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Autumn migration of Common Cranes *Grus grus* through the Italian Peninsula: new vs. historical flyways and their meteorological correlates

Toni MINGOZZI^{1,2*}, Pierpaolo STORINO¹, Gianpalmò VENUTO¹, Gianfranco ALESSANDRIA², Emiliano ARCAMONE³, Salvatore URSO¹, Luciano RUGGIERI⁴, Luciano MASSETTI⁵ & Alessandro MASSOLO⁶

¹Department of Biology, Ecology and Earth Sciences – DiBEST, University of Calabria, 87036 Rende (CS), ITALY

²GPSO Piedmont Group of Ornithological Studies, Municipal Museum of Natural Sciences, CP 89–10022 Carmagnola (TO), ITALY

³COT, Tuscan Ornithological Center, CP 726–57100 Livorno, ITALY

⁴EBN Italia, via Peyron, 10–10143 Torino, ITALY

⁵IBIMET, Biometeorology Institute, CNR, National Council of Research, Via G. Caproni, 8–50145 Firenze, ITALY

⁶Department of Ecosystem and Public Health, Faculty of Veterinary Medicine, University of Calgary, Calgary, Alberta, CANADA

*Corresponding author, e-mail: antonio.mingozzi@unical.it

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Abstract. Since the 1990s, Common Cranes migrating in autumn through Italy have increased significantly both in number and in flock size. In the present study we provided a countrywide profile of autumn crane migration across Italy between 2001 and 2007 (486 records). To investigate the association of climatic characteristics with temporal and spatial migration patterns, we used weather data and climate anomalies over 60 years (1948–2007; NCEP/NCAR Reanalysis Project database). Autumn migration showed different phenological patterns along two main migratory routes: 1) a Southern Italy route and 2) a Northern Italy route. The Southern route, across the lower Adriatic Sea was only partially described before, and more inferred than documented, whereas the Northern route, across the Po River plain, resulted as a new flyway, never described before. Crane migrations along the Northern route occurred 7 to 14 days earlier than along the Southern one. Along both routes, we detected mass migration events concurring with particular weather conditions: the use of Southern route was associated with southward winds in the Balkans, the records along Northern route with high pressure and favourable westward winds in Central Europe and in the main stop-over site (Hortobágy) of likely origin. In the last 60 years, the occurrence of the latter weather configurations has slightly, but consistently, increased, suggesting that the Northern route may have recently established as an alternative route for the cranes migrating from Eastern Europe, joining the two traditional continental routes (the West-European, and the Baltic-Hungarian).

Key words: Common Crane, autumn migration, Italy, migration routes, meteorological correlates, climate change

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INTRODUCTION

Bird migration is a complex phenomenon shaped by a wide array of factors known to influence its temporal and spatial patterns (Berthold & Pulido 1994, Newton 2008). Despite the extensive literature available, many aspects of avian migration including its adaptive significance and proximate factors responsible for its flexibility and between-population variation, remain however, largely unexplored (Bairlein & Coppack 2006).

Variation in environmental conditions and physiological status induce individuals (and ultimately: populations) to change the timing of migration and migration routes to maximize fitness in the face of new selection pressures (e.g. allowing to arrive in the right place at the right time; Lindstrom & Alerstam 1992, Stervander et al. 2005, Weidinger & Kral 2007). Weather conditions affect migration in many different ways (Newton 2008), among others by influencing bird body condition prior to and during the migration episodes

(Schaub & Jenni 2001), as well as by setting the environmental conditions for the actual migratory flight (Gauthreaux et al. 2006). With some exceptions (Thorup et al. 2006), winds, and more generally a favourable weather, play an important role in timing of migration departure and choice of migratory route (Alonso et al. 1990a,b, Bäckman & Alerstam 2003), particularly in autumn (Akesson et al. 2002). Migration routes can vary annually, depending on weather and habitat conditions (Hupp et al. 2011). Rapid changes in migration routes were recently recorded in several species, as a consequence of environmental changes (Berthold et al. 1992, Helbig 1996, Newton 2008 and references therein). Among these, climatic change may play a role, but its direct influence has never been documented, unlike other life history traits (Møller et al. 2010), including timing of migration (e.g. Sparks et al. 2005, Gordo 2007, Rubolini et al. 2007, Lehikonen & Sparks 2010). Most of the studies on the effects of climatic variation on birds have been carried out on a few well studied species, mostly small-sized passerines (Møller et al. 2010). Among larger species, Common Crane *Grus grus* (henceafter: crane) has recently received increasing attention, mainly due to recent changes in demography (population trends), breeding range and wintering areas as well as migration phenology (ICF—MPSLU 2010). A recent study has provided evidence that crane migration phenology is likely affected by increasing temperature (Filippi-Codaccioni et al. 2011).

The crane is a summer visitor throughout the Northern Europe, and parts of Central Europe. In autumn, cranes migrate to wintering areas from breeding grounds via three main migration routes (Fig. 1) (Glutz von Blotzheim et al. 1973, Cramp & Simmons 1980, Rinne 1995, Meine & Archibald 1996, Prange 2005): the West-European, the Baltic-Hungarian and the East-European.

The West-European route is taken by cranes (about 240,000 birds; Nowald 2010, Prange 2010) migrating southbound from breeding grounds in Northern (Sweden, Norway, Finland) and Central Europe (Baltic States, Poland, North-East Germany), through Western Europe to wintering areas in France, Spain, Portugal and Morocco. The Baltic-Hungarian route is used by cranes (about 120,000 birds; Prange 2011) nesting in North-Eastern Europe (Sweden, Finland, Eastern Karelia, Baltic States, Belarus) that migrate southward via a major resting site in the Hortobágy National Park, Eastern Hungary (up to 100,000 cranes; Prange 2010, Végvári & Hansbauer 2010).

