

# SPRING CRANE *Grus grus* MIGRATION THROUGH GALLOCANTA, SPAIN

## II. TIMING AND PATTERN OF DAILY DEPARTURES

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**ABSTRACT** The relationships between the daily pattern of Common Crane *Grus grus* migration departures from a staging area and variables related to weather and number of birds were studied during 1984 and 1985 (totalizing 30 days with migration) using multivariate statistical analysis. Cranes left the roost to the foraging areas between 0628 and 0715 hours. On 95% of the days with migration, the departure lasted only 71-111 minutes, generally between 0900 and 1200 hours. The timing of departure was highly correlated with air temperature at departure initiation: cranes departed earlier with higher temperatures, probably as soon as thermal updrafts had developed and facilitated soaring flight. When the number of birds departing was higher due to favourable weather conditions, the departure evenness, flock size and number of flyways used increased, and the departure interval was slightly extended through an advancement of the initial time of departure.

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### INTRODUCTION

Severe weather during migration has probably been an important selection pressure favouring adaptive physiological and behavioural strategies in birds (see Alerstam 1978). Relationships between various weather variables and the day to day variations in migration volume have been demonstrated often (Richardson 1978 and references in Alonso *et al.* 1990). However, few papers have dealt with the diurnal pattern of migration, especially in relation to proximate factors such as weather (see Alerstam & Bauer 1973, Alerstam 1975, Pennycuick 1975, Pennycuick *et al.* 1979, Karlsson & Swanberg 1984, Swanberg 1987). Assuming the success of a migratory flight depends at least in part on the timing and pattern of migration initiation from a stopover locality, the study of relationships between these variables may be relevant to understanding the selective forces acting on migration.

In this paper the relationships between weather

and non-weather variables on the timing and pattern of migration departure are explored using multivariate statistical analysis, and the latter's possible effects on the success of a migratory flight are discussed.

### METHODS

We observed visible spring migration of Cranes at Gallocanta lake, Spain (40°58'N, 1°30'W). In this paper we consider the sample of 30 days in which migration occurred during the migratory periods February-March 1984 and 1985 (total 66 days). Details of the study area and general observation methodology are given in Alonso *et al.* 1990. The timing of migration departure was defined by four variables: (a) the initial departure time, (b) the mean departure time, (c) the final departure time, and (d) the departure interval, defined as (c) - (a). Variables (a), (b) and (c) were measured as the times in minutes after sunrise at which respectively

the first flock, the weighted average and the last flock passed over any of the observation points. Times were measured relative to sunrise to allow for possible variations due to the earlier sunrise later in the migration period.

The daily pattern of departure was analysed using the following variables, all of them measured at the moment when cranes passed over the observation points: (a) mean flock size; (b) departure evenness, defined as Shannon's  $H'$  ( $= -\sum p_i \ln p_i$ ), where  $p_i$  is the fraction of birds which have departed during each 5-minutes period, from the total number of birds leaving on each day); (c) width of the migratory front, measured in km between the extreme northwesterly and southeasterly flyways used when birds cross the mountains to leave the area, and (e) mean height of departing flocks, in m above ground level, estimated ca. 10 km after take-off with respect to the nearest mountain of known height.

As predictors we used the following variables related to number of birds:

- (1) number of birds staging, defined as the highest figure from two consecutive roost counts; one on the evening, the second on the morning of departure;
- (2) 24-h relative increase in the number of birds staging, defined as the difference in (1) between the day of departure and the previous day divided by (1) on the day of departure;
- (3) migration volume, defined as the number of birds leaving the study area each day.

