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The timing of spring migration in trans-Saharan migrants: a comparison between Ottenby, Sweden and Capri, Italy

Vårflyttningens tidsmönster hos tropikflyttare: en jämförelse mellan Ottenby, Sverige och Capri, Italien

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Abstract

Some migratory birds have advanced their spring arrival to Northern Europe, possibly by increasing the speed of migration through Europe in response to increased temperature en route. In this paper we compare the phenology of spring arrival of seven trans-Saharan migrants along their migration route and test for patterns indicating that migration speed varied over the season using long-term data collected on the Italian island of Capri and at Ottenby Bird Observatory, Sweden. There was a linear relationship between median arrival dates on Capri and at Ottenby. The slope was not significantly different from one. On average, the seven species arrived 15 days later at Ottenby compared to Capri. There was a (non-significant) negative relationship between the species-specific arrival dates at Capri and the differences in median arrival dates between Capri and Ottenby, possibly indicating a tendency towards faster migration through Europe later in the season. To what extent different species are able to speed up their migration to benefit from the advancement of spring events is unknown.

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Introduction

Over the past decades many organisms have advanced the timing of spring events, most likely in response to recent climate change (e.g. Stenseth et al. 2002, Walther et al. 2002, Parmesan & Yohe 2003). For instance, recent empirical work has demonstrated changing phenology patterns in the flowering of plant species (Fitter & Fitter 2002), in the emergence from pupae in insects (Roy & Sparks 2000), and in earlier breeding by amphibians (Beebee 1995) and birds (Crick et al. 1997). Most ornithological studies demonstrating temporal trends towards earlier spring arrival or egg-laying dates have been carried out in the temperate region of Europe and North America (reviewed by Lehikoinen et al. 2004, Dunn 2004), whereas only a few publications cover the Mediterranean region or Africa (e.g. Peñuelas et al. 2002, Sanz et al. 2003, Gordo et al. 2005). Thus, at present our understanding of these patterns in migrant birds is somewhat biased towards the situation close to the breeding areas, which makes it difficult to identify to what extent arrival patterns in Northern Europe are caused by processes in Africa or along the migration route through Europe.

One hypothesis to explain how tropical migrants can advance their spring arrival to Northern Europe is that the migration speed through Europe has increased, as suggested by e.g. Hüppop & Hüppop (2003). A more rapid spring migration in response to increased temperature *en route* has recently been demonstrated in the Pied Flycatcher *Ficedula hypoleuca* (Both et al. 2005). However, the ability to speed up migration may be affected

by the "normal" speed of migration, which in turn may vary across species.

In this paper, we compare the phenology of spring arrival of seven trans-Saharan migrants along their migration route by analysing long-term data collected on the island of Capri, Italy, and at Ottenby Bird Observatory, Sweden. By analysing the relationship between arrival dates at Ottenby and on Capri we tested for patterns indicating whether migration speed varied over season. Late migrating species may be more time constrained than early migrating species, and they may therefore migrate faster.

Material and methods

Study sites

The island of Capri is situated c. 5 km off mainland Italy, in the bay of Naples, with the trapping site (40°33'N, 14°15'E) located about 400m above sea level (Pettersson et al. 1990, Hjort 2006). In spring, many migrating birds stop to rest, at least for a short time (Holmgren & Engström 2006), on this island after their passage over the Mediterranean Sea. The trapping area on Capri lies mainly within the perimeter of the walls of the old castle Castello Barbarossa and comprises c. 2 ha of macchia vegetation typical for this region of the Mediterranean. However, the plant species and especially the structural composition of the vegetation has changed over the study period, most dramatically by fires (the latest occurred in 1989), which killed the larger pine trees and favoured lower bush vegetation. This could potentially have had an effect on the species composition of the birds trapped, considering that different species have different habitat preferences and the trapping efficiencies of the nets may have changed.

On Capri data have been collected during 45 springs from 1956 to 2004 (no trapping in the period 1982–1985), with the coverage varying from 13 to 89 days per season (Table 1). Birds were trapped with mist nets throughout the study, but the number of nets used varied considerably between, and sometimes also within, years. However, we could not take into account variation in trapping effort in this study. The spring trapping season on Capri is included in the Progetto Piccole Isole, run by the Istituto Nazionale per la Fauna Selvatica (Ozzano Emilia, BO) (Spina 2006).

