SPRING CRANE *Grus grus* MIGRATION THROUGH GALLOCANTA, SPAIN
I. DAILY VARIATIONS IN MIGRATION VOLUME

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ABSTRACT The relations between numbers of Common Cranes *Grus grus* departing on spring migration and weather, progress of season and course of migration were studied at Gallocanta, NE Spain during February-March 1984 and 1985. Rain, cloudiness and strong headwinds were important factors inhibiting migration. Most cranes migrated in association with the south-western sector of a high or in the warm sector of a low. Given these fair weather conditions, the number of birds departing was mainly correlated with date and with the relative number of cranes that did not migrate the previous day, but not with the number of birds staging and only slightly with the number that arrived the previous day. The average staging period estimated for an individual crane (5-8 days) was longer than the average duration of adverse weather period without migration (0-3 days). The daily departure never included 100% of the staging birds (mean 14,3%). These facts suggest that the duration of the staging period results from a compromise between the urge to arrive in time at the breeding areas, the inhibiting effect of bad weather, and the tendency to stay longer so as to benefit from favourable feeding conditions.

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INTRODUCTION

In temperate bird species the timing of migration is genetically preprogrammed and fixed within certain limits in their annual cycle and synchronized with the environment by various proximate factors, notably photoperiod and several weather variables (Berthold 1976, 1984, Gwinner 1977, Alerstam 1978, Richardson 1978). Short term changes in weather as well as other factors such as migratory flights on the previous days may markedly affect the responsiveness of the birds and thus the numbers aloft or concentrated at stopover areas. The influence of these proximate factors seems to be especially important for species breeding at high latitudes (e. g. Ankney & MacInnes 1978, Mikkonen 1981, Ebbinge *et al.* 1982, Davies & Cook 1983, Krapu *et al.* 1985). The cranes are highly migratory and are ideal subjects to investigate the above mentioned relations. Many papers have been published describing the routes and phenology of migration of various crane species, notably the Sandhill and Whooping Cranes (*Grus canadensis* and *G. americana*) (see references in Melvin & Temple 1981, Lewis 1987) and the Common Crane (*Grus grus*) (e. g. Libbert 1936, Keil 1970, Alerstam & Bauer 1973, Mewes 1976, Vergoosen 1981, Karlsson & Swanberg 1984, Prange 1984, 1987, Salvi 1984, 1987, Petit 1986, Wessels 1987). Most of these studies describe only bivariate relations between weather and other environmental variables and migration volume (Keil 1969, 1970, Alerstam & Bauer 1973, Klose 1974, Rinne 1974, Alerstam 1975, Deppe 1978a, b, Pennycuick *et al.* 1979, Swanberg 1987b).

Common Cranes breeding in Northern Europe and migrating through the western route have their main winter quarters in Spain (Bernis 1960, Swan-

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berg 1987a, Alonso & Alonso 1988). Moreover, most of them use our study area, Gallocanta lake, as a staging area during both migration periods and a large number spend the whole winter there. During recent years this site has become the most important staging area for the species (Alonso *et al.* 1984a, 1987, Alonso & Alonso 1988). In this paper we study, through synoptic, bivariate and multivariate analyses, the relations between the numbers of cranes departing from Gallocanta and weather, progress of season, and progress of migration (including numbers of birds arrived and staging at the study area). Our objective was to identify the relative importance of these variables and to describe statistically the day to day variations in the migration departure from a staging area, rather than to obtain a predictive equation for migration intensity. Advantages of this study with respect to other radar or visible migration studies were (a) we knew the daily numbers of birds staging, which enabled us to use the fraction of birds departing as a true index of the daily intensity of migration or responsiveness of the cranes, i.e. we could compensate for the daily variations in the numbers ready to migrate; (b) in addition to weather variables we also measured other relevant variables, like numbers of cranes staging and arriving at the study area, number of preceding days without migration, and food availability; and (c) the results are highly representative for this species, as our study was carried out at one of the most important crane staging areas, and as we counted all cranes leaving the area, instead of recording a sample of birds (visual studies) or flocks (radar studies) passing through a certain area. Thus most of the usual types of bias in weather-migration studies were avoided (see Richardson 1978).

STUDY AREA

Laguna de Gallocanta (40° 58'N, 1°30'W; 990 m a.s.l.) is a saline lake with a water surface of 1400 ha. It lies approximately in the center of a flat endorreic basin of 53637 ha, most of which is cultivated farmland, mainly wheat and barley. The basin is surrounded by 150-400 m high mountains, which to the East and North are 2 to 4 km from the lake. The climate is mesothermic, with mild summers and frequent frosts between November and March. In normal years there are 75-100 dry days, an average rainfall of 400-600 mm, and mean temperatures of 10-12°C. During the study periods, temperature oscillated between -7.8°C and 19.6°C, with a mean value of 4.3°C. Precipitation occurred on 21 days, including one snowfall equivalent to 146 mm of water on 28 Feb 1984. Average wind speed was 23.8 km h^{-1}; with N, NW and WSW being the most frequent directions. Maximum recorded wind speed was 62.6 km h^{-1}, from the North.

