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The effect of wind, season and latitude on the migration speed of white storks *Ciconia ciconia*, along the eastern migration route

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The relation between wind, latitude and daily migration speed along the entire migration route of white storks was analysed. Mean daily migration speed was calculated using satellite telemetry data for autumn and spring migration of white storks from their breeding grounds in Germany and Poland to wintering grounds in Africa and back. The National Center for Environmental Prediction (NCEP) reanalysis data were used to systematically fit 850 mb wind vectors to daily migration speed along the migration route. White storks migrated significantly faster and had a shorter migration season in autumn (10 km/h) compared to spring (6.4 km/h). In autumn mean daily migration speed was significantly slower in Europe (8.0 km/h) than in the Middle East (11.1 km/h) and Africa (11.0 km/h). In spring mean daily migration speed was significantly faster in Africa (10.5 km/h) as birds left their wintering grounds than in the Middle East (4.3 km/h). Migration speed then increased in Europe (6.5 km/h) as birds approached their breeding grounds. In both spring and autumn tailwind (at 850mb) and latitude were found to be significant variables related to daily migration speed.

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Several studies have been conducted trying to determine the relationship between various weather components and the timing, intensity and spatial distribution of soaring bird migration at fixed points such as radar stations and count stations (e.g. Richardson 1990, Allen et al. 1996, Spaar and Bruderer 1996, Maransky et al. 1997, Meyer et al. 2000). In most studies, prevailing winds had the strongest effect on migration passage and rates of soaring birds. However, investigating the effect of weather along the entire migration route, across large and varied regional expanses has not been possible until recently. The use of satellite telemetry to track birds has provided invaluable information on migration routes, timing, stopover and wintering sites of several species of birds (e.g. Fuller et al. 1998, Meyburg and Meyburg 1999, Berthold et al. 2001, Hake et al. 2001). The detailed information on entire migration routes of birds, which was not available until the application of this technology, can be used to study the relation between weather and migration over broad geographic ranges. In addition, these data can provide the framework for creating migration forecasts based on weather in remote areas.

Satellite telemetry studies of migrants have shown daily and seasonal variations in migration speeds. Using data from satellite telemetry studies of migrating white storks *Ciconia ciconia* nesting in Poland and Germany and migrating to Africa (Berthold et al. 1997, Van den Bossche et al. 1999, Berthold et al. 2001) we investigated and modeled the relationship between wind, latitude and season along the entire migration route of these storks. The white storks studied used the eastern migration route passing from Europe through the Bosphorus in Turkey, and then migrating south through the Middle East crossing the Red Sea in southern Sinai and continuing to their wintering sites in Africa, south of the Sahara. In order to study the relation with weather along the entire migration route a meteorological dataset was needed covering Europe, the Middle East and north and central Africa. Both NASA (National Aeronautics & Space Administration) and NCEP (National Center for Environmental Prediction) provide such large-scale multiyear meteorological datasets through the Internet. There are several advantages in using these datasets: (1) the data are standardized over time and space, (2) they eliminate or greatly reduce the need to rely on local meteorological stations and services, (3) through the use of atmospheric models that assimilate reliable remote sensing data, meteorological fields become available for remote areas that are rarely monitored regularly by ground stations and (4) they are public domain.

Daily and seasonal variations in migration speeds may be attributed to a combination of environmental and physiological factors. The objective of this study is to analyse the relation between wind, latitude and mean daily migration speed and how these relations may change during the season along the entire migration route of white storks.

Methods

Satellite telemetry

The Argos Satellite system (Argos 1996) was used to track birds fitted with platform transmitter terminals (PTTs). The Argos system is flown aboard the National Oceanic and Atmospheric Association (NOAA) Polar Orbiting Environmental Satellites (www.argosinc.com), and as a result of the satellite's near-polar orbit, the number of passes over a PTT increases with increasing latitude, with one revolution around the earth approximately every 102 minutes. The Argos system provides location estimates that are divided into several location classes reflecting location estimate accuracy. Standard location classes (LC) are defined as follows: LC 3 with an estimated accuracy ≤ 150 m, LC 2 with an accuracy ≥ 150 m and <350 m and LC 1 with an accuracy ≥ 350 m and <1000 m, LC 0 with an accuracy of >1000 m. LC 0, A, B and Z, location estimates have failed specified quality assurance tests and therefore provide no estimation of location accuracy (Argos 1996).