Ottenby Bird Observatory (56°12' N, 16°24' E) is situated at the southernmost point of Öland, a 137 km long island c.10 km off the coast of southeastern Sweden. The trapping area in the observatory garden is 1.2 hectares and contains most of the higher vegetation within the nearest 2 km. It is surrounded by water on three sides and by grazed meadows to the north. Birds have been caught at Ottenby in funnel traps of Helgoland-type since the first year of trapping in 1946, and mist nets have been used since 1959. Since 1980 the numbers of nets and traps, their position and use in spring have been strictly standardised. We considered data for 53 spring seasons from 1952–2004 as reliable for the purpose of this study. Details on the data collection at Ottenby Bird Observatory are given elsewhere, e.g. in Stervander et al. (2005).

Species analysed

We have compiled data for seven of the most numerously trapped bird species on Capri: Redstart *Phoenicurus phoenicurus*, Willow Warbler *Phylloscopus trochilus*, Icterine Warbler *Hippolais icterina*, Garden Warbler *Sylvia borin*, Common Whitethroat *Sylvia communis*, Spotted Flycatcher *Muscicapa striata* and Pied Flycatcher *Ficedula hypoleuca*. We have used ringing recoveries from birds ringed on Capri and elsewhere in the Campania region (Naples, Sorrento, Amalfi; Scebba (1993)), and recoveries of birds ringed at Ottenby to sketch putative breeding areas, migration flyways and possible wintering areas of the investigated species. An underlying assumption when comparing arrival times between Capri and Ottenby is that the species trapped belong roughly to the same population.

Statistical analyses

We estimated the median spring arrival date for each of the seven species. The estimated medians were not dependent on whether we only analysed data from years including ringing activity on both Capri and at Ottenby, and we therefore decided to keep data from all years. Due to the large samples, any effect of variability in ringing activity within and between seasons was effectively smoothened out.

Because there are observation errors in both the Capri and the Ottenby data sets we performed a reduced major axis (RMA) to test whether the relationship between median arrival on Capri and at Ottenby differed from unity. RMA regression minimize the product of the deviations from the regression line across both the x (Capri) and the y (Ottenby) variables.

Table 1. Ringing details and trapping data from Capri. No ringing in 1982–1985. Species: P.p. = Common Redstart *Phoenicurus phoenicurus*, H.i. = Icterine Warbler *Hippolais icterina*, S.c. = Common Whitethroat *Sylvia communis*, S.b. = Garden Warbler *Sylvia borin*, P.t. = Willow Warbler *Phylloscopus trochilus*, M.s. = Spotted Flycatcher *Muscicapa striata*, F.h. = Pied Flycatcher *Ficedula hypoleuca*.
Fångsuppgifter från ringmärkningen på Capri. Ingen ringmärkning åren 1982–1985. Arter: P.p. = rödstjärt, H.i. = härmsångare, S.c. = törnsångare, S.b. = trädgårdssångare, P.t. = lövsångare, M.s. = grå flugsnappare, F.h. = svartvit flugsnappare.