METHODS

Migration data

We counted migrating birds between February 13 and March 20, 1984, and between February 17 and March 18, 1985, from 2 to 5 observatories along the mountain chain NE of the lake. Observers stood at these points from the time cranes left the roost in the morning, around 0800 h, until 1600 h. Later, possible migration departures were observed from the lake basin. Adjacent observatories were separated by 4-11 km. We used 8-12x binoculars and 20-60x telescopes and were in permanent radio contact to avoid duplications while counting the birds. The number of birds, flight height (estimated with respect to the nearest mountain of known height), and time of departure were recorded for each departing flock when it passed over the observation point.

Besides the number of birds seen migrating each day (a), this variable has been transformed in various ways (see Nisbet & Drury 1968): number of birds migrating on one day divided by the number of birds staging at the study area the previous night (b); number of birds migrating one day divided by the total number of cranes migrating through the study area that year (c); $d = c$ - the expected number of cranes on that day, calculated as the 7-day moving-average; $e = \ln d$; $f = \sqrt{d}$;

$g = \sqrt{(b+1)}$; $h = \ln(b+1)$. Transformed variable h was selected as the dependent variable to represent the daily migration volume, as it accounts for the daily differences in the number of birds staging at Gallocanta throughout the study period and reduces problems related to the lesser migratory restlessness ("Zugunruhe") during the initial and final parts of the migration period. Thus, this transformation represents the propensity to migrate better than other usual measurements like number of birds or flocks seen (see Alerstam 1978). To further avoid the problems caused by the first-year and immature cranes remaining at the study area for a longer time at the end of the staging period due to their decreased migratory responsiveness (Alonso *et al.* 1984b), we excluded the final days, when the percentage of juveniles in the area exceeded 50% of the birds.

Besides the number of birds, we also used the "logarithm of the number of flocks seen migrating plus one" as another dependent variable, to investigate wether analyses of these two variables gave consistent results (see Richardson 1978:229).

Predictor variables

Non-weather variables The following variables related to date and number of birds staging were measured each day:

(1) Number of birds staging: the cranes staging at Gallocanta were censused twice each day, during roost departure and roost entrance. The higher of two consecutive roost counts (evening and following morning) was used as the number of birds staging at the study area on each day of the migration period;

(2) Number of birds arrived in the study area the previous day = variable 1 on the previous day minus variable (1) two days ago;

(3) Retention 1, defined as the number of preceding days without migration (including those days in which the number of birds migrating were less than 1% of the yearly total);

(4) Retention 2, defined as (1) the previous day divided by the number of birds migrating the previous day + 1;

(5) Retention 3, defined as the percentage of birds that did not migrate the previous day;

(6) Retention 4, defined as (4) multiplied by the number of consecutive preceding days without migration + 1;

(7) Retention 5, defined as (5) multiplied by the number of consecutive preceding days without migration + 1;

(8) Retention 6, defined as (2) divided by (1);

(9) Retention 7, defined as the sum of variable (2) of the preceding six days;

(10) Day of year, numbered from January 1;

(11) (Day of year)^2, to study possible non-linear relations with date;

Food availability in the study area was also estimated by counting the number of recently sown wheat and barley fields – food preferred by the cranes – along a 37 km transect through the cranes' feeding areas.

Weather variables The following weather variables were calculated from values for wind speed and direction, cloudiness, precipitation and temperature measured at 1-hour intervals at the migration observatories. Their mean values for the period of usual migratory passage (0900-1300 h GMT) were used in the analyses, except for variables (10) to (14), which were taken from the nearest meteorological observatory, about 10 km NE from the study area:

(1) Wind speed at surface, in m s^{-1};

(2) Crosswind vector component of (1), in m s^{-1} (absolute value) either from the left or right side in relation to the migration direction (21°N with respect to true North);

(3) Tailwind vector component of (1), in m s^{-1}, including head winds as negative values of this variable;

(4) 24-h change in (3), with its sign;

(5) Cloudiness, estimated in eights of the visible sky;

(6) 24-h change in (5), with its sign;

(7) Precipitation, from 0 (absence of precipitation) to 3 (heavy rain or snow);

(8) Temperature, in °C;

(9) 24-h change in (8), with its sign;

(10) Barometric pressure, in mb;

(11) 24-h change in (10), with its sign;
(12) Relative humidity, in %;
(13) 24-h change in (12), with its sign;
(14) Visibility, in hectometers, mean value between 0700 and 1300 h.

Three additional weather variables were calculated from the 1200 hours GMT daily weather maps of the National Meteorological Institute:
(15) Atmospheric instability, defined as the difference in temperature (°C) between the surface and the 800 mb level, with its sign;
(16) Distance to the nearest cold front in km, with negative sign if the front was approaching (W of the study area), and positive sign if it had passed the study area (E of it);
(17) Distance to the center of the nearest low in km, with signs as in (16).