White storks tracked between 1994 through 1999 were used in this study (Berthold et al. 2001, 1997, Van den Bossche et al. 1999). The quality and number of location estimates provided by the PTTs varied between each bird and between seasons for the same bird. Therefore, only PTTs that transmitted every day or every other day and for at least half the migration route (from the wintering or breeding site to the Middle East) were used in the analysis. Following these criteria a total of 32 migration routes from 21 individuals were used (several birds had transmitters that provided data for more than one season). Sixteen storks were adults (three females, seven males and six unidentified sex) and five were juveniles. Twenty-four routes were analysed in autumn (3 adult females, 7 adult males, 6 adults of unknown sex and 5 juveniles) and eight in spring (3 adult females, 1 adult male and 2 adults of unknown sex). Storks were fitted with transmitters in autumn and satellite transmitters often did not operate for more than one season, which is why the dataset for autumn is much larger than in spring.

White stork calculations

Locations received were subjected to several stages of quality control. Initially location estimates from LC A, B and Z were automatically removed. Following this step, migration routes were mapped using ArcView (ESRI 1999a, b) Geographic Information System (GIS) software. Records that were visually erroneous in relation to their geographic and temporal position were also removed. When location estimates from LC 0–3 were not available for a period of more than 24 hours, estimates from LC A, B and Z were used. Migration was defined from the point when unidirectional movement was recorded away from the breeding site in autumn and away from the wintering site in spring (Fuller et al. 1998). End of migration occurred when movement in one clear direction stopped and birds began to move locally as they searched or settled into a particular wintering or breeding site.

Each bird was considered independent of other birds used in this study. During part of the autumn migration one or two birds were occasionally found in the same area. However, due to the level of accuracy in location estimates from the satellite transmitters it was impossible to determine if in these few cases the birds were actually in the same flock. In most cases it is clear that the birds were not migrating in the same flocks and can be treated as independent measurements. Van den Bossche et al. (1999) found that age did not significantly affect variations in daily migration distance; therefore, migration data for juveniles and adults were pooled for analysis.

Distance travelled (km) was calculated from one location estimate to the next as the great circle distance between data points. The time between successive reliable location estimates varied. In order to reduce variance in speeds due to various times of the day and night or when several hours passed between reliable location estimates, estimated average daily migration speed was calculated. Variation caused by differences in number of hours spent during actual migration cannot be accounted for; this factor cannot be determined from the satellite information. Location estimates were grouped into subsets where the time between the first and the last location estimate was closest to 24 hours. Distances between consecutive location estimates were summed for these subsets and mean daily migration speed was calculated as the accumulated distance divided by the accumulated time. The dependent variable will be labelled "daily migration speed" (km/h). Daily migration speed was the parameter analysed in relation to latitude and wind aloft (850 mb). Daily migration speed is an estimate of mean migration speed throughout the day and night and cannot be compared directly to migration speed in most publications.

Meteorological data and calculations

Data for wind at the 850 mb pressure level were extracted from the National Center of Environmental Prediction (NCEP) Reanalysis data archives. Data were provided by NOAA-CIRES Climate Diagnostics Center at Boulder, Colorado, USA (www.cdc.noaa.gov/cdc/data.nmc.reanalysis.html). The reanalysis data were created using a global data assimilation system based on various assimilated observations/measurements and atmospheric models, with output variables classified into four classes dependent upon the relative influence of observational data and model input (Kalnay et al. 1996). The 850 mb U and V wind components (wind speed along the X and Y axis respectively) used in this study belong to Class A variables, which are strongly influenced by observational/measured data and hence most reliable. Data were given for every 6 hours (00:00, 06:00, 12:00, 18:00 h UTC) with a spatial resolution of 2.5° latitude by 2.5° longitude global grid.

