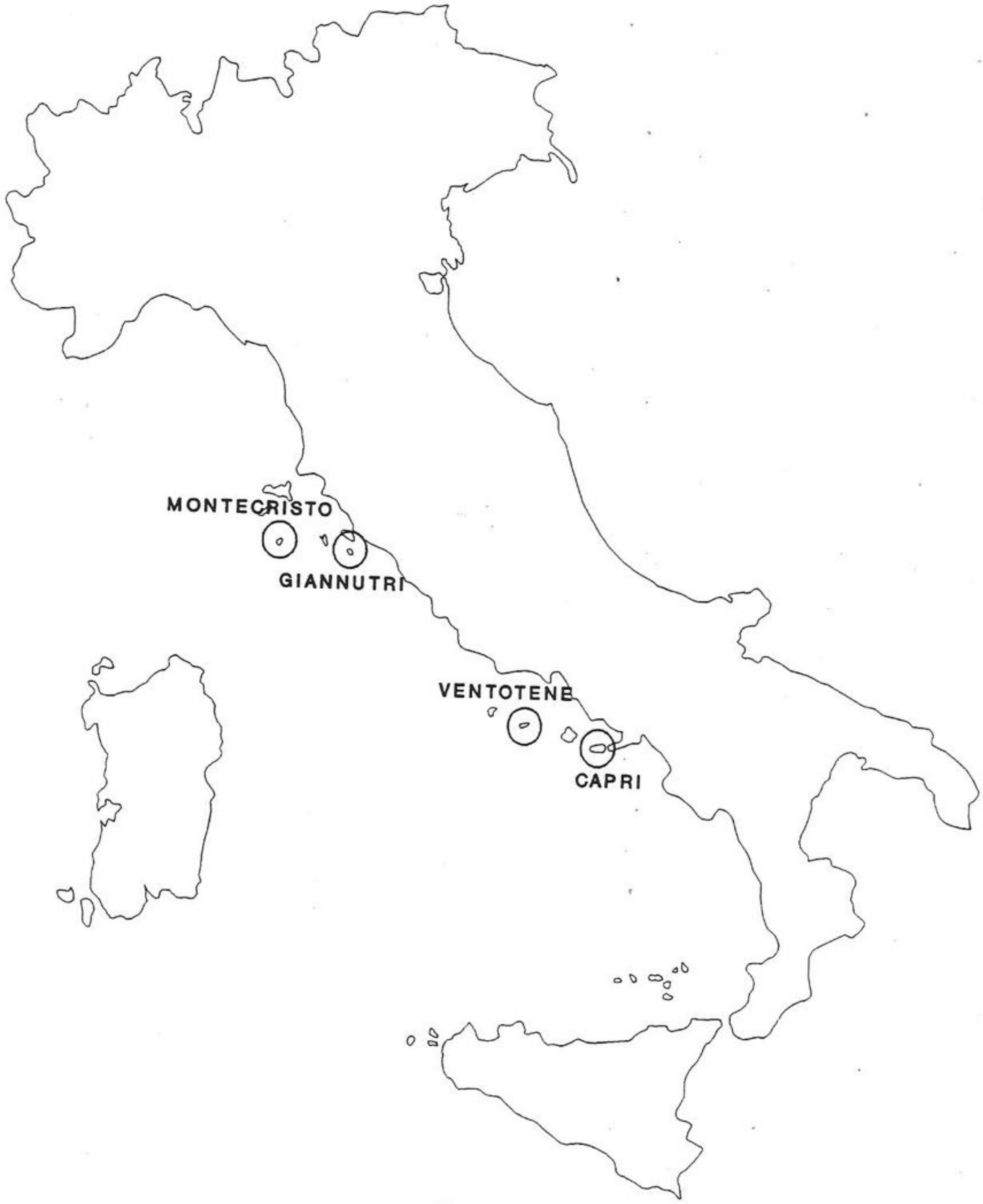

FIGURE 1

Location of the four selected islands: Montecristo, Giannutri, Ventotene, Capri (redrawn from Spina *et al.*, 1993).

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spring migration of a species may be varying from year to year, an earlier passage of males with respect to females seems to be a general feature; for instance in Whinchat, despite the already mentioned inter-annual seasonal variability, when testing the trapping distribution of males vs. females in the 4 years and in the 4 sites, 15 out of the 16 tests confirmed a significantly earlier passage of males. A summary of the variability in the time gap (expressed in days) between the median dates of males and females recorded for all species in the 4 years and on the different islands is reported in Table 2. Negative values for lower quartiles, indicating an earlier passage of females, might be due to sampling periods in the case of Barn Swallow *Hirundo rustica* and Blackcap, and still need to be interpreted for the Golden Oriole.

On the basis of these general results, we de-

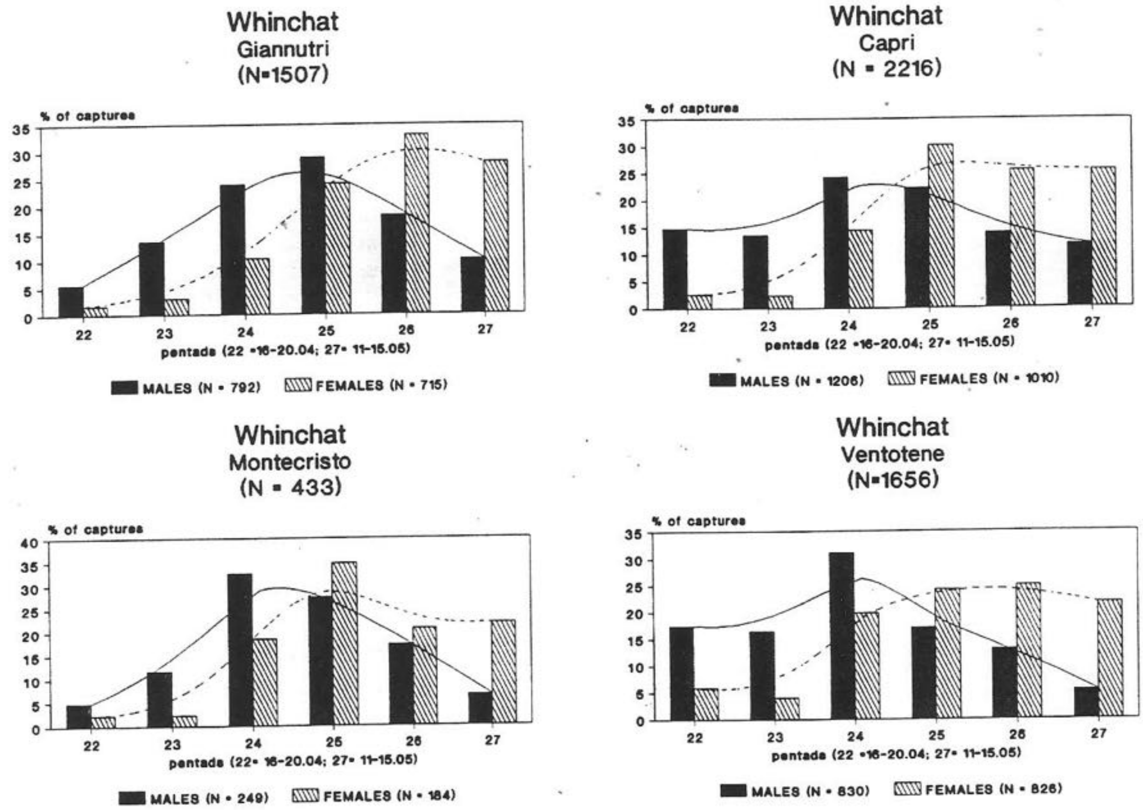

FIGURE 2

Trapping patterns of male and female Whinchat on the four sites. Percentage per pentad refers to the overall sample.