	Catch period *Fångstperiod*			Number of birds ringed *Antal märkta fåglar*						
Year	Start	Stop	Days	*P.p.*	*H.i.*	*S.c.*	*S.b.*	*P.t.*	*M.s.*	*F.h.*
1956	May 1	May 31	31	25	52	57	77	1	14	16
1957	Apr 1	May 30	60	164	320	227	445	69	125	88
1958	May 1	Jun 11	42	177	501	361	1248	26	339	54
1959	Apr 26	Jun 20	56	199	934	450	1305	53	664	264
1960	Apr 15	May 23	39	618	405	661	1327	235	347	539
1961	Mar 23	Jun 3	73	257	880	563	1472	89	880	286
1962	Mar 9	Jun 5	89	105	103	524	170	204	429	152
1963	Mar 24	May 31	69	196	436	330	683	135	578	343
1964	May 2	May 27	26	44	608	289	993	33	229	37
1965	Apr 14	May 27	44	178	420	451	557	378	203	138
1966	Apr 8	May 27	50	146	427	331	505	108	470	153
1967	Apr 11	Jun 7	58	286	368	240	384	257	194	355
1968	Apr 9	May 23	45	231	265	401	381	288	346	351
1969	Apr 1	May 25	55	197	213	408	163	384	294	180
1970	Apr 7	May 29	53	101	403	593	603	200	382	219
1971	Mar 24	Jun 5	74	140	195	305	223	140	300	144
1972	Apr 25	May 26	32	194	250	200	387	225	193	140
1973	Apr 8	May 26	49	89	403	178	266	101	327	114
1974	Apr 19	May 27	39	75	979	364	910	250	444	89
1975	Apr 11	Jun 2	53	160	374	401	546	124	722	261
1976	Apr 4	May 28	55	44	457	221	233	74	310	108
1977	Apr 19	May 23	35	94	149	188	206	70	241	110
1978	Apr 23	May 30	38	84	358	159	272	81	174	116
1979	Apr 14	May 23	40	108	624	368	666	282	58	183
1980	May 2	May 27	26	37	876	174	423	65	176	46
1981	Apr 15	May 23	39	88	485	171	180	97	195	174
1986	Apr 15	May 22	38	122	730	570	1113	273	474	465
1987	Apr 11	May 24	44	80	600	623	728	259	134	256
1988	Apr 16	May 23	38	41	366	185	237	125	280	176
1989	Mar 18	May 24	68	60	707	614	457	350	258	131
1990	Apr 5	May 23	49	95	757	902	614	197	572	465
1991	Apr 2	May 23	52	90	218	221	170	286	126	341
1992	Apr 5	May 22	48	69	798	419	350	364	538	188
1993	Apr 1	May 21	51	103	522	1105	748	433	324	453
1994	Apr 16	May 15	30	82	314	299	418	226	337	429
1995	Apr 17	May 15	29	81	236	314	302	241	199	357
1996	Apr 16	May 15	30	63	71	262	431	245	49	275
1997	Apr 16	May 15	30	185	334	519	367	422	291	358
1998	Apr 16	May 15	27	83	178	336	338	396	156	362
1999	Apr 16	May 15	29	79	451	448	876	321	245	286
2000	May 1	May 14	13	15	245	287	355	25	117	107
2001	Apr 16	May 15	27	119	79	314	284	457	298	497
2002	Apr 16	May 15	26	133	321	380	266	433	215	297
2003	Apr 16	May 15	30	74	876	320	487	317	260	566
2004	Apr 16	May 15	30	105	448	273	282	364	228	450
Total			1959	5716	19736	17006	23448	9703	13735	11119