U and V wind data that were closest geographically and temporally to each location estimate were extracted from the NCEP archive. U- and V-wind variables were used to calculate a head/tail-wind component (wind strength following or opposing the direction of migration) and a side-wind component. The first and last records within the daily migration speed subset were used to calculate migration direction and average U- and V-windspeeds for that subset were used for the calculation of head/tail-wind and side-wind components in relation to migration direction. Tail winds are expressed as positive values while negative values signify a headwind component. Crosswinds are perpendicular to the migration heading, where positive values represent winds from the left and negative values represent crosswinds from the right of the migration heading.

Statistical analysis

Spring and autumn migration routes were analysed separately. The square root transformation of daily migration speed was applied in both spring and autumn and this variable was then analysed in relation to average 850 mb tail and cross wind speed and latitude.

Data for each season were analysed according to region as follows: Europe – breeding sites in Germany and Poland to Bosphorus (41°0′N, 28°02′E), Middle East – Bosphorus to El Thor, Sinai (28°0′N, 33°01′E), Africa – El Thor to wintering site (similar to Van den Bossche et al. 1999). ArcView software (ESRI 1999a, b) was used to check coordinates close to the Bosphorus and Sinai individually. Coordinates within Sinai were considered within the Middle East, once the birds crossed the Red Sea they were considered to be within Africa. The same procedure was used for the Bosphorus, with coordinates south of the Bosphorus considered as belonging to the Middle East region, and coordinates north of the Bosphorus belonging to Europe. In spring, a distinct change in daily migration speed was found at approximately latitude 30° N. Therefore a dummy variable was created ('mlat') and defined as 1 for the Middle East and Europe and 0 for Africa.

A two-way analysis of variance (ANOVA) was conducted to test for within- and among-season effects and the interaction between season and region. To test for differences between regions within each season and for each region between seasons a one-way ANOVA model and Tukey's Studentized range tests were conducted using SPSS 9.0 (SPSS 1999).

A General Linear Model (GLM) was used to test the relation between daily migration speed, wind and latitude in spring, autumn and for Europe, Middle East and Africa. When linear relationships between the dependant and explanatory variables were not significant ($P > 0.05$) a *loess* smoother (Cleveland 1979) was applied to the particular variable and a General Additive Model (GAM), as described by Hastie and Tibshirani (1990), was fitted to test the relationship between the daily migration speed and the covariates. In the GAM, deviance is the measure used to show the fit of the model to the data. All modelling was performed using S-Plus software (MathSoft Inc. 1998).

Results

Migratory speeds of 21 adult and juvenile western Palearctic white storks migrating along the eastern flyway were studied, and results for 7 of them are exemplified in Fig. 1. Daily migration speeds of individual birds varied between days, regions and seasons (Fig. 2). The mean duration of migration in autumn for the birds studied was 26.1 ± 4.9 days (mean ± SD, $n = 23$