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cided to synthetize this phenomenon by analysing the overall samples (all years and sites) of the 16 species.

General trapping patterns of sexes and median dates

The seasonal trapping patterns of males and females across the Central Mediterranean is reported in Figs. 3-5. Although marked variations in the time gap between sexes as derived from these 4-year samples may be observed within our selected species, an earlier spring passage of males than females appears to be a widespread strategy, being observed in 14 out of 16 cases (Table 3). A significant difference in the general trapping patterns of sexes is found in 13 out of 16 species (Mann Whitney U-test, Table 3). The relatively small Ortolan Bunting *Emberiza hortulana* sample might mask a real difference in the phenology of sexes, given also the clear gap in median trapping dates recorded in our case.

Only in Subalpine Warbler *Sylvia cantillans* and Blackcap has the same median date been found for both sexes; it is worth noting that our main study period does not cover the peak migratory

TABLE 2

TEMPORAL GAP IN MEDIAN DATES OF PASSAGE OF MALES AND FEMALES IN 14 SELECTED SPECIES CALCULATED ON THE BASIS OF THE YEARLY SAMPLES ON EACH ISLAND AND EXPRESSED IN DAYS (MEDIAN OF FEMALES MINUS MEDIAN OF MALES). FOR EUROPEAN NIGHTJAR AND ORTOLAN BUNTING SUBSAMPLES WERE TOO SMALL

Species	Q.L	Q.S.	Q.U.
Barn Swallow	−1	0	1
Yellow Wagtail	1	6,5	9
Common Redstart	3	5	7
Whinchat	3	6	8
Northern Wheatear	0	1	3
Black-eared Wheatear	1	2,5	9
Subalpine Warbler	0	1	2
Whitethroat	1	2,5	7
Blackcap	−4	−1	1
Collared Flycatcher	0	0	4
Pied Flycatcher	2	3	6
Golden Oriole	−1	1	7
Red-backed Shrike	0	1	4
Woodchat Shrike	0	3	6

Q.L.: Lower quartile (25th percentile)
Q.S.: Second quartile (50th percentile)
Q.U.: Upper quartile (75th percentile).

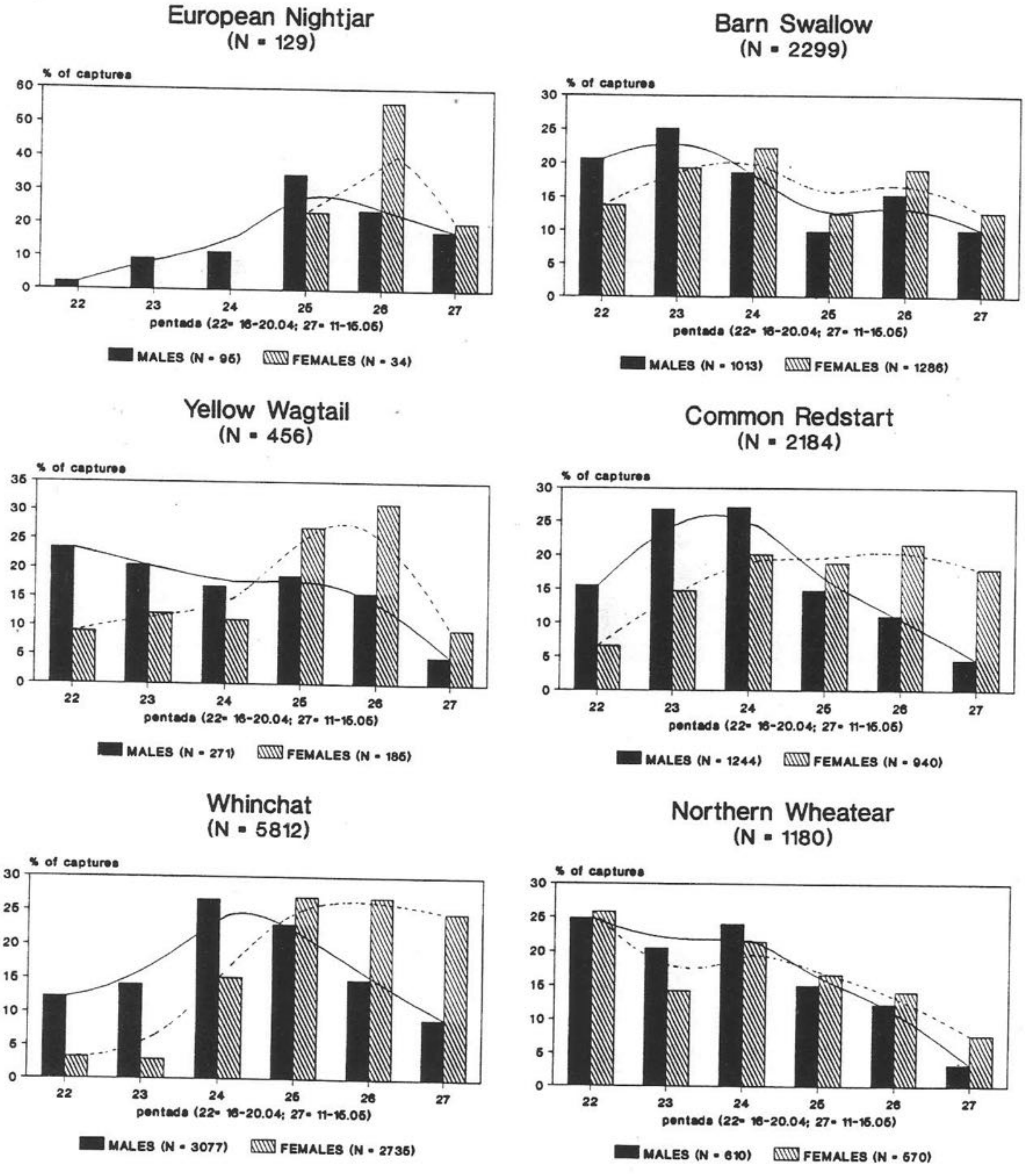

FIGURE 3

Trapping patterns of male and female European Nightjar, Barn Swallow, Yellow Wagtail, Common Redstart, Whinchat, Northern Wheatear. Percentage per pentad refers to the overall sample.