Most predictor variables were subjected to different transformations (ln, square-root or inverse) appropriate to the assumptions of multivariate analysis.

Analytical procedures

We performed synoptic, bivariate and multivariate analyses. Synoptic weather features in relation to Gallocanta were estimated by visual examination of the 1200 h GMT daily weather maps, according to Richardson (1978) and Elkins (1983).

Statistical analysis For all subsequent analyses we considered separately three data matrices, the first including all 53 migration days (until the percentage of juveniles exceeded 50% -see above), the second excluding 23 days with no migration, and the third (n = 43) excluding the last days of the migratory period (= last 10% of the yearly total migration volume of each year) considered in the first matrix. The second matrix was analysed to study possible differences caused by the inclusion of a relatively large sample of days of zero migration, which could violate the assumptions of statistical analyses used. The third matrix was included to investigate possible influences of (a) the non-reproductive birds migrating later (see above and Alonso *et al.* 1984b), and/or (b) the faster progress of migration, i.e. shorter staging during the last part of the migratory period.

A factor analysis was applied to all weather variables to elucidate relationships among them, and to reduce them to a smaller number of basic factors. We extracted five principal components and subjected the first three, which had eigenvalues 1.3 to 3.8, to Varimax rotation.

We performed stepwise multiple regression analyses relating migration volume to non-weather variables and either the original weather variables or the weather factors extracted from them; we used the BMDP2R program (Dixon 1987). To assess the reliability of the regression results, the samples of days with and without migration were subjected to a stepwise multiple discriminant analysis (BMDP 7M, Dixon *op. cit.*), which makes fewer assumptions about the nature of the data.

The results of all these analyses were very similar, supporting the conclusions derived from them. Here we only present the result from bivariate analyses and stepwise multiple regression and discriminant analyses with non-weather variables plus weather factors. Also, separate analyses for each year gave similar results; thus both years were analysed together.

RESULTS

Migration phenology

The spring migration of cranes takes place at Gallocanta between mid February and late March. The staging population peaked on March 8 in 1984 (6107 cranes) and March 9 in 1985 (20 878). The total numbers of cranes migrating through Gallocanta were 16 351 and 31 945, respectively for 1984 and 1985. The maximum numbers of birds departing from the area on one day were, respectively, 4353 or 72.8% of the staging population that day (March 5, 1984) and 93 28 or 44.7% (March 9, 1985). Daily mean numbers of departing cranes were 867 (21.2% of the staging population that day) in 1984 (18 days with migration) and 2530 (30.0% of staging population) in 1985 (12 days with migration). In 1984 the number of birds staging in the study area decreased regularly between March 19 and April 8, when the last 11 cranes left the area.

The durations of the periods of arrivals and departures at Gallocanta were similar in both years. The number of birds arriving one day was not significantly correlated (r = 0.281, n = 53, $p > 0.05$) with the number of birds departing the next day, suggesting that cranes tended to stage at the study area for more than one night. Moreover, the weighted mean arrival dates were March 1 and March 5, respectively for 1984 and 1985, while the respective weighted mean departure dates were March 9 and 10. Thus, the estimated average staging periods for an individual bird at Gallocanta were 8 and 5 days, respectively for 1984 and 1985. Furthermore, cranes were never observed to fly over Gallocanta without stopping there.

Synoptic features of crane departures

The results of the synoptic analysis indicate that most cranes (54.6% of total migrating birds, in 16 days, Fig. 1) migrated in association with the southwestern part of an anticyclonic ridge, as a low pressure area moved away to northeast and another was approaching from the west. This situation coincides with short periods of calm or light following winds (southerly to southwesterly) under typical fair weather conditions: clear skies and sunny days