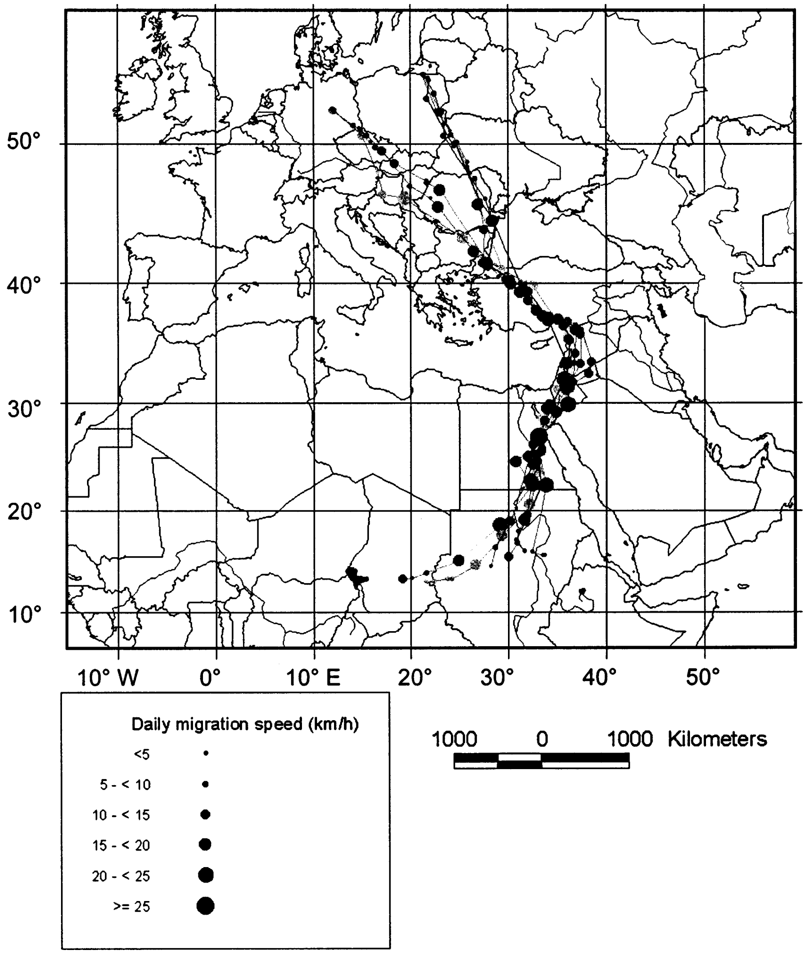

Fig. 1. Map (Mercator projection) of 1996 autumn migration routes of seven white storks used in analysis. Size of the symbol represents relative daily migration speed; each route represents an individual bird.

routes), 24.7 ± 3.8 days without stopovers, with an average speed of 10.0 ± 5.9 km/h ($n = 543$ days). In spring the mean duration of migration of was 49.1 ± 15.0 days ($n = 8$ routes), 36.0 ± 8.3 days without stopovers and the mean migration speed was 6.4 ± 5.6 km/h ($n = 314$). The mean daily migration speed was significantly faster in autumn than in spring ($F_{1,851} = 51.36$, $P < 0.001$). There was also a significant difference between regions ($F_{2,\ 851} = 27.1$, $P < 0.001$) as well as an interaction between season and region ($F_{2,\ 851} = 26.8$, $P < 0.001$).

Autumn

In autumn the white storks began migrating at slower speeds as they left their nesting sites and then migrated faster as they reached the Middle East and their wintering grounds in Africa (Table 1). Daily migration speed in the Middle East (11.1 km/h) and Africa (11.0 km/h) were significantly faster than in Europe (8.0 km/h) (Table 2). Migration speed was significantly related to latitude and tailwind at 850 mb (Fig. 3: residual deviance = 467.4, null deviance = 593.9, GAM).

In Europe there was a significant relation between daily migration speed, latitude ($T = -6.4$, $P < 0.001$) and average tailwind at 850mb ($T = 2.8$, $P = 0.005$; $r^2 = 0.19$, $P < 0.001$, GLM). Migration speed increased with average tailwind and as birds migrated farther south. When stopovers (over 24 h) were removed, the relation between migration speed, wind and latitude remained very similar. In the Middle East there was a significant relation between daily migration speed, day of year ($T = -3.8$, $P < 0.001$) and average tailwind at 850mb ($T = 3.4$, $P < 0.001$; $r^2 = 0.14$, $P < 0.001$, GLM). Migration speed increased with tailwind and earlier days in the season. In Africa there was a significant and positive relation between daily migration speed and average tailwind at 850 mb ($T = 5.3$, $P < 0.001$) and latitude ($T = 5.0$, $P < 0.001$; $r^2 = 0.39$, $P < 0.001$, GLM). During autumn migration tailwinds were prevalent in all regions.