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season for these two species (Spina *et al.* 1993). In Blackcap, when testing the trapping patterns of sexes in each year and site (see above), 15 out of 16 cases resulted in no significant differences ($p > 0,05$, Mann-Whitney U-test).

Phenology of sexes in earlier and later migrants

Our main study period between mid-April and mid-May seems appropriate to investigate the differential migration of sexes in most of the selected species, since it covers their main spring passage periods (Spina et al. 1993); exceptions are represented by the earlier and later migrants, peaking before (Northern Wheatear *Oenanthe oenanthe*, Subalpine Warbler, Blackcap) or after (Whitethroat *Sylvia communis*, Red-backed Shrike *Lanius collurio*) the sampling period. For the former three species we therefore took into account also

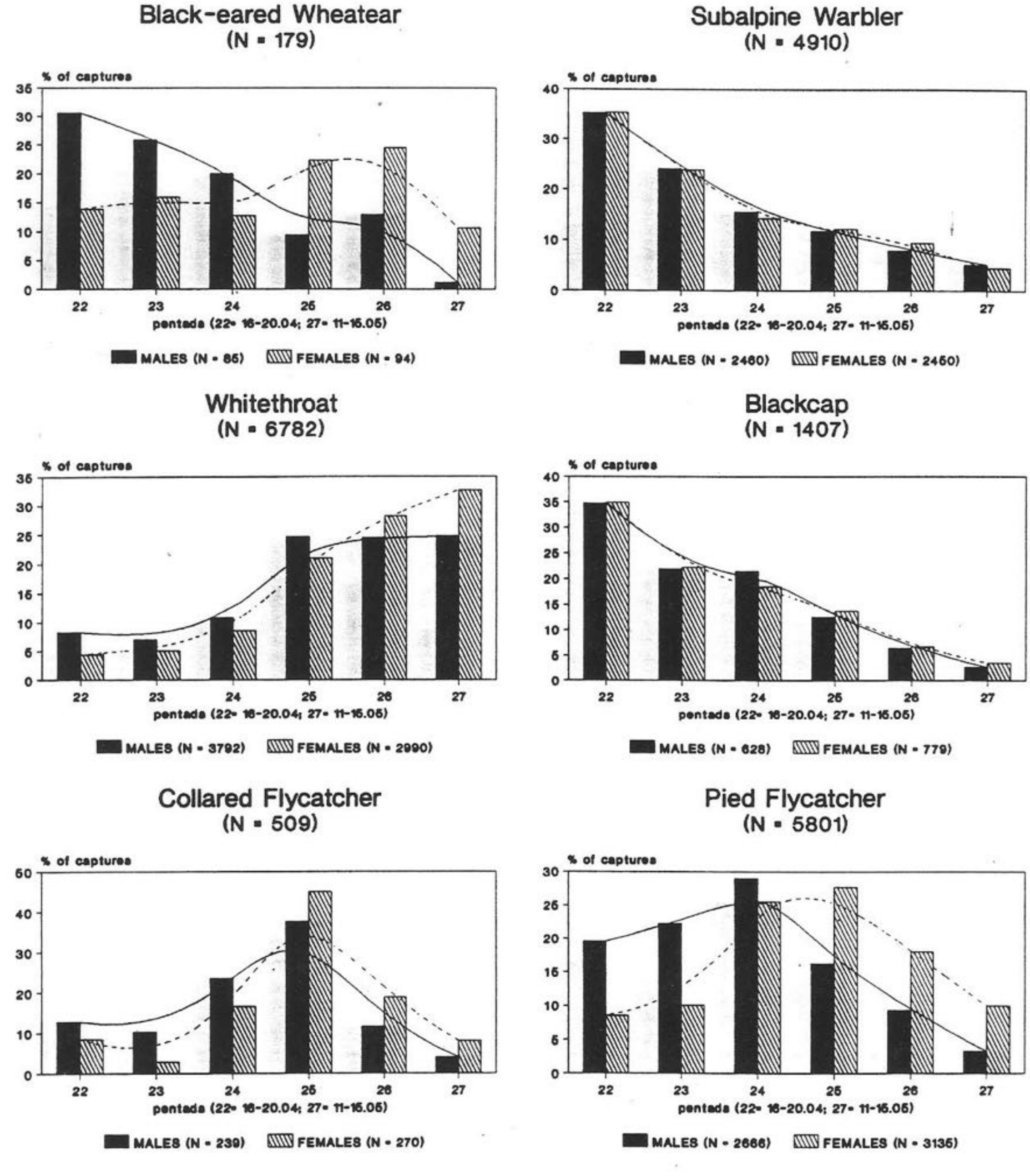

FIGURE 4

Trapping patterns of male and female Black-eared Wheatear, Subalpine Warbler, Whitethroat, Blackcap, Collared Flycatcher, Pied Flycatcher. Percentage per pentad refers to the overall sample.

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data collected earlier in the season in 1989 (mid-March to mid-April), calculating the percentage of males and females with respect to the total number of birds ringed in each pentad (Fig. 6a). Although the earlier phase of migration has been sampled in only one season, the general trapping patterns which derive from this analysis suggest how also in these earlier migrants males are passing through the Central Mediterrenean ahead of the females. In the case of the Blackcap, an even earlier sampling would be needed to get a better idea of the incidence of males at the start of the spring movements.

Similarly, since we did not cover the final stages of spring migration after mid-May, the same kind of calculation has been plotted for the two species