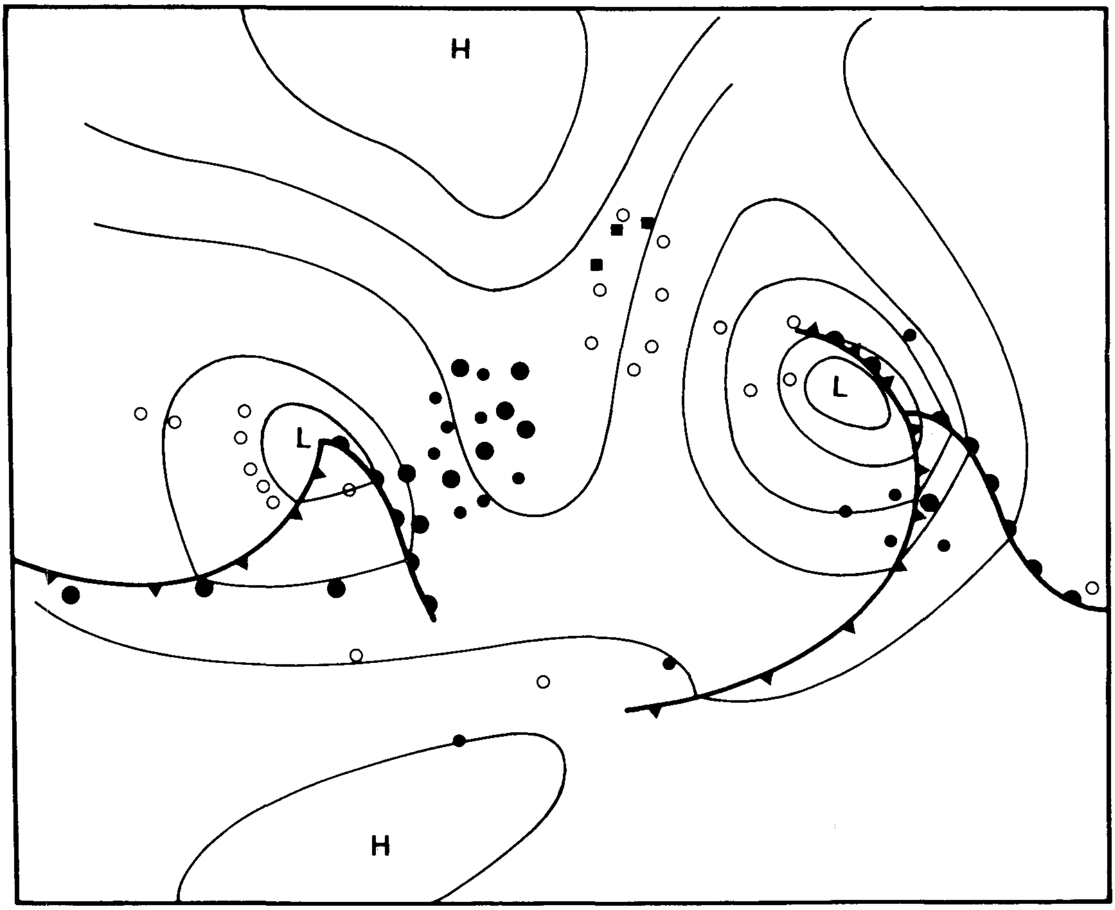

Fig. 1. Typical synoptic situation during the spring migratory period of the Common Crane. Modified from Elkins (1987). Each dot or square represents one migration day (n = 45 972 migrating cranes); larger dots represent days of migration volume both ≥ 1000 birds and ≥ 25% of birds staging; black squares indicate last days of 1985 migration period, after a long period of adverse wind conditions (see text); open dots are days with no migration

with high pressure, usually with extensive thermal activity. Most of the other cranes (30.8% in 5 days) migrated in warm sector conditions, i.e. behind the warm front of a low, with westerly to southwesterly winds. A few birds (3.2%), migrated immediately behind cold fronts (4 days) or before occluded fronts (1 day). These occasions generally involved a predominantly westerly wind. Finally, some cranes (11.5% in 4 days) migrated under light headwind conditions, but most of them were birds migrating during the last days of 1985 migratory period (see Fig.1), after some consecutive days of unfavourable wind conditions.

Bivariate relationships between migration volume and weather and non-weather variables

When we analysed all days in the migration periods, conditions tending to favour migration departure were tailwind, increasing tailwind within the last 24 hours, and absence of clouds and rain. Low wind speeds, low values of the crosswind component, high temperatures and rapid temperature increases also seemed to favour inception of migration. In our study area, high wind speeds usually coincided with strong or moderate crosswinds, as suggested by the significant partial correlation coefficient between these two variables while considering them together with the tailwind component (r = 0.835, n = 53, $p < 0.001$). Moreover, there was an inverse partial relationship between tailwind and absolute wind speed, while accounting for the influence of crosswinds (r = -0.456, $p < 0.001$) this suggesting that wind speed tended to be low on days with prevalence of following winds.

When only days with migration were considered, the 24 hours increase in temperature remains the most significant variable, while all other correlations with weather variables became non-significant. Although this may partly result from the reduced sample size, it suggests that the effect of most weather variables was mainly the inhibition of migration departure.

In the sample of all days, migration increased with date, 24-h increase in the number of birds staging and percentage of birds that did not migrate the previous day(s) (Table 1). After exclusion of the days without migration, the correlation values with date and retention variables increased.

Effect of the food availability

During spring staging in Gallocanta, cranes foraged mainly on recently sown cereal fields (Alonso *et al.* 1984a). The weight of cereal seeds sown in our study area just before the beginning of the spring staging period was: 1302 x 10^3 kg in 1984 and 1502 x 10^3 kg in 1985. Assuming that 5% of this cereal was readily available for the birds (own obs.), there was excess food for the staging cranes. However, a snowfall on February 28, 1984, prevented the cranes from feeding during 3 days and hindered foraging for another 3 days. The daily migration volume during these 6 days varied between 149% and 1026% of that predicted by multivariate equations (see below). These differences are significant ($p < 0.001$) and suggest that the sudden decrease in food availability determined the early departure of the cranes.