The following weather variables, all of them except (10) averaged for the main departure period (0900-1300 hours GMT, see results) were also used as independent variables:

- (1) surface wind speed in  $\text{m s}^{-1}$ ;
- (2) crosswind vector component of (1), in  $\text{m s}^{-1}$  (absolute value), either from left or right in relation to the migration direction ( $21^\circ\text{N}$ );
- (3) tailwind vector component of (1) in  $\text{m s}^{-1}$ , including headwinds as negative values;
- (4) cloudiness, estimated in eighths of the visible skies;
- (5) relative humidity, in %;
- (6) temperature, in  $^\circ\text{C}$ ;

(7) temperature, in  $^\circ\text{C}$  at the time of usual departure initiation (0900 hours GMT);

(8) early morning temperature increase, defined as the difference in  $^\circ\text{C}$ , with its sign, between the time of roost departure and 0900 hours;

(9) barometric pressure, in mb;

(10) atmospheric instability, defined as the difference in temperature between surface and the 800 mb level, with its sign, measured at 1200 hours GMT;

Precipitation was not included since there was no precipitation on days with migration.

The assumption of normality was checked for each variable and appropriate transformations (ln, square-root or inverse) were applied. Relationships between variables were first explored through linear regression analysis. Later, a stepwise multiple regression analysis (BMDP2R, Dixon 1983) was performed for each dependent variable studied. In each of these analyses we included as predictors all variables related to weather and number of birds plus certain variables related to timing or pattern of departure suspected to have a possible causal relationship with each dependent variable analysed. So, departure interval was included as a predictor in analyses of departure mean time, evenness, mean flock size, width of the migratory front and number of flyways used; the number of flyways was used as a predictor in the equations for interval and mean flock size; mean flock size in those for evenness, width of front and number of flyways, and departure mean time in that for mean flock size.

## RESULTS

### Daily routine during migration

A typical migration day began with cranes departing from the roost to foraging areas, as on days without migration during winter (see Alonso *et al.* 1984). Cranes flew from the roost between 0628 and 0715 hours GMT, although a few birds remained at or near the roost after that time, especially late in the season. Birds foraged as usual until around 0900 hours. At this time some flocks started to show premigratory behaviour consisting of sus-

tained circling flight with calling and little wing flapping. As these soaring birds approached the mountain chain NE of the feeding areas small flocks frequently combined into a larger group in a thermal. The crossing of these mountains was by way of three or four passes. Occasionally, a flock flew back to the feeding grounds after having tried to cross the mountains and leave the area. Other birds continued foraging after leaving the roost and showed no premigratory behaviour, or only some soaring during early afternoon. When migration occurred, the percentage of birds departing varied between 0.4 % and 72.8 % per day, with a mean of 14.3 % (*SE* 3.3, *n* = 30 days of migration).

The time of departure of individual flocks varied between 0824 and 1455 hours GMT, respectively 1 h 54 min and 8 h 15 min after sunrise, for the entire premigratory period, although most (95.3 %) departed between 0900 and 1200 hours. The mean departure time was 1055 (*SE* 11 min, *n* = 30 days), the mean initial time 1019 and the mean final time 1150. The mean departure interval was 91.2

minutes (*SE* 9.9, 30 days), with a maximum of 222 minutes. The flock size varied between 1 and 550 birds, with a mean of 46.2 (*SE* 1.8, 908 flocks). The departure front varied between 1 and 18 different flyways and was up to 21.7 km in width, with a mean of 5.3 flyways (*SE* 0.7) spanning 8.3 km (*SE* 1.0). The average height of the birds as they passed by observation points was 371 m (range 200-700) above lake level.

### Bivariate relations between weather variables and timing and pattern of migration

The timing of departure is significantly related to absolute and crosswind speeds, early morning temperatures, relative increase in the number of birds staging and migration volume (Table 1). All these variables tend to advance departures. Departure intervals increase with high temperature and migration volume and decrease with high cloud cover.