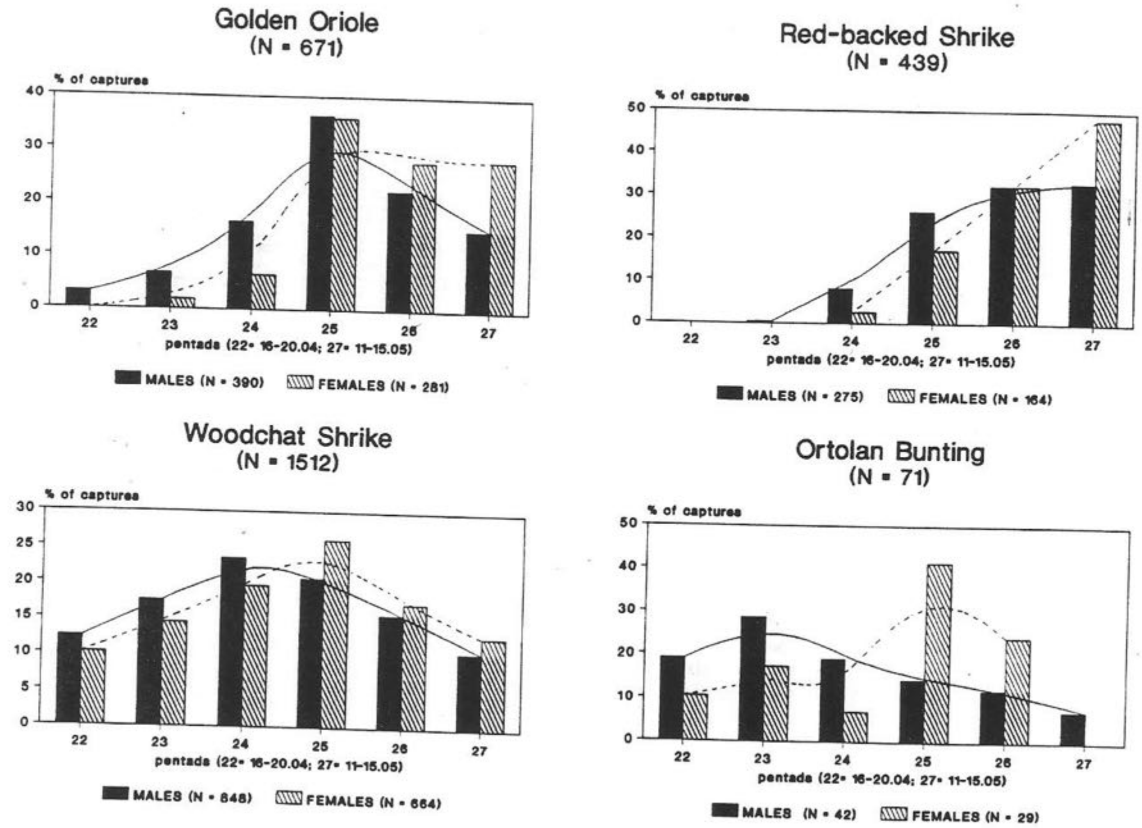

FIGURE 5

Trapping patterns of male and female Golden Oriole, Red-backed Shrike, Woodchat Shrike, Ortolan Bunting. Percentage per pentad refers to the overall sample.

TABLE 3

SAMPLE SIZE MEDIAN TRAPPING DATE AND MANN-WHITNEY U-TEST (DATE VS SEX) FOR MALES AND FEMALES IN 16 SPECIES REFERRED TO THE OVERALL SAMPLES COLLECTED ON THE 4 ISLANDS DURING THE 4 YEARS (1988, 1990-92)

Species	Sample Size		Median Trapping Date (Day/Month)		2-tailed P	
	Males	Females	Males	Females		
European Nightjar	95	34	04.05	08.05	0,0026	
Barn Swallow	1 013	1 286	27.04	30.04	0,0000	
Yellow Wagtail	271	185	28.04	03.05	0,0000	
Common Redstart	1 244	940	27.04	02.05	0,0000	
Whinchat	3 077	2 735	30.04	06.05	0,0000	
Northern Wheatear	610	570	27.04	28.04	0,0251	
Black-eared Wheatear	85	94	23.04	01.05	0,0000	
Subalpine Warbler	2 460	2 450	23.04	23.04	0,6356	N.S.
Whitethroat	3 792	2 990	05.05	08.05	0,0000	
Blackcap	628	779	24.04	24.04	0,9650	N.S.
Collared Flycatcher	239	270	01.05	02.05	0,0004	
Pied Flycatcher	2 666	3 135	27.04	02.05	0,0000	
Golden Oriole	390	281	04.05	06.05	0,0000	
Red-backed Shrike	275	164	08.05	10.05	0,0001	
Woodchat Shrike	848	664	30.04	02.05	0,0014	
Ortolan Bunting	42	29	26.04	03.05	0,0961	N.S.

N.S. not significant (Significance level = P < 0,05) of later migrants which show strong movements for both sexes still at the end of our study period (Whitethroat, Red-backed Shrike, Fig. 6b); again it is evident how males precede females in the northward movements.

Phenology of age classes

We also took into account the seasonal trapping patterns of adults (EURING code 6) and yearlings (EURING code 5) in the 13 out of 16 species which can be aged in spring. For this purpose, we analysed the temporal relationships between median trapping dates of adults with respect to yearlings with reference to single years (Table 4) and sites (Table 5). For this purpose we excluded 2 species (Yellow Wagtail, Ortolan Bunting), for which too small and scattered sub-samples had been collected in the single years or sites; a few small sub-samples from given years or sites referred also to some of the other species were excluded as well.

Given the high frequency of earlier movements by adults, we plotted (Figs. 7-11) and analysed the age-related seasonal trapping patterns for the two sexes as derived from the general pooled samples for all 13 species (all years and sites). Median trapping dates of adult birds are earlier than those of yearlings in 18 out of 26 cases (Table 6); the same median date is found in 3 of 26 cases, while earlier passage of yearlings has been recorded in 5 of 26 cases. A slightly higher incidence of earlier movements of adults is suggested in females (10 of 13) than males (8 of 13) although, when testing these qualitative differences in age-related trapping patterns within our sample of species, the level of statistical significance is reached in 7 out of 13 cases in males and in 5 out of 13 in females (Table 6, Mann-Whitney U-test).

Our results seem to indicate, for both sexes, an earlier passage of adults than yearlings as being a fairly widespread strategy.

DISCUSSION

Earlier passage of males than females during spring migration has been found to be a widespread feature in our selected species, apparently irrespective of the location of the main winter quarters in Africa. This general picture from an intermediate stage of spring migration does not allow to estimate whether the differences in timing originate at the departure from the winter quarters, or at any stage en route. Males might be passing earlier when coming from winter quarters north of those reached by the females (Ketterson & Nolan 1983), as recorded for Yellow Wagtail or Blackcap (Terrill & Berthold 1989; Wood 1992); they might also precede females by flying faster, as suggested for the Willow Warbler (Hedenstroem & Pettersson 1986; Bezzi & Gustin 1991).