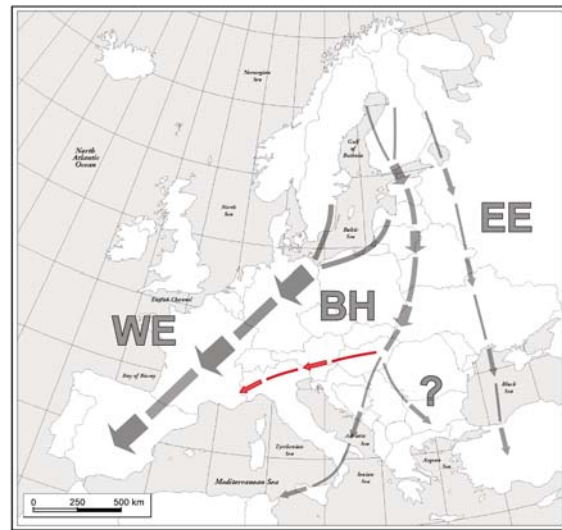


Fig. 1. Current migration routes of Common Crane in Europe. European routes (WE = West-European; BH = Baltic-Hungarian; EE = East-European) indicated by literature are showed by grey arrows. The red arrow shows the North Italy route presented in this paper. Arrow thickness is representative of the intensity of migration flows.

Cranes stage at Hortobágy between mid-September and the second half of November (Végvári & Tar 2002) and are presumed to continue their migration via two secondary flyways (Meine & Archibald 1996, Prange 2005): a southern route through the Balkans and Turkey, to wintering areas in Eastern Africa, and a southwest route across the Adriatic sea, the southern Italian Peninsula, Sicily and the Mediterranean to wintering grounds in North-Western Africa. However, whereas the first route is currently well documented, the latter is not (Nowald 2010). The third major flyway of European cranes, the East-European route, is proved to be taken by cranes nesting in Finland and Estonia that migrate via Ukraine, Crimean Peninsula and Turkey southward to Ethiopia (Nowald 2010).

Since the 17th century, crane populations have undergone a large decline in Europe, with a minimum reached in the 1960s, due to the negative impacts of habitat loss and degradation, changes in land use and agricultural production methods (Meine & Archibald 1996). Afterwards, thanks to legal protection and habitat restoration, European populations started to increase and most national populations were restored to numbers and in range size, which brought the crane to be removed from the IUCN red list (Prange 1997, Birdlife International 2004, Prange 2005). In fact, since the 1990s cranes have re-occupied most of their former territories, and the total European

population has been estimated at 74,000–110,000 breeding pairs (Birdlife International 2004), even more nowadays (Prange 2011). Despite the increase of the European population in the last 50 years, no new (or not previously described) major migration routes have been reported (Prange 2011).

In Italy, the crane had become extinct as a breeding bird around 1920 (Brichetti 2009), and until the 1980s the species was regarded here as a “scarce” migrant (Brichetti 1981, Heinze 1983), except for Sicily, where migrating flocks of hundreds of birds were occasionally recorded (Iapichino & Massa 1989). Since the 1990s, the number and size of flocks migrating through the country have increased significantly (Brichetti & Fracasso 2004), probably reflecting the general increasing trend in European populations (Birdlife International 2004). Although recently unprecedented occurrences of migrating cranes (including big numbers and new sites) have been recorded across Italy (e.g. Caula 2006, Prange 2006, Ruggieri & Sighele 2007), there was no attempt to summarize these and describe the spatial and temporal patterns of the autumn migration of the species across the Italian Peninsula.

The present paper thus aims to provide a comprehensive account of autumn crane migration across Italy in the seven-year period between 2001 and 2007. In particular, we aimed to describe: a) the migratory population trend, b) the spatial (routes) and temporal (phenology) patterns of migration, and c) the weather correlates of the observed patterns.

METHODS

Migration data

Countrywide sighting data (date, time, locality, flock size, flight direction) of autumn migration (herein considered as ranging from 1st September to 31st December) were collected from 2001 to 2007 and compiled by the *Gru Italia DataBase* working group (GRUITDB, Italian Crane database, Dept. of Biology, Ecology and Earth Sciences – DiBEST, University of Calabria). The GRUITDB includes data from the Crane Database for Calabria Region, the GPSO (Gruppo Piemontese Studi Ornitologici, Piedmont Group of Ornithological Studies, <http://www.gpso.it>) archive for the Region of Piedmont (archives 1980–2000), the COT (Centro Ornitologico Toscano, Tuscan Ornithological Center, <http://www.centronitologicotoscano.org>) archive for the Region of

Tuscany, EBN Italia (EBN Italia mailing archive; www.ebnitalia.it). Other data were regularly entered into GRUITDB by other collaborators across the Peninsula (Friuli, Veneto, Marche, Abruzzo, Sicily; see Acknowledgements).

Given the large scale of the study, a large number of observers was involved, in line with the recent appreciation of citizen participation to global or regional studies (Devictor et al. 2010). To account for unequal skills of observers, an in-depth data screening was performed. Data of suspected reliability were directly discussed with the observers, otherwise eliminated. Data with incomplete temporal or spatial references, or referred to nocturnal observation, were not included in the analysis. Finally, the records reported on the same date and within the same municipality were treated as a single record to avoid double counts. Similarly, records that could represent the same birds (e.g. similar flock sizes recorded in close localities on the same observation dates) were not counted twice. For each observation, flock size and flight directions were also reported, if available.

Crane abundance data were classified into 8 semi-logarithmic classes (1 = 1–50, 2 = 51–100, 3 = 101–200, 4 = 201–400, 5 = 401–800, 6 = 801–1,600, 7 = 1,601–3,200, 8 = 3,201–6,400 birds), and geo-referred to municipality using ArcGis 9.2 (ESRI Inc., CA, USA). We defined as mass migration the events in which more than 70% of the overall seasonal migrating cranes across Italy passed within 24 hours.

Migration start and end (along a specific route or all over the country) were defined by the first and last recorded observation date in a given year, respectively. We also reported the mean migration dates as well as the peak (the day in which the largest number of cranes occurred) migration event dates, and the dates in which the 25% (25 percentile) and 75% (75 percentile) of all migrating birds were observed along a specific route or all over the country. In addition, the overall duration (number of days) of the seasonal migration was calculated.