Weather factors in the study area, en route and at destination and their relationships with migration volume

To study the relationships between migration volume and the weather that would affect the migrating cranes after departure, during their migratory flight, as well as at their next stopover locality, we measured 17 meteorological variables respectively, at departure time in the study area, at 1200 h and 90 km NNE along the migratory flyway (Zaragoza), and at 1800 h and 170 km NNE (Monflorite). These variables were subjected to factor analysis (Table 2). The first factor in the study area and en route, and the second at destination represents the presence or absence of a typical low pressure situation, combining variables related to cloudiness and precipitation. The second weather factor in the study area and en route, and the first at destination represent situations of a low center to the east and a high center to the west, with strong total and lateral winds, vs. the western sector of a high, with warm southerly winds and cold fronts still far to the west. The third factor defines different weather situations for each of the three localities.

Table 1. Product-moment correlation values between weather and non-weather variables and the volume of migration[a].

Variables	All days (n=53) No. birds	No. flocks	Only days with migration (n=30) No. birds	No. flocks
Wind speed	-0.308*	-0.303*	-0.014	0.033
Crosswind component	-0.267	-0.309*	0.003	-0.078
Tailwind component	0.319*	0.287*	0.153	0.015
24-h Δ in tailwind comp.	0.359**	0.402**	0.193	0.318
Cloudiness	-0.422**	-0.469**	-0.161	-0.265
24-h Δ in cloudiness	-0.340*	-0.347*	-0.193	-0.207
Visibility	0.204	0.252	-0.101	0.017
Precipitation	-0.384**	-0.402**	-[b]	-[b]
Relative humidity	-0.013	-0.092	0.203	-0.031
24-h Δ in rel. humidity	-0.045	-0.068	0.126	0.077
Temperature	0.294*	0.315*	0.086	0.133
24-h Δ in temperature	0.320*	0.273*	0.400*	0.321
Barometric pressure	0.059	0.186	-0.149	0.186
24-h Δ in barometric press.	0.001	-0.010	0.041	0.019
Instability	0.152	0.138	0.102	0.068
Distance to nearest cold front	0.048	0.019	0.200	0.147
Distance to low pressure center	0.007	-0.005	0.161	0.159
Day of year	0.277*	0.182	0.567**	0.343
Day of year^2	0.264	0.165	0.555**	0.319
Number of birds staging	0.082	0.225	0.054	0.477**
24-h Δ in no. birds staging	0.482**	0.527**	0.281	0.399*
Retention 1	0.129	-[c]	-[c]	-[c]
Retention 2	0.082	-[c]	-[c]	-[c]
Retention 3	0.332*	0.295*	0.584**	0.525**
Retention 4	0.165	-[c]	-[c]	-[c]
Retention 5	0.327*	0.293*	0.561**	0.510**
Retention 6	0.167	0.148	0.210	0.174
Retention 7	0.086	0.070	0.040	-0.006

* $p < 0.05$, ** $p < 0.01$

[a] migration volume is expressed as (number of birds migrating + 1) and ln(number of flocks migrating + 1)

[b] not computed since there was no precipitation on migration days

[c] not computable due to the definition of this variable

The number of birds departing from Gallocanta was inversely correlated with factors I and II at this locality, i.e. with cloudiness, precipitation, humidity, low temperature and low pressure. The number departing was also positively related with high temperature and pressure at destination at the expected time of arrival there (Table 2). However, after partial regression analysis of all 9 factors shown in Table 2 with migration volume, the only correlation remaining significant was with the second factor at the study area (r = 0.459, p < 0.01). This suggests that cranes decided to depart from Gallocanta depending more on local weather rather than on expected meteorological conditions along the migratory route or at their next stopover.

Table 2. Relationships between orthogonal factors derived by Varimax rotation and original weather variables at Gallocanta (study area), Zaragoza (en route) and Monflorite (at destination), after sorting and deletion of correlations ≤ 0.5 and simple product-moment correlations between weather factors at each locality and the migration volume [a]. Sample of all days (n = 53).

Locality	study area			en route (90 km NE)			at destination (170 km NE)		
Factors	I	II	III	I	II	III	I	II	III
Variance explained (%)	18.21	16.48	13.07	19.12	14.29	13.08	18.83	16.67	13.31
Accumulated variance (%)	18.21	34.69	47.76	19.12	33.41	46.49	18.83	35.50	48.81
Wind speed	-	0.648	-	-	-0.514	-	0.789	-	-
Crosswind component	-	0.694	-	-	-0.691	-	0.705	-	-
Tailwind component	-	-	0.656	-	0.731	-	-0.687	-	-
24-h Δ in tailwind component	-	-	-	-	0.517	-	-0.668	-	-
Cloudiness	0.557	-	-	0.614	-	-	-	-0.676	-
24-h Δ in cloudiness	-	-	-	0.513	-	-	-	-	-
Visibility	-0.774	-	-	-	-	-	-	-	-
Precipitation	0.764	-	-	0.586	-	-	-	-0.636	-
Relative humidity	0.778	-	-	0.518	-	0.622	-	-0.753	-
24-h Δ in relative humidity	0.576	-	-	-	-	0.534	-	-0.632	-
Temperature	-	-0.654	-	-0.670	-	-	-	-	0.712
24-h Δ in temperature	-	-0.669	-	-0.589	-	-	-	-	0.569
Barometric pressure	-0.514	-	-	-0.631	-	-	-	-	0.533
24-h Δ in barometric press.	-	-	-	-0.657	-	-	-	-	-
Instability	-	-	0.515	-	-	-	-	-	0.671
Distance to nearest cold front	-	0.537	-	-	-	-	-	-	-
Distance to low pressure center	-	-	-0.523	-	-0.594	-	0.520	-	-
Correlation coefficient between factor and migration volume [a]	-0.273*	-0.427**	0.044	-0.201	0.039	-0.095	0.046	-0.161	0.301*