TABLE 4

COMPARISON OF MEDIAN TRAPPING DATES OF ADULTS (EURING CODE 6) AND YEARLINGS (2ND-YEAR BIRDS EURING CODE 5) OF 11 SPECIES WITH RESPECT TO THE TOTAL SAMPLES (ALL ISLANDS TOGETHER) COLLECTED IN EACH YEAR. CHI-SQUARE ADULTS VS YEARLINGS = 7,577, P = 0,006

	No. of cases
Adult males earlier than yearling males	24
Adult males later than yearling males	10
Same median date for adult and yearling males	9
Adult females earlier than yearling females	26
Adult females later than yearling females	7
Same median date for adult and yearling females	9
Adults earlier than yearlings	50
Adults later than yearlings	17
Same median date for adults and yearlings	18

TABLE 5

COMPARISON OF MEDIAN TRAPPING DATES OF ADULTS (EURING CODE 6) AND YEARLINGS (2ND-YEAR BIRDS EURING CODE 5) OF 11 SPECIES WITH RESPECT TO THE TOTAL SAMPLES (ALL YEARS TOGETHER) COLLECTED IN EACH ISLAND. CHI-SQUARE ADULTS VS YEARLINGS = 8,906, P = 0,003

	No. of cases
Adult males earlier than yearling males	27
Adult males later than yearling males	4
Same median date for adult and yearling males	12
Adult females earlier than yearling females	27
Adult females later than yearling females	5
Same median date for adult and yearling females	6
Adults earlier than yearlings	54
Adults later than yearlings	9
Same median date for adults and yearlings	18

TABLE 6

MEDIAN TRAPPING DATE (DAY/MONTH) OF THE DIFFERENT SEX AND AGE CLASSES AND MANN-WHITNEY U-TEST DATE VS AGE IN 13 SPECIES REFERRED TO THE OVERALL SAMPLES COLLECTED ON THE 4 ISLANDS DURING THE 4 YEARS (1988, 1990-92)

	Males				Females			
Species	Adults	Yearlings	2-tailed P	Sample size (Ad./2Y)	Adults	Yearlings	2-tailed P	Sample size (Ad./2Y)
Yellow Wagtail	26.04	28.04	0,231 N.S.	50/165	03.05	03.05	0,9158 N.S.	19/117
Common Redstart	26.04	28.04	0,1512 N.S.	326/764	29.04	05.05	0,0143	113/325
Whinchat	29.04	30.04	0,0112	968/1944	03.05	06.05	0,0093	493/1907
Northern Wheatear	28.04	27.04	0,4027 N.S.	180/414	25.04	28.04	0,0570 N.S.	132/307
Black-eared Wheatear	21.04	26.04	0,0016	40/44	01.05	01.05	0,7996 N.S.	33/46
Subalpine Warbler	25.04	23.04	0,0052	243/1393	23.04	23.04	0,8465 N.S.	98/1370
Whitethroat	05.05	06.05	0,0001	721/2202	07.05	08.05	0,0000	220/2068
Blackcap	26.04	25.04	0,3611 N.S.	99/379	27.04	28.04	0,4717 N.S.	105/407
Collared Flycatcher	01.05	30.04	0,4262 N.S.	106/81	02.05	04.05	0,9190 N.S.	43/94
Pied Flycatcher	28.04	27.04	0,0069	446/1520	01.05	03.05	0,0001	588/1845
Golden Oriole	01.05	05.05	0,0000	107/160	05.05	07.05	0,1429 N.S.	55/134
Woodchat Shrike	29.04	02.05	0,0000	339/453	30.04	03.05	0,0016	268/362
Ortolan Bunting	20.04	30.04	0,3367 N.S.	3/20	25.04	03.05	0,0640 N.S.	4/17

N.S. = not significant (Significance level: $P < 0,05$)

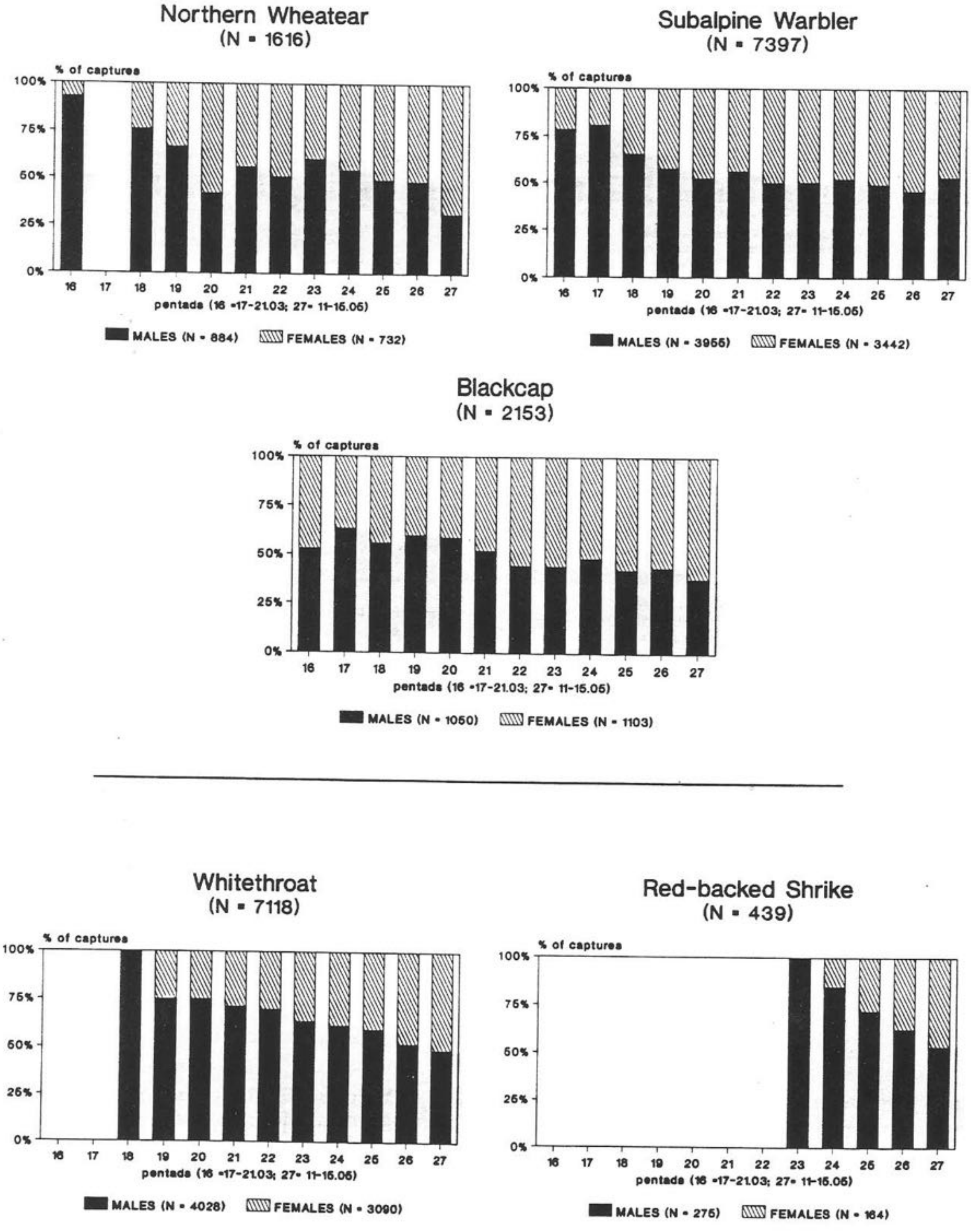

FIGURE 6

(A) Percentage of male and female Northern Wheatear, Subalpine Warbler, Blackcap with respect to the total number of birds ringed in each pentad, taking into account also data collected earlier in the season (1989).