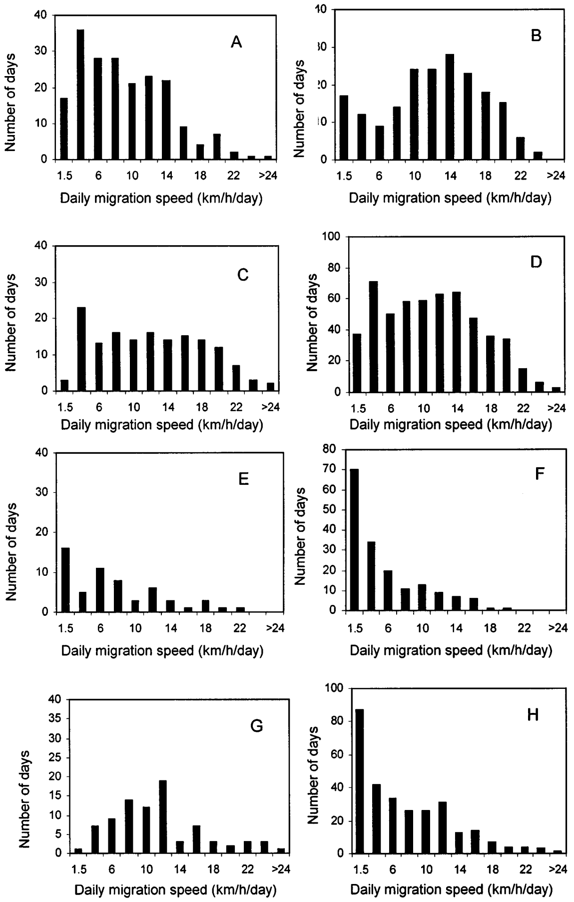

Fig. 2. Frequency of distribution of daily migration speeds in autumn for Europe (A), the Middle East (B), Africa (C) all regions combined (D) and in spring for Europe (E) the Middle East (F), Africa (G) and all regions combined (H). Scale for daily migration speed: $x \le 1.5$, $1.5 < x \le 4$, $4 < x \le 6$, etc. In most cases, values under 1.5 km/h can be considered stopovers.

Spring

In spring, daily migration speeds differed significantly between the three regions (Table 2). Storks migrated faster in Africa (10.5 km/h), at the beginning of the migration season, and then migrated significantly slower in the Middle East (4.3 km/h) and Europe (6.5 km/h). Storks, all adults, first made stopovers over 24 h in the Middle East, occasionally lasting several days.

Table 1. Mean daily migration speeds (km/h) and standard deviation for each season and region; n = number of days.

		Europe	Middle East	Africa
Autumn	Mean	8.0	11.1	11.0
	SD	5.3	5.7	6.2
	n	199	192	154
Spring	Mean	6.5	4.3	10.5
	SD	5.5	4.5	5.4
	n	58	172	84

Table 2. Significance of one- and two-way ANOVA for daily migration speeds (km/h) between and within season and regions.

	Model	P value
Autumn	Europe vs Middle East	<0.001
	Europe vs Africa	<0.001
	Middle East vs Africa	ns
Spring	Europe vs Middle East	0.009
	Europe vs Africa	<0.001
	Middle East vs Africa	<0.001
Autumn vs Spring	Europe	ns
	Middle East	<0.001
	Africa	ns
Season		<0.001
Region		<0.001
Season times Region		<0.001

Daily migration speed was significantly related to region (variable 'mlat'; T = – 10.9, $P < 0.001$), tailwinds at 850 mb (T = 5.6, $P < 0.001$) and crosswinds (T =