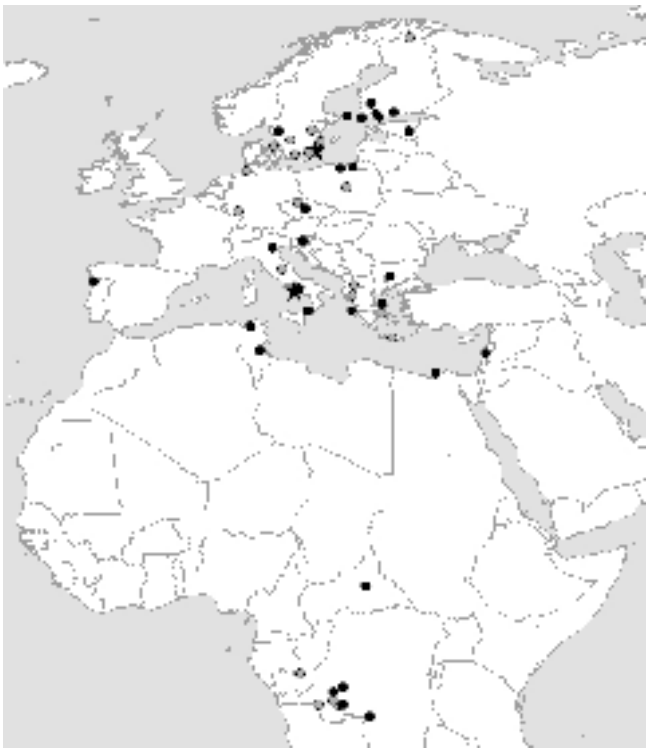

Figure 1. Map showing the recoveries of Spotted Flycatchers *Muscicapa striata* ringed or controlled at Ottenby (grey circles) and Capri (black circles). The black stars indicate the location of Ottenby and Capri. The sample from Capri also includes recoveries of birds ringed or recovered elsewhere in the Campania region (from Scebba 1993).
Återfyndskarta för grå flugsnappare Muscicapa *striata som ringmärkts eller kontrollerats vid Ottenby (grå cirklar) eller Capri (svarta cirklar). De svarta stjärnorna anger Ottenbys och Capris geografiska läge. Caprimaterialet inkluderar återfynd från hela Campania regionen (från Scebba 1993).*

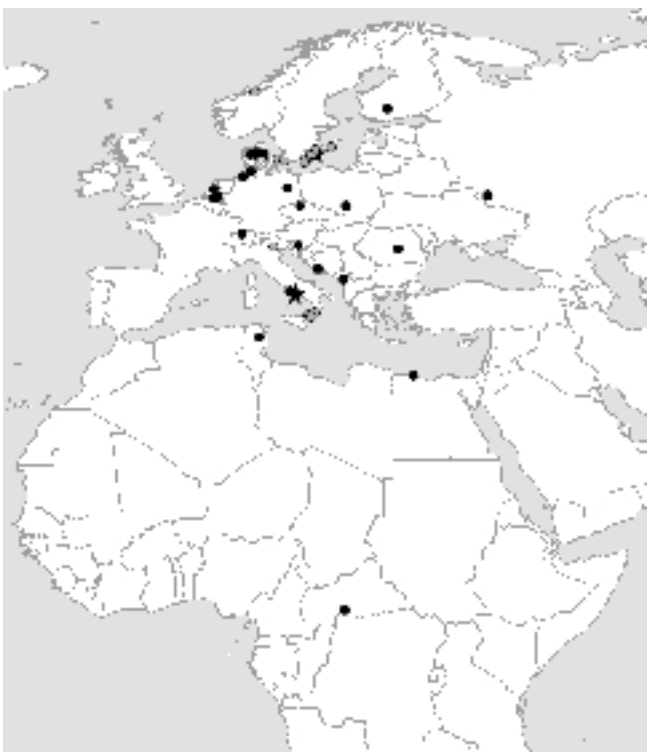

Figure 2. Map showing the recoveries of Icterine Warblers *Hippolais icterina* ringed or controlled at Ottenby (grey circles) and Capri (black circles). The black stars indicate the location of Ottenby and Capri. The sample from Capri also includes recoveries of birds ringed or recovered elsewhere in the Campania region (from Scebba 1993).
Återfyndskarta för Härmsångare Hippolais icterina *som ringmärkts eller kontrollerats vid Ottenby (grå cirklar) eller Capri (svarta cirklar). De svarta stjärnorna anger Ottenbys och Capris geografiska läge. Caprimaterialet inkluderar återfynd från hela Campania regionen (från Scebba 1993).*