Meteorological analysis

To investigate the association of migration meteorological correlates, such as air temperature (e.g. Hüppop & Winkel 2006), wind direction and speed (e.g. Weber & Hederström 2000), and the temporal (such as 25th and 75th percentiles of arrival date) and spatial (South vs. North) migration patterns in Italy, weather data from

NCEP/NCAR Reanalysis Project were used (Kalnay et al. 1996). This dataset includes over 80 different variables (e.g. atmospheric pressure, air temperature, relative humidity, wind direction and speed) calculated on 2.5×2.5 degree latitude/longitude grids (about 250×250 km). We first examined the association between the monthly (August to December) mean air temperature (measured at an elevation in which the air pressure was of 850 hPa, i.e. geopotential height), in an area of 5×5 degrees lat-long (500×500 km) centered in Hortobágy and the following 4 phenological timepoints (of the different routes): i) the migration starting date; ii) when 25% of cranes had passed; iii) when at least 75% of the population had passed, and iv) at the end of migration.

Secondly, we examined the association between the intensity of migration (number of cranes observed during migratory peaks) and their weather correlates such as: i) the air pressure (expressed in m, as the height above sea level at which atmospheric pressure equals 500 hPa; i.e. the higher the elevation, the lower the pressure) during the peak migration days; ii) the air temperature ($^{\circ}\text{C}$) (at 850 hPa geopotential height to compensate for differences at different pressure values); iii) the Zonal and Meridional wind components (in m/s) at 925 hPa geopotential height (as above). Zonal wind component corresponds to wind motion along the x-axis (positive for a West to East direction, negative otherwise), whereas Meridional component refers to motion along the y-axis (positive for a South to North direction, negative otherwise). These weather variables have been measured in three areas of 5×5 degrees (500×500 km) centered in Piedmont and in Calabria (respectively, North-Western and Southern Italy), as well as in Hortobágy. For each area, the meteorological parameters were collected during the migration peaks, as well 1 and 2 days before.

Moreover, to obtain the weather profile during the mass migration events, we generated maps of the mean composite anomalies of 850 hPa geopotential height, temperature, and Zonal and Meridional wind components in Europe. The composite anomalies have been computed as the difference between the mean of the values observed during the recorded peak days (i.e. 2 peaks in Northern Italy and 3 in Southern Italy) and the mean monthly value calculated for a 30 year reference period (1968–1996). In addition, to characterize the climate trend in Northern Italy during the study period, we used a 60-year climat-

ic series (1948–2007), and we expressed the trend as the Number of Good Weather Days (NGWD) from 20th October to 5th November (the 15-day period where the migratory peaks have been recorded). A GWD was defined as a day with mean 500 hPa geopotential height in North-Western Italy higher than the 90% percentile distribution of geopotential height calculated in the same area during the peak days of migration along the Northern route.

Statistical analyses

Wilcoxon test for paired samples (Siegel & Castellan 1988) was used to compare migration characteristics (the number of migrating flocks, start, end and duration of migration) in Northern and Southern Italy. The probability levels were computed using a complete randomization method (permutation or exact test; p_{exact}) or, when computation was not possible, a Monte Carlo (Mehta & Patel 1996, Good 2000) simulation based on 10,000 sampled tables (p_{MC}). The associations between the meteorological conditions and the temporal characteristics of migration were analyzed using Pearson's product moment correlation (Sokal & Rohlf 1995). The significance of climatic and population trends from 2001 to 2007 and of NGWD trend during 1948–2007 were tested using a linear regression, with the adjusted R^2 (R^2_{Adj}) as a measure of model fit.

Throughout the text means are reported along with their standard errors (SE). Statistical analyses were carried out using SPSS 15.01 (SPSS Inc., USA).

Flight directions ($n = 275$ records) were analyzed with reference to eight "biogeographical" regions (Sardinia was excluded, having only three directional records). Descriptive statistics (mean and SE) of circular data were calculated using ORIANA 4.02 software (Kovach Computing Services, Anglesey, Wales, UK).

RESULTS

Migration trends

During the 7-year study period, 486 records of migrating cranes, totalling 33,062 individuals were collected from Italy throughout the year.

The number of crane sightings during the autumn migration showed a steady and significant increase over the course of the study (range = 13–115; $n = 486$ records; $R^2_{\text{Adj}} = 0.584$, $F_{1,5} = 9.429$, $p = 0.028$) (Fig. 2). Likewise, a significant increase in the total number of individuals

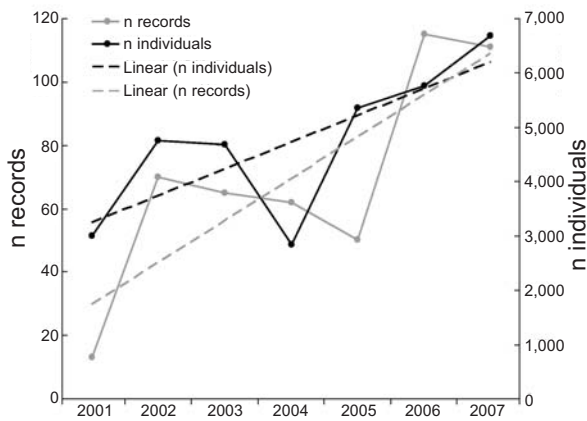


Fig. 2. Trends of Common Crane records (grey dots with continuous line; linear trend in hatched grey line) and number (black dots with continuous line; linear trend in hatched black line) in Italy during autumn migration from 2001 to 2007.

recorded during autumn migration was found over the seven years (range = 2,996–6,683 individuals per autumn season; $n = 33,062$ cranes; $R^2_{Adj} = 0.485$, $F_{1,5} = 6.646$, $p = 0.050$). At a local scale, in the Piedmont region (one of most intensively investigated Italian regions) the crane was a scarce visitor till the 1990s, with 54 records in the 21-year period from 1980 to 2000 and a total of 338 cranes, 8.62 ± 1.33 cranes/flock, range 2–30, with 45 observations of single individuals (GPSO Archives). However, in next 7 years, i.e. in the period of this study (2001–2007), numbers of

migrating cranes observed in Piedmont increased dramatically with mean flock being six-fold larger (183 records; 6,318 cranes; mean flock size 48.14 ± 8.07 individuals, range 2–780, with 12 observations of single individuals; GPSO Archives), with unprecedented massive migrations in 2006 and 2007. Despite that the number of observers per year in Piedmont was lower (mean \pm SE, 27.00 ± 8.40) from 1980 until the mid '90s than from 1996 until 2007 (69.33 ± 10.93), no relation between the number of cranes and the sampling effort was detected ($Rho_{Spearman} = -0.054$, $df = 10$, $p = 0.757$) in this latter period. Nonetheless, a significant increase of migrating cranes occurred ($R^2_{Adj} = 0.299$, $F_{1,10} = 5.696$, $p = 0.038$). As it was not feasible to estimate the sampling effort nationwide, we made the assumption that the absence of significant association between sampling effort and frequency of records in Piedmont was valid across the rest of the peninsula as well.