Mean flock size, and departure evenness tend to increase with increasing migration volume. This

**Table 1.** Product-moment correlation values between weather variables<sup>a</sup> and variables defining the timing and pattern of migration departure<sup>b</sup> (*n* = 30 days, bold means significant, *p* < 0.05).

migration variables	weather variables												
	WS	CWC	TWC	C	RH	T	TDI	TIEM	BP	I	NB	INB	MV
IDT	<b>-0.50</b>	<b>-0.39</b>	0.13	0.16	0.07	-0.02	<b>-0.76</b>	<b>-0.41</b>	-0.20	0.26	-0.21	<b>-0.45</b>	<b>-0.52</b>
MDT	<b>-0.54</b>	<b>-0.42</b>	0.03	0.05	0.04	-0.01	<b>-0.75</b>	<b>-0.36</b>	-0.18	0.27	-0.14	<b>-0.43</b>	<b>-0.41</b>
FDT	<b>-0.48</b>	<b>-0.41</b>	0.09	-0.19	0.05	0.10	<b>-0.53</b>	-0.09	-0.08	0.27	0.05	<b>-0.43</b>	0.05
DI	0.13	0.06	-0.15	<b>-0.44</b>	-0.02	0.14	<b>0.44</b>	<b>0.45</b>	0.19	-0.03	0.34	0.12	<b>0.75</b>
MFS	0.05	-0.02	0.09	-0.07	<b>0.44</b>	0.06	0.23	0.01	-0.09	0.04	0.30	0.16	<b>0.55</b>
DE	0.31	0.27	-0.01	-0.23	0.05	0.05	0.35	0.26	0.14	-0.08	0.27	0.29	<b>0.65</b>
WoF	0.11	0.06	-0.18	<b>-0.45</b>	-0.13	0.24	<b>0.56</b>	<b>0.40</b>	<b>0.37</b>	-0.04	<b>0.37</b>	0.16	<b>0.65</b>
NoF	0.28	0.23	0.18	-0.18	-0.01	0.26	<b>0.41</b>	0.20	0.25	-0.01	<b>0.43</b>	0.34	<b>0.70</b>
MFH	-0.05	-0.06	0.06	0.06	-0.10	0.14	0.07	-0.07	0.06	<b>0.39</b>	0.01	-0.17	-0.21

<sup>a</sup>(weather variables) WS= wind speed, CWC= crosswind component, TWC= tailwind component, C= cloudiness, RH= relative humidity, T= mean temperature, TDI= temperature at departure initiation, TIEM= temperature increase in early morning, BP= barometric pressure, I= instability, NB= number of birds staging, INB= 24-h relative increase in number of birds, MV= migration volume

<sup>b</sup>(migration variables) IDT= initial departure time, MDT= mean departure time, FDT= final departure time, DI= departure interval, MFS= mean flock size, DE= departure evenness (measured as  $H' = -\sum p_i \ln p_i$ , see Methods), WoF= width of migratory front, NoF=number of flyways, MFH= mean flying height.

variable and the number of birds staging in the study area are also positively related to the width of the departing front and the number of flyways used to leave the area. Increasing temperatures and barometric pressures and decreasing cloudiness also were associated with a wider departure front.

### Multivariate relationships

**Timing of departure** The timing of migration departure is determined mainly by the temperature at departure initiation. Departure begins earlier with high temperatures at that time. This variable accounts for a 80.5 %, 91.0 % and 82.0 % of the variance explained respectively in the initial, mean and final time equations (Table 2). A separate partial correlation between all three times showed higher association between initial and mean times ( $r = 0.93$ ) than between final and mean times ( $r = 0.56$ ),

the difference between both correlation values being significant at  $p < 0.05$ . The apparent opposite effect of the mean temperature during the departing period and temperature at departure initiation (see Table 2) on the departure time reflects the non-linear relationship between both independent variables and the departure time. An increase in the number of birds departing determines an advance in both initial time and mean time and a delay in final time. Final time is advanced with increasing cloudiness.

The departure interval depends mainly on the number of birds departing. Increasing numbers prolong the interval, while both delayed time of departure initiation and cloudiness tend to make it shorter. Partial correlation between duration of departure interval and initial and final times of departure showed significant partial correlations be-

**Table 2.** Results of the stepwise multiple regression analyses for the variables defining the timing of migration departure. Dependent and significant independent variables and partial correlation ( $r_c$ ) are given;  $n = 30$  days (see Methods for complete list of independent variables used in each case).