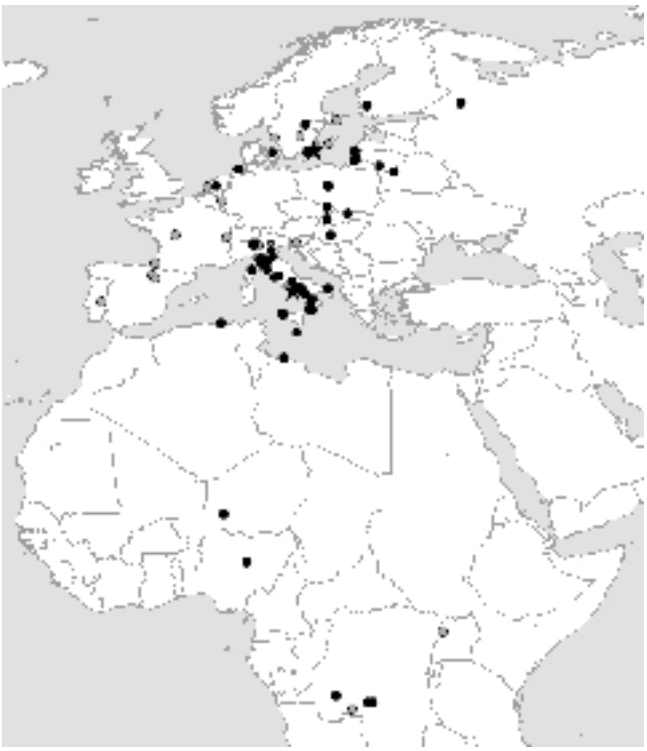

Figure 3. Map showing the recoveries of Garden Warblers *Sylvia borin* ringed or controlled at Ottenby (grey circles) and Capri (black circles). The black stars indicate the location of Ottenby and Capri. The sample from Capri also includes recoveries of birds ringed or recovered elsewhere in the Campania region (from Scebba 1993).
Återfyndskarta för Trädgårdssångare Sylvia borin *som ringmärkts eller kontrollerats vid Ottenby (grå cirklar) eller Capri (svarta cirklar). De svarta stjärnorna anger Ottenbys och Capris geografiska läge. Caprimaterialet inkluderar återfynd från hela Campania regionen (från Scebba 1993).*

Results

The ringing recoveries indicate that Spotted Flycatchers and Icterine Warblers (Figures 1 and 2) passing Capri follow a central flyway in Europe and Africa, and are later found in the general direction of Ottenby. A similar pattern was also found for Redstarts, Willow Warblers, Common Whitethroats and Pied Flycatchers (not shown). On the other hand, the recoveries of Garden Warblers suggest a more eastern origin of the birds trapped at Capri compared with those trapped at Ottenby (Figure 3).

Figure 4 shows the linear relationship between median arrival dates on Capri and at Ottenby for each species. The point estimate of the slope was 0.87 ($t_5 = 8.45$, $P < 0.001$), which is not significantly different from one (95% confidence interval: 0.61–1.14). On average, the seven species migrated 15 days (0.79 SE) later at Ottenby compared to Capri. In order to see if migration speed varied over the season we tested if there was a relationship between species-specific arrival dates on Capri and the differences in median arrival dates between Capri and Ottenby. There was a non-significant negative correlation between the species-specific arrival dates on Capri and the differences in median arrival dates between Capri and Ottenby ($r = -0.57$, $P = 0.18$; Figure 5).

Discussion

The strong and positive relationship between migration dates at Ottenby and on Capri suggests that there are either common underlying environmental factors affecting long-distance migrants along their migration route, or that arrival dates are mainly reflecting a specific endogenous time-programme. In long-distance migrants, the onset of migration is known to be under strong endogenous control (Berthold 1996, Gwinner 1996), although the speed of migration through Europe can be affected by local conditions en route, as recently shown in the Pied Flycatcher (Both et al. 2005).

The difference in median arrival date on Capri and at Ottenby may indicate variation in migration speed between species. We find that the Willow Warbler, being the earliest migrant of the species

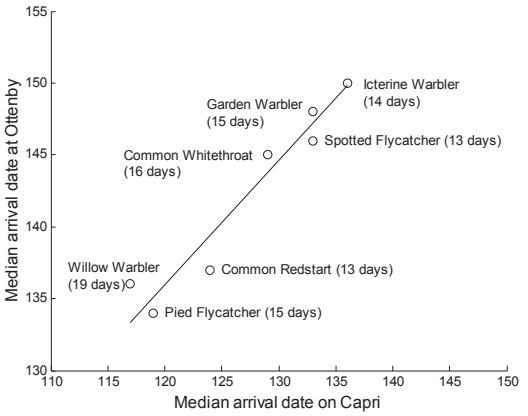

Figure 4. The relationship between median arrival dates on Capri and at Ottenby for seven trans-Sahara migrants, as well as the difference (in days). The line is the estimated slope in a reduced major axis regression (RMA).
Förhållandet mellan mediandatum för vårfångst av sju trans-Saharaflyttare på Capri och vid Ottenby, liksom skillnaden i antal dagar. Den heldragna linjen är den skattade regressionslinjen i en RMA regression.