Migration phenology

On average, autumn migration started in Italy on Oct. the 17th (range, Sep. 14th–Nov. 10th), and ended on Dec. the 20th (range, Nov. 20th–Dec. 31st), for a mean duration of 60.1 ± 6.1 days (range, 16–100 days). The migration phenology slightly differed between Northern and Southern Italy (Fig. 3). In Northern Italy the migration started

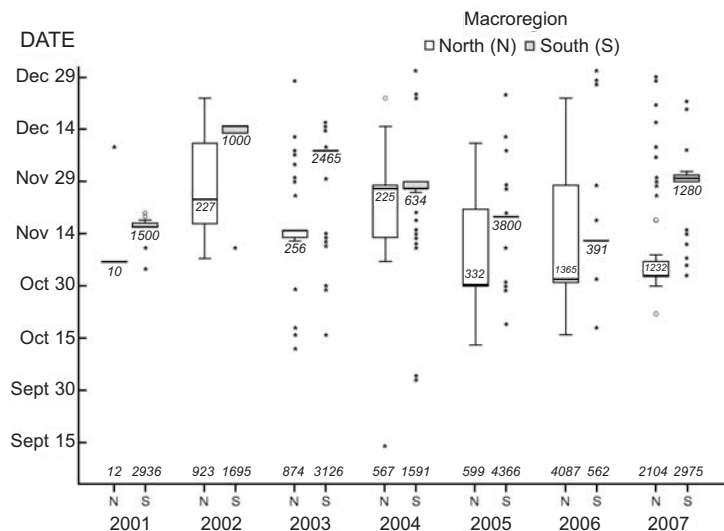


Fig. 3. Temporal distribution of autumn migratory flow (in term of number of individuals) of Common Crane in Northern and Southern Italy from 2001 to 2007. Boxes represent inter-quartile distance; thick line, median; whiskers, extreme values. Circles and asterisks represent outliers (that extend for more than 1.5 times the interquartile distance) and extreme outliers (i.e. extend more than 3 times the inter-quartile distance), respectively. Numbers along the x axis represent the total number of migrating crane along the North and South route (N and S, respectively), whereas in graphs the numbers represent the number of cranes during mass migration events.

Table 1. Common Crane counts (and %) during autumn migration in Northern, Central (Sardinia included) and Southern (Sicily included) Italy from 2001 to 2007.

| Years | Northern Italy | | Central and Sardinia | | Southern and Sicily | |
|-------|----------------|------|----------------------|------|---------------------|------|
| | N | % | N | % | N | % |
| 2001 | 12 | 0.4 | 48 | 1.6 | 2,936 | 98.0 |
| 2002 | 923 | 19.4 | 2,132 | 44.9 | 1,695 | 35.7 |
| 2003 | 874 | 18.7 | 739 | 15.8 | 3,066 | 65.5 |
| 2004 | 547 | 19.3 | 702 | 24.7 | 1,591 | 56.0 |
| 2005 | 599 | 11.2 | 385 | 7.2 | 4,366 | 81.6 |
| 2006 | 4,087 | 70.9 | 1,115 | 19.3 | 562 | 9.8 |
| 2007 | 2,104 | 31.5 | 1,604 | 24.0 | 2,975 | 44.5 |

7 days earlier than in the South (Oct. 17th. vs. Oct. 24th, respectively; start date, Wilcoxon, $Z = -2.117$, $p_{\text{exact}} = 0.047$; 25% percentile date, Wilcoxon, $Z = -2.366$, $p_{\text{exact}} = 0.016$). Conversely, the mean end dates were comparable (North — 21st Dec. South — 19th Dec.), and no significant difference was found between the duration of migration between North and South (North — 64.3 ± 8.19 days; South — 55.86 ± 9.28 days; Wilcoxon, $Z = -1.863$, $p_{\text{exact}} = 0.063$).

Records of autumn migration (Fig. 4A) were not distributed homogeneously across the country (Sardinia included) with a larger amount in the North ($n = 225$, 46.30%) as compared to Central ($n = 114$, 23.46%) and Southern Italy ($n = 147$, 30.25%). On the other hand, observations of large flocks (> 400 birds) mostly clustered in Southern Italy (Table 1; 52.0% of total; $n = 17,191$ individuals), while on the North (27.7% of total cranes; $n = 9,146$ individuals). Sightings clusters in the North West region (Piedmont) (Fig. 4A) were mainly from two unprecedented massive migrations with a north-east to a south-west axis in 2006 (no less than 2,258 cranes counted in 12 hours from Oct. 31st to Nov. 1st), and in 2007 (greatest flux on Nov. 2nd, with 937 cranes in 6 hours). On the whole, cranes observed in Piedmont in 2006 and 2007 represented 62.8% ($n = 2,565$ individuals), and the 90.3%

Table 2. Autumn migration peak events (number of birds) of Common Crane in Calabria in 2001, 2003 and 2005 and their relative abundance in respect to the total migration flow in the rest of Italy.

| Years, and time windows | Italy (total) | Calabria | rest of Italy |
|-------------------------|---------------|---------------|---------------|
| 2001, 9–23 Nov | 2,935 | 2,186 (74.5%) | 749 (25.5%) |
| 2003, 1–15 Dec | 2,852 | 2,542 (89.1%) | 310 (10.9%) |
| 2005, 12–26 Nov | 4,053 | 3,480 (85.9%) | 573 (14.1%) |

($n = 1,900$ individuals) of the totals for the Northern Italy in respective seasons.

In the southern region (Calabria), the great clusters of observations (Fig. 4A) corresponded to three mass migration events (autumn 2001, 2003, 2005) involving thousands of individuals: a minimum of 1,500 in 3 hours on Nov. 16th 2001 in Rende-Cosenza municipalities; no less than 3,000 in 15 hours in the province of Cosenza on Dec. 8th 2003; 3,420 individuals counted in 4 hours on Nov. 19th 2005 in Rende-Cosenza municipalities. The intensity of these massive migratory events in Calabria (Table 2) is evident from the fact that the number of cranes recorded during the 15-day window of maximum passage accounted for 89.1% (2,542/2,852 total) and 74.5% (2,186/2,935) of the entire migratory records throughout the rest of Italy in 2003 and 2001, respectively.