Dependent variable	independent variable <sup>a</sup>	$r_c$	expl.% <sup>b</sup>	total expl.%
Initial departure time	TDI	-0.843**	63.7	79.1
	T	0.630**	0.9	
	MV	-0.506**	14.5	
Mean departure time	TDI	-0.836**	68.3	75.1
	T	0.618**	0.2	
	MV	-0.292	6.6	
Final departure time	TDI	-0.728**	45.0	54.9
	T	0.489**	4.4	
	C	-0.301	4.3	
	MV	0.295	1.2	
Departure interval	MV	0.607**	37.9	69.4
	ITD	-0.449*	20.5	
	C	-0.399*	11.0	

\*  $p < 0.05$ , \*\*  $p < 0.01$ .

<sup>a</sup> TDI= temperature at departure initiation, T= mean temperature during the departing period, MV= migration volume, C= cloudiness, ITD= initial time of departure.

<sup>b</sup> measured as  $100 \cdot b \cdot r$ , where  $b$  = standardized multiple regression coefficient, and  $r$  = simple correlation coefficient (see Harris 1975, Alerstam 1978).

**Table 3.** Results of the stepwise multiple regression analyses for the variables defining the timing of migration departure. Dependent and significant independent variables and partial correlation ( $r_c$ ) are given;  $n=30$  days (see Methods for complete list of independent variables used in each case).

Dependent variable	independent variable <sup>a</sup>	$r_c$	expl.% <sup>b</sup>	total expl.%
Mean flock size	MV	0.556**	30.7	48.9
	RH	0.446*	18.2	
Departure evenness <sup>c</sup>	MV	0.713**	44.6	56.5
	CWC	0.459*	7.8	
	MFS	-0.282	4.1	
Width of migratory front	DI	0.789**	58.3	76.0
	BP	0.346	6.8	
	TDI	0.330	10.9	
Number of flyways	MV	0.782**	49.6	68.9
	CWC	0.476**	7.2	
	BP	0.450*	7.5	
	TWC	0.392*	4.6	
Mean flying height	AI	0.407*	15.2	21.7
	MFS	-0.284	6.5	

\*  $p < 0.05$ , \*\*  $p < 0.01$ .

<sup>a</sup> MV= migration volume, RH= relative humidity, CWC= crosswind component, MFS= mean flock size, DI= departure interval, BP= barometric pressure, TDI= temperature at departure initiation, TWC= tailwind component, AI= atmospheric instability.

<sup>b</sup> measured as in Table 2.

<sup>c</sup> see Table 1 and Methods.

tween interval and both times ( $r = -0.97$  and  $r = 0.95$  respectively, both  $p < 0.001$ , difference between them not significant). However, the coefficient of variation of the initial time (31 %) is higher than that of the final time (19 %), this indicating that the absolute duration of the migration departure is probably more dependent on the variations in the time of departure initiation.

**Pattern of departure** The results of multiple regression analyses for the variables defining the pattern of migration differ from those suggested by simple correlations. The number of birds departing remains the most important variable in the equations for mean flock size, departure evenness and number of flyways, while the duration of the depart-

ure interval is the relevant variable in the definition of the width of the departing front (Table 3). Departure evenness and the number of flyways used by the birds increase with increasing crosswinds. Finally, high barometric pressures, temperatures at departure initiation and tailwind components also enlarge either the migration front or the number of flyways.

## DISCUSSION

Our results suggest that the diurnal timing and pattern of crane migration departures from a staging area is determined by the proximate influence of a few weather variables together with the volume of