(B) Percentage of male and female Whitethroat, Red-backed Shrike with respect to the total number of birds ringed in each pentad, taking into account also data collected earlier in the season (1989).

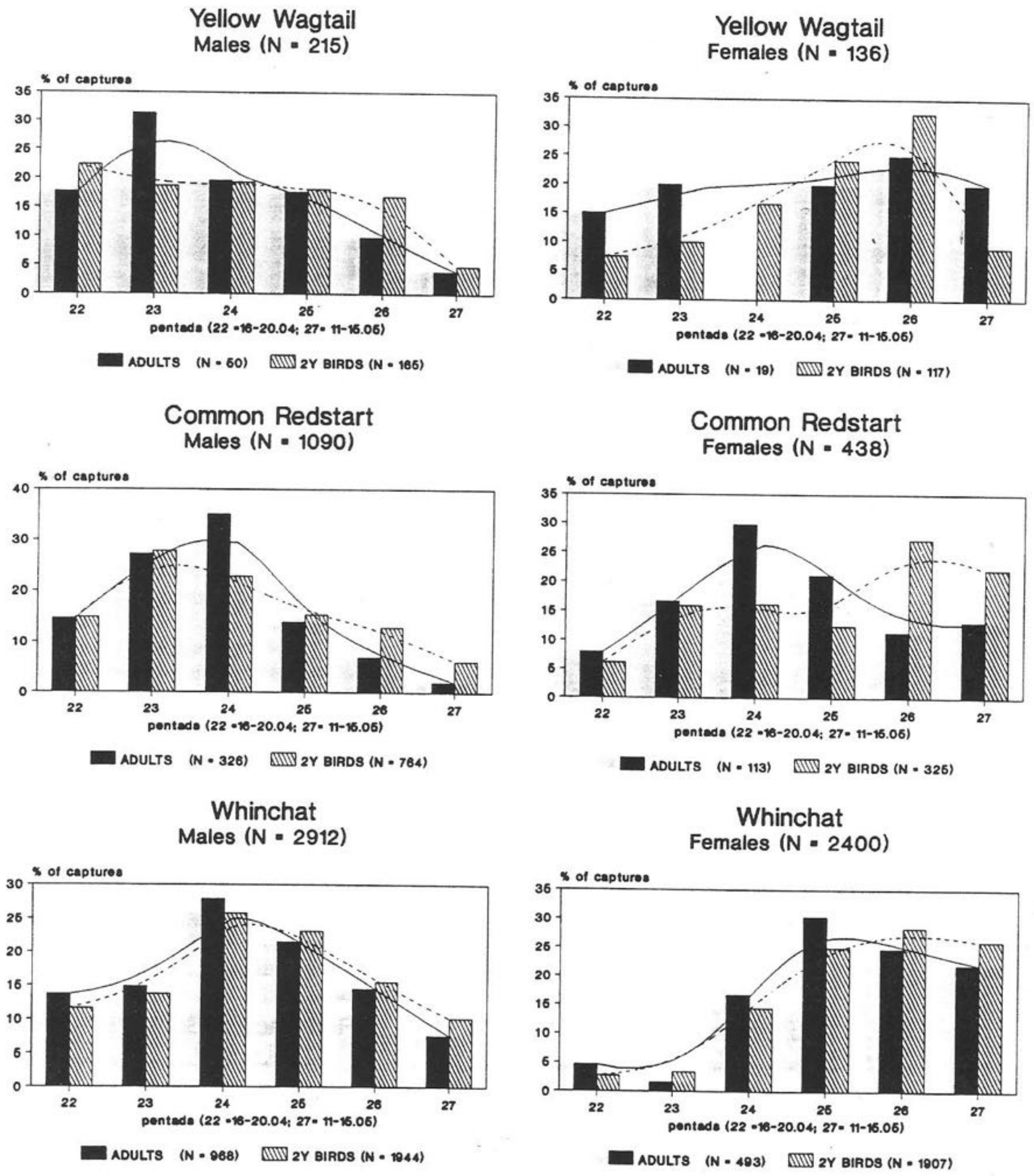

FIGURE 7

Trapping patterns of adults (EURING code 6) and yearlings (2-Year birds EURING code 5) for male and female Yellow Wagtail, Common Redstart, Whinchat. Percentage per pentad refers to the overall sample.

From our results, this general strategy seems to be positively selected both in polygynous and monogamous species, suggesting that an already defined territory on the arrival of females could be a positive prerequisite for breeding.

Another general feature of spring migration, again suggested in many of our study cases, seems to be represented by earlier movements of adults than inexperienced yearlings. In these species of long-distance migrants, endogenous circannual rhythms act as important control mechanisms of the different phases of migration; in particular, the amount of migratory activity has proved not to be related to age (Berthold 1986). The same endogenous rhythms may be extremely important for triggering the spring departure from the winter quarters, although interactions between circannual rhythmicity and external factors are to be