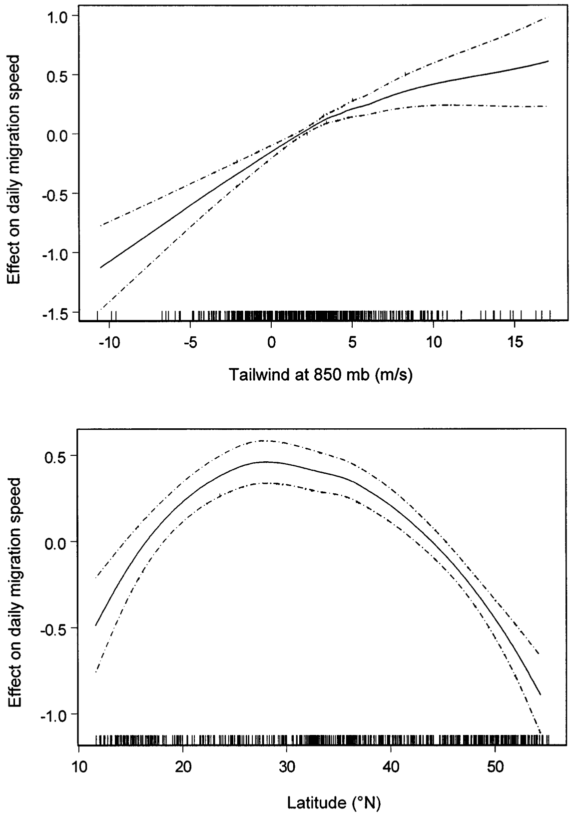

Fig. 3. Plots from the autumn GAM of the effect of the best fitting function of each covariate (x-axis) on the square root of daily migration speed (y-axis). The scale of the y-axis reflects the relative importance of each covariate in the model. Covariates: (upper panel) Loess smoothers of average 850 mb tailwind (m/s) and (lower panel) latitude. Dashed lines represent two standard error boundaries around the covariate. Lines along the x-axis represent a rugplot of data points used in the analysis showing the density of data over the range of each covariate.

-4.1, $P < 0.001$; $r^2 = 0.32$, $P < 0.001$, GLM). Migration speed was faster south of 30°N and increased with tailwind, and crosswinds from the south-west.

In Africa there was a significant and positive relation between daily migration speed and average tailwind at 850 mb ($T = 5.3$, $P < 0.001$; $r^2 = 0.25$, $P < 0.001$, GLM). Headwinds dominated in the region (mean headwind 1.55 m/s). In both the Middle East and Europe there was a significant positive relationship between daily migration speed and average tailwind at 850 mb and crosswinds from the left of the migration track ($r^2 = 0.14$, $P < 0.001$, $r^2 = 0.13$, $P = 0.01$, respectively, GLM).

Discussion

Mean daily migration speed of white storks was significantly faster during southbound migration than northbound migration when birds are returning to their nesting sites (10.0 km/h vs 6.4 km/h, respectively, and migration duration was significantly longer in spring than in autumn (mean migration duration with stopovers was 49 days in spring vs 26 in autumn). Mean daily migration speed also differed significantly between regions along the storks' migration path in both autumn and spring. The tailwind aloft (850 mb) consistently had a significant effect on daily migration speed both between and within each season.

The location of the birds (latitude) was generally one of the significant variables related to changes in daily migration speed. In autumn white storks increased their mean daily migration speed when they left Europe and migrated faster in the Middle East and Africa. In spring, there was a sharp decrease in mean daily migration speed north of latitude 30° N and storks migrated significantly slower in the Middle East and then increased their speed in Europe as they approached the nesting grounds. The mean daily migration speed and the relationship with wind differed between seasons. Leshem and Yom-Tov (1996b) also recorded a significantly longer white stork passage over Israel in spring (43 days) than in autumn (28 days). During spring migration six adult storks made stopovers lasting between 4 and 29 days.