migration. The duration of departure is restricted to an average of 91 minutes (95 % of the cases between 71 and 111 minutes) during the morning, a short interval compared to a whole day. In particular, the initial and mean departure times were highly determined by the air temperature, although this variable has little influence on the number of birds departing (see Alonso *et al.* 1990). The earlier departure with higher early morning temperatures suggests that a threshold temperature value exists below which migration departure could be uneconomical, surely due to the absence or poor development of thermal upcurrents at this time of the day. The importance of thermals as a source of energy has been demonstrated for several soaring bird species (Pennycuick 1972, Alerstam 1975, Pennycuick *et al.* 1979, Kerlinger & Gauthreaux 1984, 1985). Although cranes are not considered as primarily soaring migrants (see e.g. Beason 1978, Pennycuick *et al.* 1979), the fact that birds wait for some hours before departing on migration strongly suggests that there must be a high energy saving through soaring. Cranes leaving Gallocanta thus behave as "energy expense minimizers" rather than "migration speed maximizers". This is in accordance with the imperative for migratory bird species breeding at high latitudes to maintain the highest possible energy reserves until the beginning of the reproductive season (see e.g. Ankney & MacInnes 1978, Mikkonen 1981, Ebbinge *et al.* 1982, Davies & Cook 1983, Krapu *et al.* 1985). Departure timings similar to those at Gallocanta have been described for crane species in various areas (Williams 1970, Nesbitt 1975, Pennycuick *et al.* 1979, Melvin & Temple 1981, Petit 1986) as well as for other soaring species (e.g. Kerlinger & Gauthreaux 1985), although it seems that closer to breeding areas cranes sometimes start their daily migratory journey earlier (Alerstam & Bauer 1973, Rinne 1974, Karlsson & Swanberg 1984, Prange 1987, Swanberg 1987, Wessels 1987). The tendency to wait for thermals decreases as cranes approach breeding areas (see also below, night migration). In the case of cranes migrating northwards from staging areas around the Baltic sea, the reason for bimodal departure patterns including departures

between 0500 and 0900 hours (Alerstam & Bauer 1973, Rinne 1974), is probably a lack of thermal activity over the sea. This encourages some cranes to use flapping flight and not to wait until mid morning.

With respect to the time at which departures cease, a high percentage of the total variance remains unexplained. We suggest that the relevant variable is the distance to the next stopover. Sotonera, South of the Pyrenees, and Camp de Captieux in France, are the next traditional stopovers Northeast from Gallocanta, respectively at 160 and 380 km. At 30 km h<sup>-1</sup>, given average migration speed measured in Southern Europe during spring (Fernández 1981, Petit 1986), cranes would need slightly more than 5 hours and almost 13 hours to reach Sotonera and Camp de Captieux, respectively. Thus, 95.3 % of the flocks, leaving Gallocanta between 0900 and 1200 hours would arrive at Sotonera at 1420-1720 hours, and Camp de Captieux at 2140-0040. Assuming a migration speed of 45 km h<sup>-1</sup> (average for several references at higher latitudes, e.g. Keil 1969, Alerstam 1975, Melvin & Temple 1981, Knoblauch 1984, Swanberg 1987, Wessels 1987), arrival at Sotonera would occur at 1230-1530 hours, and at Camp de Captieux at 1730-2030. Mean recorded arrival time at Sotonera is indeed 1545 hours (sample of 19035 birds, see Acín & Acín 1985), close to our predicted interval. Only 6.2 % of flocks arrived after dark, the last recorded at 2030 hours. This coincides with predictions for the latest flocks leaving Gallocanta. In Camp de Captieux the mean arrival time during 1985 was 1630 hours (sample of 17501 birds, Dupuy pers. comm.), earlier than our prediction. Only 14.4 % of the cranes arrived after 1900 hours, with latest records between 2030 and 2100. Moreover, on three days in which departures from Gallocanta and arrivals at Sotonera could be recorded simultaneously, more than 50 % of the cranes arrived at this last stopover, while mass departures from Gallocanta were followed by mass arrivals at Camp de Captieux one or two days later. This suggests that after leaving Gallocanta, most cranes stopover one night at Sotonera before crossing the Pyrenees.

Migration departures have never been recorded

during late afternoon or night (Alerstam & Bauer 1973, Rinne 1974, Heidt 1986, Swanberg 1987, pers. obs.). If thermal currents are important in defining the timing of departure, observations of cranes flying by night might be due to (a) proximity to a predetermined destination area (Rinne 1974, Nesbitt & Hintermeister 1984, Swanberg 1987, pers. obs.), or (b) scarcity or lack of suitable stopovers over long distances, or (c) birds frightened from roosts or accidentally lost (pers. obs.).