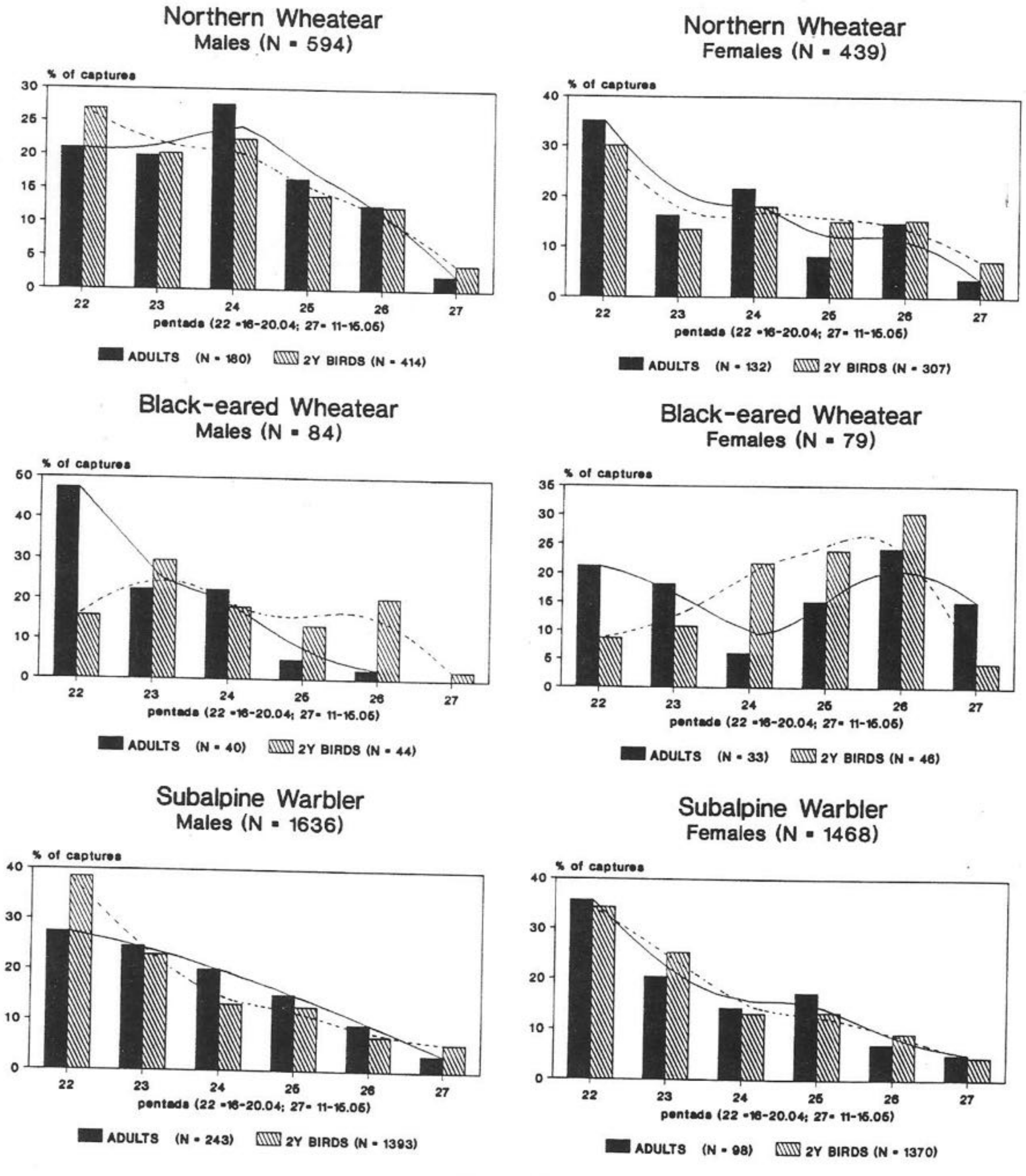

FIGURE 8

Trapping patterns of adults (EURING code 6) and yearlings (2-Year birds EURING code 5) for male and female Northern Wheatear, Black-eared Wheatear, Subalpine Warbler. Percentage per pentad refers to the overall sample.

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taken into account also in Africa (Gwinner 1990).

Given these general assumptions, in our case we might accept that birds of the same sex, belonging to both age classes from a given population, should not differ as to the onset of their pre-migratory phase by the end of the wintering period. They might therefore presumably be leaving together from their communal African quarters; faster movements of adults, often characterized by more pointed wings (Alatalo *et al.* 1984), could then be one of the possible explanations for such shifted passage. Both occupancy of the best territories by more experienced adult birds and avoidance of direct conflict upon settlement by yearlings with respect to potentially dominant adults might explain the incidence of this strategy.

The general occurrence of both earlier passage of males and adults is a clear indication of the adaptive value of these features of spring migration.

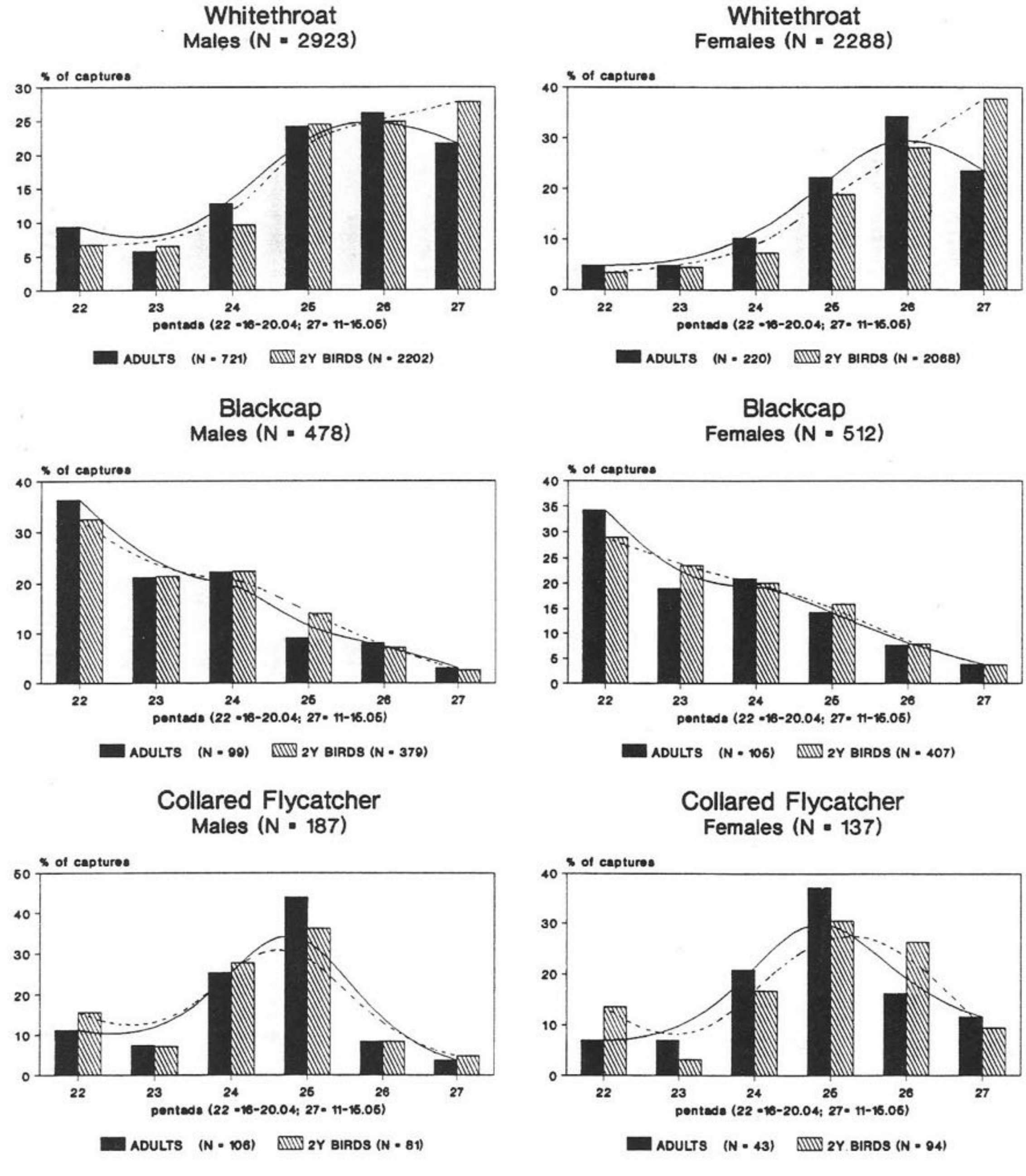

FIGURE 9

Trapping patterns of adults (EURING code 6) and yearlings (2-Year birds EURING code 5) for male and female Whitethroat, Blackcap, Collared Flycatcher. Percentage per pentad refers to the overall sample.