Beside the two regions mentioned above, we identified three more areas with intense migration countrywide, namely (Fig. 4A): i) the area around Garda Lake (North Italy), at the foothills of the Central Alps; ii) the large area corresponding to the lower Adriatic regions (from Abruzzi to Apulia); iii) the north-western tip of Sicily which accounted for 72.1% ($n = 1,743$) of all the cranes recorded in the island ($n = 2,418$; Fig. 4A).

Migration routes

Flight directions ($n = 275$ records) related to eight “biogeographical” regions (Fig. 4A) revealed a complex pattern of migration routes over Italy (Fig. 4B). Three main routes were clearly identifiable: i) one Northern Italian route (NORTHIT route; 1 in Fig. 4B), and ii) two Southern Italian routes (SOUTHIT/a and SOUTHIT/b routes; 2a and 2b in Fig. 4B).

The NORTHIT route (1 in Fig. 4B) goes along East-West axis across the Po River plain to the western alpine arch, and then to Provence (Southern France), although we cannot exclude that flocks observed along both the northern Adriatic and the Tyrrhenian coasts might be coming from this route, as the flight directions over the Romagna region seemed to indicate (broken lines in Fig. 4B).

The SOUTHIT/a route (2a in Fig. 4B) has a large front along the middle Adriatic regions (from Marche to Northern Apulia). Moreover, our data suggest that, once over the land, the crane flocks might head to at least two sub-flyways along the Southern Italian Peninsula (Fig. 4B): i) a branch heading southward along Calabria, the Messina Strait and then Sicily to reach Tunisia

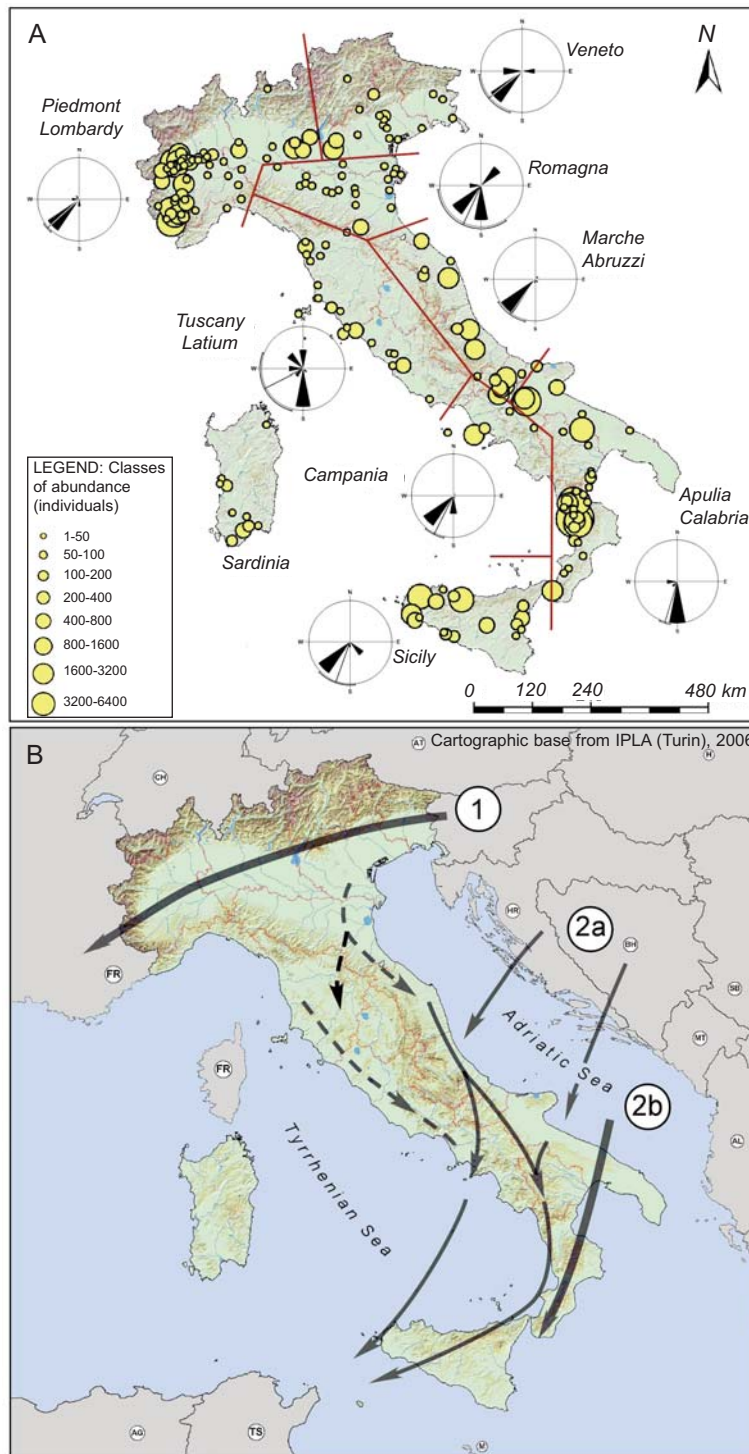


Fig. 4. Autumn migration routes of Common Crane in Italy from 2001 to 2007. A — spatial distribution of records (dots of variable size, $n = 486$) and main flight directions (rose diagrams). Records (i.e., total number of cranes for each municipal area) are clustered in 8 semi-logarithmic classes of bird abundance. Rose diagrams (see text for details) show flight directions as percentage of observations ($n = 275$) related to eight regional sectors (highlighted by red lines), from north to south: Piedmont and Lombardy (observations $n = 100$); Veneto (11); Romagna (9), Tuscany and Latium (22), Marche and Abruzzi (14), Campania (23), Apulia and Calabria (85), Sicily (11). Each black wedge is 45° wide and the length of each wedge (the radius from the centre) represents the percentage of observations falling within that range. The black line running from the centre of the diagram to the outer edge is the mean angle of directional data (mean vector), while 95% confidence interval (C.I.) for the mean is indicated by the arcs extending to either sides. B — main migratory routes (arrows and number: 1 NORTHIT route; 2a and 2b: SOUTHIT routes). Arrow thickness indicates the intensity of migration flows; broken lines indicate the migratory routes less supported by directional data.