When the number of birds departing one day is large, due to favourable weather conditions (Alonso *et al.* 1990), the departure interval is extended by advancement of the initial rather than a delay of the final time. The higher coefficient of variation of the initial time, its closer association with mean time and the higher partial correlation of migration volume with initial time than mean and final times support this conclusion. This suggests that when it is possible to migrate, cranes depart earlier so as to optimize the energy from thermal activity that peaks at midday and decreases in the afternoon (see also Pennycuick *et al.* 1979, Kerlinger & Gauthreaux 1984, 1985). Such behaviour enables the cranes to travel longer distances, as suggested by the significantly earlier mean departure time on days in which mass departures from Gallocanta and mass arrivals at Camp de Captieux coincided ( $t = 2.3$ ,  $p < 0.05$ ,  $n = 28$  days) and/or minimize the risks derived from having to continue migrating by night or being forced to roost en route. The only other weather condition that has an influence on the timing of departure is cloudiness. Cloud cover decreases the departure interval as a consequence of the advancement of final departure time (see also Kerlinger & Gauthreaux 1985). The extreme of this is the absolute suppression of migration on very cloudy days (see Alonso *et al.* 1990).

Although the number of birds departing only slightly affects timing, it is the variable most closely related to the pattern of departures. The increase in flock size as migration volume increases agrees with the positive correlation between the daily number of birds seen aloft and mean flock size en route in cranes and other species (Rinne 1974,

Richardson 1978, Blanchon 1983, Wessels 1987). However, this correlation does not exist or is even inverse in the case of flocks at foraging areas or entering the roost during winter (Alonso *et al.* 1987, Veiga *et al.* in press). Thus, specific advantages may exist favouring flock size increase during migration. The flock size also increases between departure (46.2 birds) and en route (106.8 birds,  $p < 0.01$ ), remaining stable to the destination (108.2 birds,  $p > 0.05$ ). The coalescence of small flocks into larger ones in thermals by local enhancement observed at the departure area continues en route and probably ceases when thermal activity decreases, as described for pelicans by O'Malley & Evans (1982) and for hawks by Kerlinger & Gauthreaux (1985) for similar reasons to those discussed by these authors.

Finally, the pattern of migration is also influenced by the wind. Strong and persistent crosswinds drift migrating flocks during the departure period, with a consequent increase in the spatial and temporal dispersion of the migration inception (i.e. number of different flyways used that day and evenness of departure). Increasing barometric pressure and tailwinds, which facilitate the crossing of the mountains by the birds leaving Gallocanta have a similar effect. The significant partial correlation between atmospheric instability and the height reached by flocks while leaving the area agrees with the suggestion that when thermal activity is strong crossing the mountains is easier. Probably the crosswinds also facilitate mountain crossing, as they produce updrafts along the NNW-SSE oriented mountain chain.

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## SAMENVATTING

Onderzocht werden de verbanden tussen (1) het dagelijkse patroon van wegtrekken van Kraanvogels uit een pleisterplaats tijdens de voorjaarstrek (30 dagen met trek in 1984 en 1985) en (2) het weer en het aantal vogels. Hierbij werd gebruik gemaakt van multivariate statistische methoden.

Kraanvogels verplaatsten zich van de roest naar het fourageergebied tussen 0628 en 0715 uur. De wegtrek uit het gebied duurde slechts 71 tot 111 minuten in 95% van de dagen met trek en vond meestal plaats van 9 tot 12 uur. De vogels vertrokken vroeger bij hoge temperaturen, waarschijnlijk zodra zich opstijgende warme lucht ontwikkelde (gunstig voor zweefvlucht). Als door gunstige omstandigheden het aantal wegtrekkende vogels toenam, dan nam ook de gelijkmatigheid van het vertrekpatroon, de troepgrootte en het aantal trekwegen toe. Bovendien was dan de tijdsduur tussen de vertrekkende troepen verlengd in samenhang met een vroeger begin van de trek.