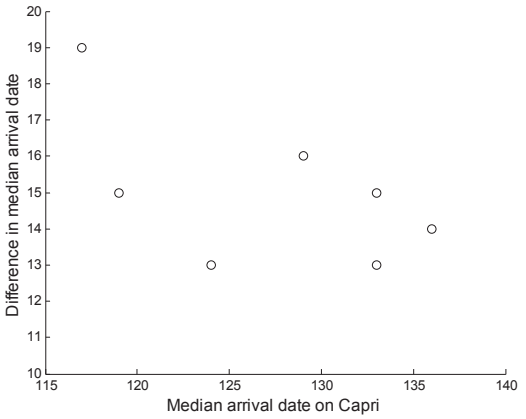

Figure 5. The differences in median arrival dates between Ottenby and Capri plotted against the species-specific arrival dates on Capri. r = −0.57, P = 0.18
Skillnad i medianankomst mellan Ottenby och Capri vid olika (artspecifik) medianankomst på Capri. r = −0.57, P = 0.18

analysed, is also the species having the largest difference (19 days) in median arrival dates between the two sites. In the same vein, late migrating species such as the Spotted Flycatcher and the Icterine Warbler show a difference of only 13 and 14 days, respectively. However, the overall pattern is weak even though some of the extremes are behaving as expected. It would be interesting to know to what extent the migration speed is limited by the time needed to stop-over. A number of recent studies (e.g. Saino et al. 2004, Both et al. 2005) have shown that arrival time is affected by environmental conditions en route, such that migration speed increases when conditions en route are favourable. If this is a general pattern the timing of migration may not constrain adaptations to climate change as much as previously thought (e.g. Both & Visser 2001, Both et al. 2005).

Competition for territories is an important factor affecting the timing of migration (Kokko 1999). A close look at Figure 4 shows that all species falling below the regression line (i.e., migrating faster than predicted by the linear model) are using cavities as nesting sites. If cavities are limited one may expect severe competition for territories. In fact, comparative evidence indicates that, among trans-Saharan migrants, hole-nesting species migrate earlier than other species in the Mediterranean (Rubolini et al. 2005). However, to what extent different species are able to speed up their migration to benefit from the advancement of spring events is currently unknown.

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Sammanfattning

Klimatförändringar har gjort att många organismers fenologi har tidigarelagts i norra Europa. Flera tropikflyttande fågelarter anländer allt tidigare och en förklaring till hur detta är möjligt är att flyttningen genom Europa går allt snabbare då vårtemperaturen ökar. Hur pass mycket olika arter kan öka sin flyttningshastighet är okänt och borde bero på deras ”normala” hastighet. I denna artikel jämför vi datum för medianankomst på Capri (Italien) och Ottenby (Sverige) på våren hos sju arter som alla övervintrar söder om Sahara. Ringmärkningsåterfynd visar att några arter (t.ex. grå flugsnappare och härmsångare; Figur 1 resp. Figur 2) passerar Capri längs en central flyttningsväg genom Europa och återfinns senare i riktning mot Ottenby. Återfynd av andra arter ringmärkta på Capri (t.ex. trädgårdssångare; Figur 3) pekar på ett östligare ursprung än Ottenby. I Tabell 1 redovisas fångstperioder och antal fångade fåglar under våren på Capri för de sju arter vilkas ankomsttider analyseras i denna uppsats.

Jämför man medianankomst på Capri och Ottenby (Figur 4) finner man att det är ett linjärt förhållande med en lutning på 0.87 som dock inte skiljer sig statistiskt från 1. I genomsnitt passerar de sju studerade arterna 15 dagar senare på Ottenby än på Capri. Det finns även en icke-signifikant antydan till att ju senare en art flyttar desto snabbare flyttar den genom Europa, att döma av skillnader i medianankomst på Ottenby och Capri (Figur 5). Det är okänt i vilken utsträckning olika arter skulle kunna öka sin flyttningshastighet för att dra nytta av vårens allt tidigare ankomst i norra Europa. Det är därför viktigt att man studerar vilka egenskaper som gör att en art har (eller saknar) förmågan att anpassa sig till klimatförändringar.