The regional and seasonal differences in mean daily migration speed can be explained by at least three main factors: the physical condition of the bird, tailwind assistance and thermal convection. In autumn, as birds leave the breeding sites, they must feed in order to make the long journey to their wintering grounds in Africa. Conditions in Europe are still such that food sources are available. In autumn, when birds reach the Middle East and North Africa, food and water sources are scarce and migration speed increases significantly. In spring, white storks migrate quickly as they leave Africa and then significantly decrease mean migration speed when they first reach the Middle East. After crossing the Sahara where food sources are scarce the storks need to rest and refuel at the first appropriate sites. Following the rainy winter season, more food and water sources are available in the Middle East in spring compared to autumn. Van Den Bossche (pers. com.) observed that white storks stop to feed while migrating north in spring once they reach the Negev in Israel (latitudes 30°–32°N). Delaying arrival at the breeding sites in order to feed after leaving Africa may also be due to decreased food supplies in wintering areas as a result of climatic changes, desertification and locust extermination (Dallinga and Schoenemakers 1989).

Wind assistance may explain part of the seasonal differences in mean daily migration speed. During this study the winds prevalent in spring were generally less advantageous than in autumn in all regions. Nevertheless, in Africa there was no significant difference in mean daily migration speed between spring and autumn. White storks probably take advantage of excellent soaring conditions in Africa during both seasons, hence the greater mean migration speed there. However, prevailing headwinds during spring and lack of stopover sites in Africa may force the storks to land and feed once they reach the Middle East. Once storks have refuelled their speed increases in Europe, although it is still slower in spring than in autumn when tailwinds were significantly stronger. Liechti et al. (1996) also found that the average ground speed of white stork migration in southern Israel was higher in autumn than in spring, due to a difference in prevailing tailwinds.

The relation between tailwinds and soaring bird migration has been well documented and several studies have shown that many species tend to take off or pass study sites in peak numbers when winds are following relative to flight directions (Richardson 1990). Maransky et al. (1997) found that more red-tailed hawks *Buteo jamaicensis* passed the study site when winds were following and strong (20 km/h and above), having a greater effect later in the season. Spaar and Bruderer (1996) found that cross-country speed of steppe eagles *Aquila nipalensis* increased with increasing tailwinds in southern Israel. Alerstam and Hedenström (1998) suggested that as soon as wind speed exceeds a bird's airspeed the range of possible track directions will become restricted and birds may not be able to maintain preferred migration direction should wind direction change.

In spring, in the Middle East and Europe, crosswinds had a significant effect on migration speed, with winds from the left of the migration track being preferred by the storks. In the Middle East winds from the left (generally westerly or south westerly winds) are preferable to easterly or northeasterly winds that may cause storks flying downwind to drift out over the Mediterranean Sea, a major ecological barrier for white storks. In Europe, winds from the left of the migration axis, south-westerly winds, are accompanied by warm humid air, in contrast to the cold dry air that originates from the north-east. Richardson (1990) summarizes studies showing peak northward migration corresponding to days with warm southerly winds, increasing humidity and temperature and decreasing pressure, as highs move away to the east or lows approach from the west. Crosswinds may play a more significant role in migration speed in spring than in autumn because of the prevalent headwinds in the latter season.

Thermal convection is the third factor that probably has a significant effect on the regional differences in mean migration speeds, explaining in part the faster daily migration speeds at more southern latitudes. Higher migration altitudes due to better soaring conditions were reported in Africa for several species of soaring birds including white storks (Pennycuick 1972). Migrating white storks were not only recorded at higher altitudes in Africa than in Israel (Leshem and Yom-Tov 1996a), but average cross-country speeds were also higher (43.9 ± 1.2 km/h vs 38.7 ± 9.6 km/h). The differences in height bands and cross-country speeds between Africa and Europe would probably be even higher. Unfortunately, thermal convection is not measured directly especially across such large regions and although thermal convection can be modelled, these models must be calibrated to local topography (Shannon et al. 2002, Shamoun-Baranes et al. 2002).

In summary, differences in daily migration speed of white storks were related to wind assistance, location and season. Seasonal and regional differences in daily migration speed are probably explained by a combination of differences in the physical condition of the bird and feeding behaviour, prevailing winds and other factors, particularly thermal convection. Understanding of these relationships can be used to forecast changes in migratory behaviour based on changes in meteorological conditions. Furthermore, it provides an excellent method for future studies on different species tracked over several years using satellite telemetry and for comparing migratory behaviour in different regions around the globe.

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