* $p < 0.05$, ** $p < 0.01$

[a] migration volume was the ln of the number of birds departing from the study area divided by the number of birds staging there the previous night plus 1 (see Methods)

Multivariate relationships of migration to weather factors and non-weather variables

The multiple regression equation resulting from stepwise analysis of weather factors and a selection of non-weather variables at the study area explained a 47.4% of the day-to-day variations in migration volume for the sample of all days (Table 3). This equation predicts large migration departures with progress of season, high negative values of weather factor II (i.e. high temperatures and 24-h increases in temperature, and low absolute and lateral wind speeds, see Table 2), and high positive absolute and relative values of 24-h increase in the number of birds staging.

The same trends remained after exclusion of the last 10% of migration volume in both years (= last 10 days, see Methods) this suggesting that the final part of migration did not depend on significantly different predictor variables.

When the days without migration were excluded from the analysis, the weather factor II was also excluded as a predictor. Date and the percentage of birds that did not migrate the previous day were the most relevant variables, together with the

Table 3. Partial correlation coefficients (r_c) and % explained variance (expl.%) between migration volume[a] and weather factors and non-weather variables at the study area based on stepwise multiple regression analysis.

variable	all days (n=53)		day with migration (n=30)	
	r_c	expl.[b] %	r_c	expl.[b] %
Day of year	0.391**	8.5	0.654**	37.2
Day of year ^{2}	-	-	-	-
No. of birds staging	-	-	-	-
24-h Δ in no. staging	0.527**	22.3	-	-
Retention 3	-	-	0.425*	13.8
Retention 5	-	-	-	-
Retention 6	0.282*	3.3	0.414*	5.7
Retention 7	-	-	-0.461*	0.6
Factor I	-	-	-	-
Factor II	-0.402**	13.3	-	-
Factor III	-	-	-	-
total variance explained by the equation		47.4		57.3

* $p < 0.05$, ** $p < 0.01$

[a] migration volume measured as ln(number of birds migrating/total number of birds staging + 1) (see Methods)

[b] % variance explained by each variable in the equation, estimated as $100 \cdot b \cdot r$ (Harris 1975, Alerstam 1978), where b = standardized regression coefficient of this variable, and r = simple correlation coefficient between the variable and migration volume.

relative number of birds arriving on the previous day.

As with the original weather variables, a stepwise multiple discriminant analysis was performed with the sample of all days. In this case, the weather principal component II and the 24-h increase in number of birds staging are the only significant variables discriminating between days with migration and days without migration, with an accuracy of 69.8% (Jackknife procedure).

Stepwise multiple regression and multiple discriminant analyses were also performed with the original weather plus non-weather variables. The results from these analyses were very similar to those performed with weather factors, with tailwind, low cloudiness and precipitation values, progress of season, relative number of birds arriving on the previous day, and 24-h increase in the number of birds staging, as the most important predictors or discriminant variables.

Selection of wind direction during departures

Previous bivariate and multivariate analyses indicate that wind conditions are important predictors of migration volume, but they say little about the real wind selection by departing birds, in terms of direction preferred relative to the frequencies of the various wind directions in the study area. To further investigate this aspect, we established eight wind direction classes with respect to the cranes' migration direction (21°N, with respect to true north, pers. obs.), plus one class of days with no wind during the main departure period (0700 to 1100 h GMT) (see Fig. 2). The frequency distributions of wind directions did not differ statistically between years (χ^2 = 4.58, 8 df, $p > 0.05$). The most