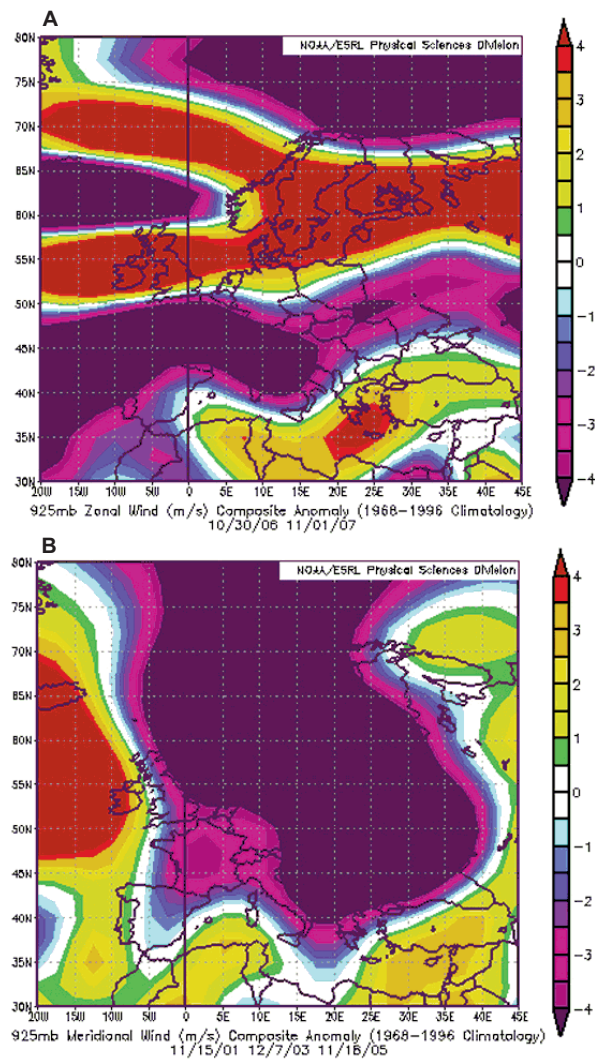


Fig. 5. Anomalies (from the mean over the whole period) detected for Zonal (A, west to east direction) and Meridional (B, south to north direction) wind components in Europe in the years of Common Crane mass migrations in Northern and Southern Italy (respectively, 2006 and 2007, and 2001, 2003 and 2005) in the period from 2001 to 2007. Data from NCEP/NCAR Reanalysis Project calculated on a 2.5×2.5 degree grids. Negative wind anomalies indicate that the wind is blowing in the opposite direction (i.e., negative anomaly for the Zonal, west-east component indicates an east-west wind, for the Meridional component indicates a north-south wind).

through the Sicilian Channel; ii) another branch through the Apennines and the Campania region across the lower Tyrrhenian Sea towards North-western Sicily. This second way is supported by regular observations of flocks migrating over the Campania islands (Procida and Vivara) heading SW towards the open sea (D. Zeccolella, EBN Italia).

The SOUTHIT/b route (2b in Fig. 4B) was indicated by mass migrations events occurred in Calabria in autumns 2001, 2003, 2005. Such events have no corresponding observations from either northernmost or southernmost Italian regions, suggesting a route probably originating from the northeast Balkan regions, and heading southward along the Eastern Sicilian coast.

Meteorological correlates

The duration of the autumn migration both in Northern and Southern Italy was positively correlated to mean December air temperatures in Hortobágy ($r = 0.825$, $p = 0.022$; $r = 0.807$, $p = 0.028$, for the N and S Italy, respectively). Whereas no meteorological parameter seemed to be associated to the timing of crane migration along the Northern route, the migration along the Southern route showed a strong significant association with October temperatures in Hortobágy (i.e. significantly advanced when T_{Oct} in Hortobágy were above average; $r_{25\text{perc}} = -0.852$, $p = 0.015$; $r_{75\text{perc}} = -0.818$, $p = 0.025$).

Analyses of the meteorological conditions on days with recorded peak numbers and 1 and 2 days prior showed that, along the Northern route, the number of cranes on the peak-flow day and on the day before were positively related to good weather conditions (same day, $r_{\text{geopot500hPa}} = 0.533$, $p = 0.050$; 1 day before, $r_{\text{temp850hPa}} = -0.580$, $p = 0.030$ and $r_{\text{geopot500hPa}} = -0.591$, $p = 0.026$). Peak-flow events were associated with anomalies in zonal wind currents occurring the day before ($r_{\text{zonalwind}} = -0.548$, $p = 0.043$). Conversely, along the more Southern route (2b in Fig 4B) the intensity of the migratory flow was correlated not to the weather conditions along the route itself, but to bad weather conditions at the stopover (Hortobágy) on the days before the peak-flow (same day, $r_{\text{temp850hPa}} = -0.642$, $p = 0.005$; 1 day before, $r_{\text{temp850hPa}} = -0.514$, $p = 0.035$; $r_{\text{geopot500hPa}} = -0.700$, $p = 0.002$; 2 days before, $r_{\text{geopot500hPa}} = -0.520$, $p = 0.032$).

Both Northern and Southern migration flows were clearly associated with patterns of wind configurations. The intensity of Northern migratory flows increased/decreased in the presence of negative anomaly of the Zonal wind component, a stronger westward air circulation from the Balkans (Fig. 5A), which probably facilitated migration along this route. Interestingly, a slight but significant increase in the number of days with favourable weather conditions (high geopotential height and null or negative Zonal

wind) along the NORTHIT route has been observed over the last 60 years ($R^2_{Adj} = 0.136$, $F_{1,58} = 10.256$, $p = 0.002$). Likewise, the Southern migration flow seemed to be strongly associated to a Meridional wind component anomaly with currents flowing southward from Eastern European regions to the Southern Adriatic regions of Italy (Fig. 5B).