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Results from the Progetto Piccole Isole EURING (I.N.F.S.): paper N. 9.

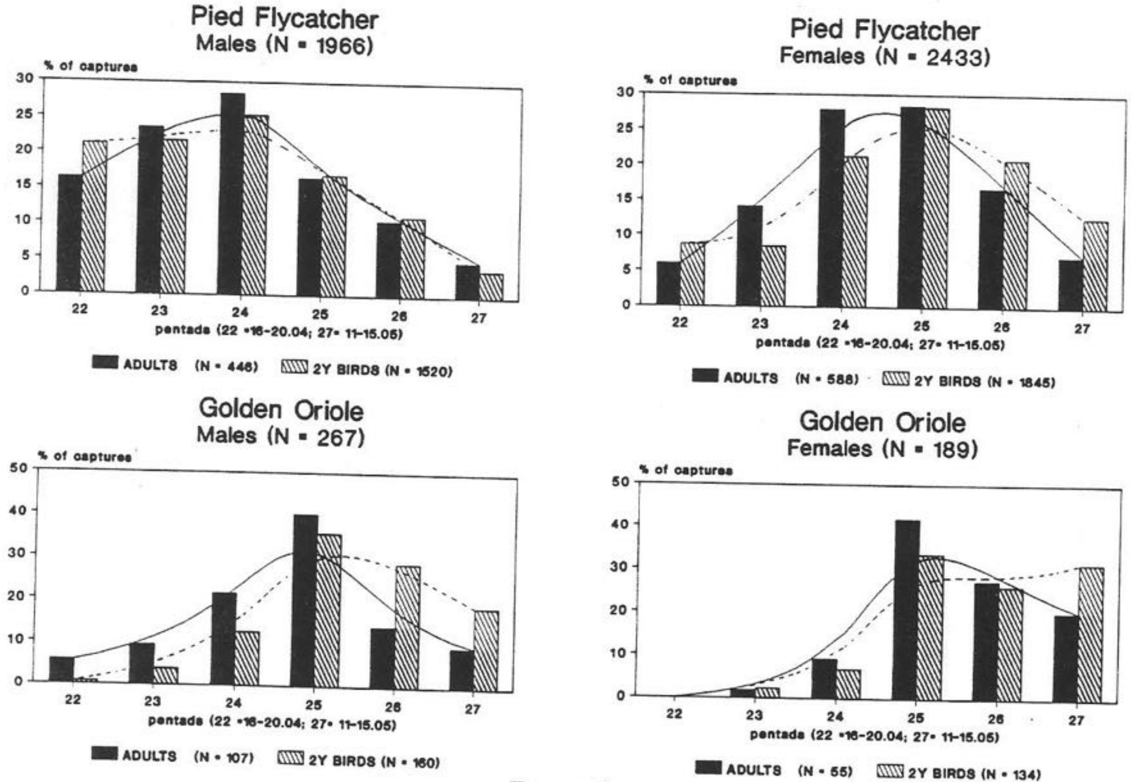

FIGURE 10

Trapping patterns of adults (EURING code 6) and yearlings (2- Year birds EURING code 5) for male and female Pied Flycatcher, Golden Oriole. Percentage per pentad refers to the overall sample.

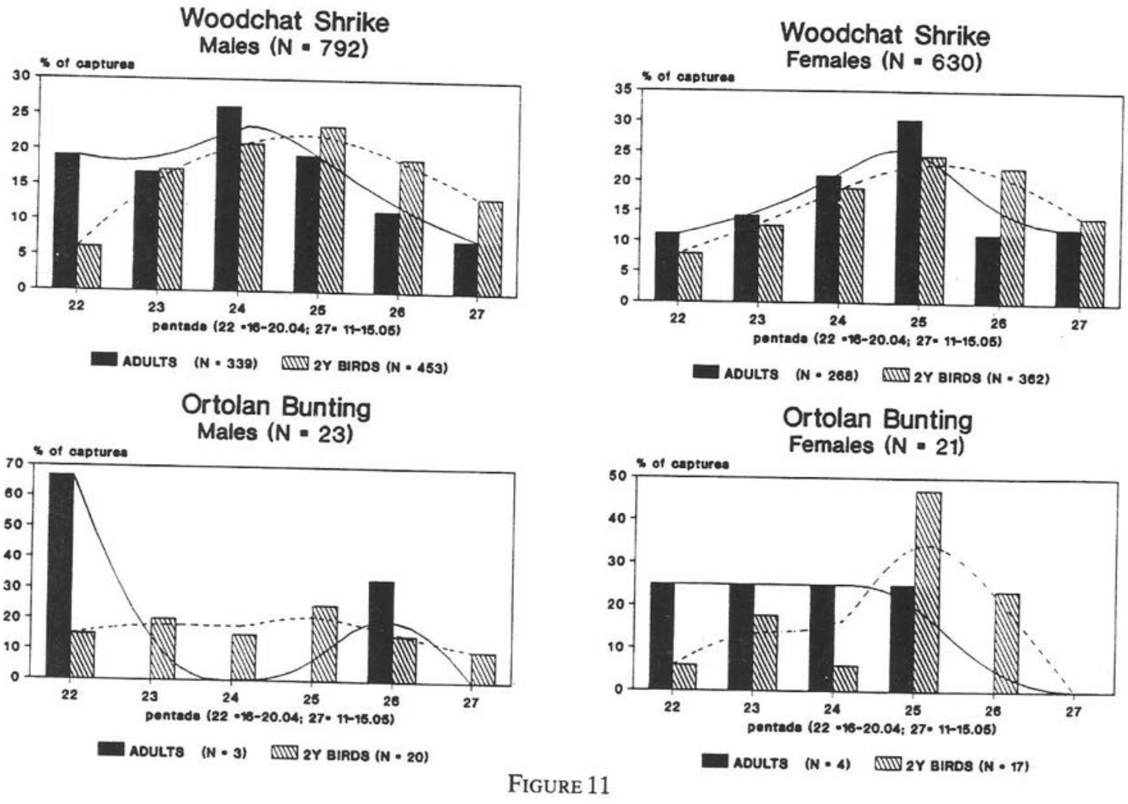

FIGURE 11

Trapping patterns of adults (EURING code 6) and yearlings (2-Year birds EURING code 5) for male and female Woodchat Shrike, Ortolan Bunting. Percentage per pentad refers to the overall sample.

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