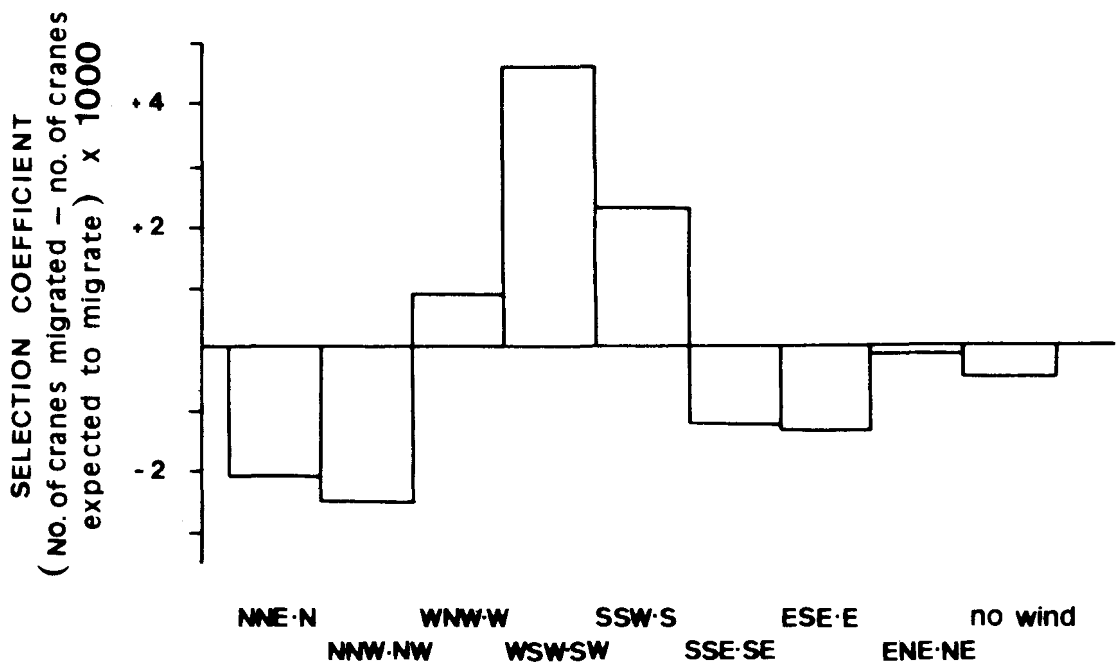

Fig. 2. Selection of wind direction during cranes' migration departures from Gallocanta, measured as the difference between the number of cranes migrated and the number of cranes expected to migrate according to the frequencies of each wind direction (average for 1984-85). All differences are statistically significant at 0.01 (*t*-test for percentages).

frequent direction was North (27.3% of all days in 1984 and 40.0% in 1985). Headwinds (NW to NE) were dominant in a 36.4% and 70.0% of all days, respectively in 1984 and 1985, while tailwinds (SW to SE) were only present in a 21.2% and 5.0% of the days, respectively in both years. According to these frequencies we calculated the expected number of cranes that should have departed with each of the nine wind classes considered and subtracted these values from the observed departure figures to estimate the wind selection indexes (Fig. 2). The distributions of total days with each wind and migration days with each wind were significantly different (χ^2 = 18.32, 8 *df*, $p < 0.025$). Cranes clearly selected SW, S and to a lesser extent also W wind directions, avoiding all other winds, specially N and NW (Fig. 2). The positive selection of westerly winds was determined by two days (3496 cranes) at the end of the 1985 migratory period, after some consecutive days of adverse wind conditions.

DISCUSSION

Previous studies have shown the importance of weather in regulating bird migration (reviews in Lack 1960, Richardson 1978). Some authors have demonstrated the influence of certain weather characteristics on the migration of some holarctic crane species (Keil 1969, 1970, Alerstam & Bauer 1973, Rinne 1974, Nesbitt 1975, Deppe 1978a, b, Melvin & Temple 1981, Swanberg 1987b, older references in Rinne *op. cit.*). Few studies, however, analysed simultaneously a large set of variables and none included non-weather characteristics. Whereas some of them did not find clear correlations between crane migration and weather at ground level (Keil 1970, Deppe 1978b), most concluded that precipitation, cloudiness, wind and temperature were relevant. Our results indicate that rain, cloudiness and strong headwinds are important factors restricting the daily volume of spring migration in the Common Crane. The agreement between the results from the different analyses used indicate that these conclusions are robust.

Cranes are probably very sensitive to these conditions, which has surely been decisive in favouring marked waves of migration in cranes and other soaring species (Richardson 1978). When migration is possible, the fraction of cranes departing one day depends mainly on date and the relative number that did not migrate the previous day. This suggests that cranes decide to migrate depending principally on their urge, i.e. the more (a) the later in the season; and (b) the lower was the number of birds departing the previous day. This supports Nisbet & Drury's (1968) hypothesis that responsiveness increases as the season progresses. Our data suggest that this effect increases exponentially through the migratory season.

The increase in responsiveness after one or more days of non-migration due to adverse weather is also consistent with another hypothesis of these authors, namely that the act of migration reduces the responsiveness on the next day. This is especially true near the end of the migratory season, when cranes departed into suboptimal conditions such as opposing or cross winds. Interestingly, the migratory impulse is not influenced by the number of birds staging, and only slightly by the number of birds that arrived in the study area the previous day. If one considers only the sample of days with migration the highest variance is accounted for by the fraction of birds that did not migrate the previous day in which migration was possible.