DISCUSSION

General migration trends

According to our data, the frequency of migrating cranes in Italy has remarkably increased, both in terms of flock records and total bird numbers. Despite the difficulties related to the use of data collected opportunistically by birdwatchers (citizen database; homogeneity of sampling effort, double counts), we believe that the resulting picture is correct. The recent data, collected in 2008–2010, i.e. after the period analyzed in this paper seem to confirm these findings, in particular the notable migration of cranes observed in Italy in autumn of 2009 ($n = 383$ records, $n = 36,934$ individuals).

The recent increase in numbers of cranes migrating through Italy in autumn is possibly a consequence of the demographic situation of the European population, which affects the numbers of cranes passing the country. The six-fold increase in the Piedmont region (Northwest) is exemplary of this trend, as well as the increase in mean flock size and the unprecedented mass migration events. The existence of such an increasing trend in Italy, is complemented by similar trends recorded in other European areas, along both the West-European route (e.g., Gallocanta, Spain: increase from a few bird staging between 1970 and 1973, to about 56,000 in 1989–1990; Bautista et al. 1992) and the Baltic-Hungarian route (e.g. Hortobágy, Hungary: a few thousands birds in early 1980s (Kovács 1987), 60,000 in early 1990s (Végyvári 2002), peaking to 100,000 birds in 2007 (<http://champagneardenne.lpo.fr/grus-grus/index.htm>). However, the overall consistent increase of migration flows through Italy in the last 20 years may not only reflect merely an overall increase in the European population, but probably also involves the use of new migration routes, or the re-use of an ancient migration route that existed before crane numbers decreased between the 17th and 20th century.

Migration routes

Italy has already been stated as a “bridge” for the cranes migrating in autumn from Northeast Europe to North Africa (Meine & Archibald 1996, Prange 1999), but the role of the Peninsula is now appearing more complex and relevant than previously thought. Our study provided data supporting presence of at least three migration routes, even if their links to the recognized European flyways are still to be proved.

The NORTHIT route appeared as a new migration flyway for cranes in Southern Europe, joining, across Northern Italy, the two traditional continental routes: the West-European, and the Baltic-Hungarian. Given the presence of this migration route, it is now likely that cranes nesting in North-Eastern Europe and previously wintering in Northern Africa may have partially joined the wintering populations of the Iberian peninsula or Morocco. However, it is worth to note that the two massive migration waves recorded in Piedmont (2006 and 2007) were not observed in the neighbouring Provence-Alpes-Côte d’Azur region (South-eastern France), where just few sightings were recorded (<http://champagneardenne.lpo.fr/sommaireC2.htm>). Evidence from satellite telemetry and/or ringing records are needed to confirm wintering destination of cranes flying along NORTHIT route.

The SOUTHIT route (2a and 2b, Fig. 4B) represents the other main migratory flyway across Italy, mostly used with a one-week delay from the previous one. The SOUTHIT/a route corresponds to the “historical” Italian branch of the Baltic-Hungarian route. The existence of such a flyway, first suggested by Libbert (1936, 1938), then rejected by Schenks (1938), and held up again by Glutz et al. (1973), was, till recent years (e.g. Meine & Archibald 1996, Prange 1999) more inferred than documented (Schneider-Jacoby 2008), with no sound data to support it (Brichetti 2009). Our data confirmed the existence of this route, that i) is consistent with recent autumn observations on crane migration in Croatia and Bosnia-Herzegovina along the so-called “Adriatic flyway” (Schneider-Jacoby 2008, Denac et al. 2010, Stumberger & Schneider-Jacoby 2010), and ii) it is supported by recent satellite telemetry tracking (<http://www.satellittikurjet.fi>; Nowald 2010). The secondary branch of the SOUTHIT/a route across the lower Tyrrhenian Sea was only supported by sightings from Procida and Vivara islands. However, it should be noted that the same migration flyway was described for a migratory bird of

prey, the Honey Buzzard *Pernis apivorus* (Agostini 2004).

The SOUTHIT/b route evidenced by the massive migratory events in Calabria coupled with lack of corresponding records in either northernmost (e.g. Apulia, Basilicata) or southernmost (Sicily) Italian regions, appears as a new route not described so far. It may represent also an alternative spatial variant of the SOUTHIT/a route, used occasionally. More evidence is needed to understand this situation.

Both SOUTHIT and NORTHIT routes could be used by cranes coming from Eastern Europe. In particular, it is very likely that these cranes come from the resting site in Hortobágy National Park. This is supported by the synchronicity of the departures from Hortobágy and the mass migration events registered on Calabrian territory, particularly in autumn of 2001 (<http://champagne-ardenne.lpo.fr/grus-grus/index.htm>). In case of the NORTHIT route, the absence of records of migrating cranes from areas located further north, i.e. Austria and Switzerland (<http://www.ornitho.ch>; R. Lardelli, pers. comm.) supports this hypothesis. In accordance with the evaluations of Meine & Archibald (1996), during mass migration events, about 20,000 cranes proceed from Hungary to North Africa across the Adriatic Sea. Interestingly, most of the cranes (ca 50–60%) staging in Hortobágy during our study period (2001–2007) left the stop-over site between the end of October (26–27th Oct.) and the first week of November (4–5th Nov.; data from the European Crane Working Group; <http://champagne-ardenne.lpo.fr/grus-grus/index.htm>), which is consistent with the peaks of migration flows recorded for the NORTHIT route.

Meteorological influence on alternative migratory strategies

Our data suggest that the crane population stopping over Eastern Hungary and migrating across Italy shows at least two different migratory strategies. The one already described in literature (Prange 2010, Nowald 2010, Stumberger & Schneider-Jacoby 2010) is to fly southward through the Adriatic Sea and Southern Italy to reach North Africa (SOUTHIT/a and SOUTHIT/b routes) when winds blow from North-East to South-West (Bora wind) in mid-late November or later.