The high correlation with date agrees with the fact that spring migrations are faster and less variable in date that autumn migrations, reflecting the adaptive value of early arrival at the breeding areas. The urge is different for the various age-classes, breeding adults arriving much earlier than immatures (Prange 1974, 1984, 1987, Mewes 1976, Jähme 1983, Karlsson & Swanberg 1984, Swanberg 1987b, Neumann pers. comm.). Most first-year birds, which arrive in Gallocanta with their parents along the whole staging period, become independent before the latter leave the area and remain there until the end of the season (Alonso *et al.* 1984b).

The average staging period estimated for an individual crane – 8 and 5 days respectively for 1984 and 1985 – is somewhat shorter than staging periods measured in radiotracked Sandhill Cranes (Drewien & Bizeau 1974, Crete & Toepfer 1978, Melvin & Temple 1981, Krapu *et al.* 1985), and similar to that recorded for a colour banded Common Crane at Hornborga, Sweden (13 days in 1987, 8 in 1988, Swanberg, pers. comm.). Nevertheless, it is still much longer than the mean duration of adverse weather periods without migration – 0.8 days (range 0-3) in 1984 and 0.6 days (range 0-2) in 1985 –. On the other hand, the daily departure volume never reaches 100% of the staging birds. These two factors clearly reflect the staging condition of our study area. The importance of cereal farmlands as staging areas during spring migration for replenishing fat reserves has been demonstrated in the Sandhill Crane (Krapu *et al.* 1985, Reinecke & Krapu 1979, Krapu 1987). These reserves are frequently vital for arctic breeding species between arrival at breeding areas and nest initiation (Ankney & MacInnes 1978, Davies & Cook 1983). As in these and other bird species (King & Farner 1963) we also observed an increased food intake rate during spring staging at Gallocanta in relation to the average for the whole winter (Alonso *et al.* 1987). The staging condition of our study area is also illustrated by the higher-than-expected number of departing birds as a consequence of a sudden reduction in the food availability, due to a snowfall before the peak departing period. Summarizing, the short staging period in Gallocanta results from a compromise between the urge to arrive in time at the breeding areas, and both the inhibiting effect of bad weather and the tendency to stay and benefit from favourable feeding conditions.

The weather characteristics inhibiting crane departures – precipitation, cloudiness and strong headwinds – are those that affect survival, energy requirements and orientation en route (Richardson 1978). Radiotagged Sandhill Cranes interrupt migration with these conditions, resuming it when weather allows (Melvin & Temple 1981). Absence of rain, clouds and headwinds at departure also enhance the probability of encountering favourable weather during the flight and at destination (Nisbet

& Drury 1968, Blokpoel & Richardson 1978, present study). Clearly energy saved by flying with favourable conditions is of survival value, as birds may be subjected to conditions which prevent feeding, during stopovers and upon arrival in breeding areas. Although the correlation found in the present study between the volume of migration and fair weather at destination of course does not demonstrate a bird's predictive ability, it does show that the association, whether causal or not, does exist. This correlation is probably of adaptive value as weather is likely to be more severe further north. The initiation of migration into the southwest of a high pressures area could be an adaptation facilitating fair weather en route for birds migrating northwards in the Northern hemisphere. The facts that (a) migration departures are concentrated into this particular sector od the synoptic pattern, (b) crane migration correlates with fair weather at destination, and (c) cranes select WSW-SW winds, which are suboptimal with respect to strictly tailwinds (SSW-S) in terms of energy expenditure minimization, suggest that birds depart with some anticipation to benefit from the maximum northward flow of warm air between high and low pressure centers. Moreover, this situation is less likely to develop into cyclonic disturbances. The continuous eastward passage of highs and lows thus provides with successive optimal situations for migration on the west part of highs or anticyclonic ridges, which cause wavelike migrations.

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SAMENVATTING

De voorjaarstrek van kraanvogels werd onderzocht in Gallocanta, in noord-oost Spanje, februari-maart 1984 en 1985. De wegtrek uit de pleisterplaats was duidelijk minder bij regen, bewolking en tegenwind. De meeste wegtrek trad op als het gebied in de zuid-west sector van een hogedrukgebied lag of in het warme deel van een lagedrukgebied. Binnen deze gunstige omstandigheden was het aantal wegtrekkende vogels vooral gecorreleerd met de datum en met het aandeel niet trekkende kraanvogels van de vorige dag, maar niet met aantal aanwezige dieren, en slechts zwak met het aantal dat de vorige dag was gearriveerd.

De gemiddelde verblijfsperiode van een individu was 5 tot 8 dagen, langer dan de gemiddelde duur van een slecht weer periode (0 tot 3 dagen). Dagelijks vertrok gemiddeld 14.3 % van de verblijvende vogels, nooit vertrokken ze allemaal.

Deze feiten wijzen er op dat de duur van het verblijf een compromis is tussen de diverse soorten van drang: (1) op tijd in het broedgebied te arriveren, (2) vliegen bij slecht weer te vermijden en (3) langer te blijven en zodoende meer te profiteren van gunstige voedselsituaties.