Beside this, our data also highlights possible development of a new strategy in recent decade. Some cranes take advantage of early favourable

weather conditions of mid- to late October (in Western Europe in general, and in Northern Italy in particular) to migrate west rather than south from Hortobágy (end of October-first week of November; NORTHIT route). We have no data to suggest the possible destination areas of these birds; nonetheless, the most accredited destinations are the Iberian wintering grounds in Spain (Gallocanta) or France (Aquitaine) (Fig. 4B, route 1), and possibly also Morocco. Probably, some birds migrating along the NORTHIT route may detour southward along the Adriatic or Tyrrhenian Italian sides (Fig. 4B) wintering in central Italy (Tuscany, Latium) (Corsi & Dragonetti 2010, N. Baccetti, pers. comm.) or migrating to Northern Africa through Sicily. The proximate causes of the onset of this new route are not known, and we can only speculate. Probably, it is a multi-factorial process triggered by several factors such as environmental conditions (i.e. favourable weather for migration as: westward winds, higher atmospheric pressure, higher temperature), behavioural factors and genetic variation in the propensity for specific migration directions. It is well known that in many bird populations, the direction of migration can have genetic basis (e.g. predisposition to migrate in different directions; Berthold 1991, Berthold et al. 1992, Berthold & Pulido 1994, Tankersley & Orvis 2003, Thorup et al. 2007). However, in cranes, a tendency of immature birds to migrate along different routes than adults has been shown in Spain (Alonso et al. 2008), so more research is needed to gather data on how the different components interact in determining the phenology and direction of migration routes for this species.

The trigger for the establishment of the NORTHIT route might then have been the co-occurrence of adequate climatic configurations, and the presence of individuals whose genetic predisposition is to migrate west (west-migrants). Even if we expected a low frequency of west-migrants in the subpopulation of cranes stopping-over Hortobágy, the increase of the crane population might have made this fraction of individuals detectable. Alternatively, we cannot exclude that the west-migrants birds belong to the population of cranes that usually do not stop over in Hungary and move westward immediately after leaving the breeding grounds in Northern Europe, but for some unknown reasons, have detoured south and then, after the stop-over in Hungary, headed westwards towards Northern Italy (NORTHIT route).

The contemporary favourable weather conditions along the NORTHIT route had likely increased the probability of migration success (surviving to the successive migration), through a decrease in flight costs (e.g. Liechti & Bruderer 1998, Liechti 2006). If pioneering west-migrants succeeded, the fraction of birds migrating westward in the following years could increase. This reinforcement may happen due both to possible micro-evolutionary process (Berthold et al. 1992), if the west-migration attitude has some genetic basis (Berthold 1991, Berthold et al. 1992, Berthold & Pulido 1994, Pulido et al. 2001), and due to plastic phenotypic responses (e.g. Tøttrup et al. 2008). The latter, epigenetic way of transmission can easily develop by social interactions that could induce juveniles and immature individuals (that are not necessarily genetically west-migrants) to follow adult ones (i.e. experienced west-migrants, parents, etc.) in their migratory route. Given the observed climatic trend (NGWD trend detected for NW Italy in the last 60 years), we predict this route to establish as a regular and important alternative to the Southern one, and consequently we expect the number of individuals that migrate earlier and westward (from Hortobágy) to increase in the near future.

CONCLUSIONS

Our data strongly suggest that: 1) the number of cranes migrating through Italy has consistently increased in the last 20 years; 2) Italy serves as a main land "bridge" for cranes migrating from Eastern-Europe to North-Africa through Mediterranean via the Adriatic Sea; 3) a new route through Northern Italy has been onset in recent years.

Furthermore, our meteorological analyses suggested that the establishment of this novel route was likely related to favourable weather conditions along the route itself, and that the climate trend, coupled with the population growth, might enhance the migration along this route.

The onset of a new route may be the expression of a new migratory strategy whose success depends upon its outcome (i.e. if it gives an increased or comparable fitness), and possibly upon future climatic scenarios. In our case, the northern and southern Italian routes (the Adriatic flyway) have probably different energetic costs, and occur in different times depending on the onset of favourable weather conditions. The Adriatic flyway is likely to be more exhausting as

it goes across sea and it is usually used later in the season when the late south-migrants can take advantage of the strong southward winds blowing in late November in the Balkans. Conversely, the birds heading west migrate earlier when earlier favourable weather conditions occur (i.e. high geopotential pressure) along the NORTHIT route, and they are more likely to direct to the wintering grounds in Spain, or in Morocco. Both strategies are likely to coexist, as their success may be frequency-dependent (high density wintering individuals, less resources available).

To verify our hypotheses though, more hard data are necessary, with satellite tracking and individual tagging being pivotal here, particularly for the cranes that stop-over in Hungary (Hortobágy). Also a more standardized methodological approach, relying on appropriate temporal and spatial sampling protocols, and co-ordination of observations along the possible and confirmed migratory routes could improve the knowledge of the temporal and spatial patterns of crane migration in South Europe.

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STRESZCZENIE

[Jesienna wędrówka żurawi przez Włochy: związki szlaków przelotu z warunkami pogodowymi]

Europejskie żurawie lecą na zimowiska trzema głównymi trasami przelotu (Fig. 1). Od lat 90. XX wieku liczba żurawi lecących jesienią przez Włochy wzrasta zarówno w odniesieniu do liczby osobników, jak i wielkości stad migrujących ptaków. W pracy zebrano dane o przelocie żurawi nad Włochami z lat 2001–2007, do analiz zależności wędrówek od pogody wzięto pod uwagę także dane meteorologiczne dla znanego dużego miejsca przystankowego na Węgrzech (Hortobágy) oraz dane o warunkach pogodowych z lat 1948–2007.

Stwierdzono stały wzrost liczby wędrujących ptaków (Fig. 2), a także inny wzorzec fenologiczny dla północnych i południowych Włoch — ptaki wędrujące na północy kraju lecą wcześniej o 7–14 dni niż na południu (Fig. 3), a liczba ptaków obserwowana nad poszczególnymi częściami kraju różni się pomiędzy latami (Tab. 1, 2). Na podstawie liczby i kierunku przelotu wędrujących ptaków (Fig. 4A) zaproponowano przebieg dwóch głównych szlaków wędrówkowych żurawi na tym obszarze (Fig. 4B): północnego i południowego. Dotychczas istnienie tego drugiego było sugerowane w literaturze, natomiast szlak północny jest nowo opisaną drogą wędrówkową. Masowe przeloty żurawi powiązane są z konkretnymi warunkami pogodowymi, przelot szlakiem północnym związany jest z wiatrami zachodnimi wiejącymi w centralnej Europie (Fig. 5). W ostatnich 60-ciu latach częstość występowania takich warunków pogodowych wzrasta, co może sugerować, że powstanie nowego szlaku wędrówkowego wiąże się ze zmianami klimatycznymi.