DAILY ACTIVITY AND INTAKE RATE PATTERNS
OF WINTERING COMMON CRANES Grus grus

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ABSTRACT Daily activity patterns of wintering Common Cranes Grus grus were studied at Gallocanta, NE Spain, and related with changes in foraging site, distance to roost and flocking behaviour. Per cent time spent feeding, feeding bout length, and food intake rate showed two peaks, in early morning and late afternoon. Vigilance, preening and other activities followed an inverse pattern, peaking at midday, when birds usually gathered at drinking sites. The feeding habitat and location, and the flock size changed between the morning and the evening foraging peaks. During the morning cranes showed a higher locomotor activity, foraging in smaller flocks, at higher distances from the roost, and on grounds with higher food availability. On the contrary, during the afternoon birds showed lower locomotor activity, aggregated in larger flocks, and foraged closer to the roost, on grounds with lower food availability. We explain these daily changes as a consequence of the risk-sensitive foraging behaviour of the cranes. Birds shifted from a risk-prone foraging with higher intake rate in the morning to a risk-averse one with lower intake rate in the evening.

INTRODUCTION

During the non-breeding season, birds must perform few activities in order to survive, the most important being feeding, drinking, avoiding predators and preening. However, since these activities are usually incompatible, each individual has to make several decisions about timing, duration and sequence of these activities, to maximize fitness (Sibly & McFarland 1976, McCleery 1978, Caraco 1980, McNamara et al. 1987). Time allocation decisions are related with the hunger state of the individual through a feedback process, and therefore change throughout the day constituting the animal's daily routine.

Individuals must also make decisions about the foraging patch, and in the case of gregarious species, about the flock size and distance to the roost. These decisions are probably not independent from time allocation decisions and may also change throughout the day. According to the models of risk-sensitive foraging (Caraco et al. 1980, Stephens 1981, Stephens & Krebs 1986), birds should shift throughout the day from a risk-prone behaviour during the morning, when they have negative energy budgets, to a risk-averse behaviour during the evening, when they have positive energy budgets. In this paper we study the daily changes in time budget, feeding patch selection, flock size and food intake rate of wintering Common Cranes Grus grus dispersing daily from a central roost to feed. We test if daily changes observed in this behaviour follow the predictions of the risk-sensitive foraging theory. If the hypothesis of a progressive shift to a less risky foraging situation is correct, we should expect a decrease in the distance to the roost, an increase in flock size, and a decrease in mean food availability of the sample of foraging patches used, throughout the day.

METHODS

The study was carried out at Laguna de Gallocanta, NE Spain (40° 58' N, 1° 30' W), during the winter seasons 1980-81 to 1985-86, with the exception of...
1983-84. Most cranes arriving from their breeding areas in Northern Europe stage at Gallocanta some days or weeks in November-December on their way to SW Spain and a variable number remain there throughout the whole winter. During our study, yearly peak numbers of cranes staging during migration varied between 5900 (February 1983) and 21 000 (February 1985), and average wintering numbers varied between 3000 (January 1983) and 10 000 (December 1985-February 1986).

We spent 1-2 days per week in the field and gathered data continuously between cranes’ roost departure and roost entrance. Thus, our samples were evenly distributed throughout day and season. Flocks were located opportunely during regular circuits of the study area by vehicle. We did not repeat the same circuit to avoid possible relationships between a particular site, habitat or daytime, and activity of the birds. All flocks were located on maps scale 1:50 000, to calculate the distance to the roost afterwards. We recorded date, time, flock size, foraging effort (measured as the percentage of birds head-down), percentage of juveniles, and type of ground (cereal sown field, cereal stubble field, sunflower stubble field, ploughed field, pasture, drinking place, others). We estimated the density of each flock by means of the interindividual distance, measured in bird-lengths, along a transect line through the flock. Food availability was also measured in 1984-86 in stubble fields used by focal birds after finishing behavioural observations, as the mean and variance of twenty 25x25 cm random samples of the number of cereal seeds found on the ground.

From each flock we recorded the behaviour of 1-10 adults and 1-5 juveniles, in a number approximately proportional to the relative flock size. Individuals were selected randomly, but at more or less regular distance intervals along the flock’s longest diameter to avoid biases due to individual’s position in the flock (Inglis & Lazarus 1981). Birds were aged as adults or juveniles (first winter birds) on the basis of their head and neck colour (Cramp & Simmons 1980). We observed adults and juveniles in succession, in order to control for possible age differences in our sample due to flock size, food availability, ground type, or any other physical or social factor (see Alonso et al. 1987).

From 1980 to 1983 focal individuals were observed for three minutes through 60-90x Questar telescopes. Time spent in the following activities was measured to the nearest second: feeding (head down), vigilance (head up), and preening. All other activities, including flying and resting (which included all head up postures lasting more than one minute), were also measured in the field but included as ‘others’ for analysis. During 1984-86 we reduced observation time of focal birds to one minute, and recorded the rate of food intake, easily identified by the characteristic swallowing movement, and the number of paces. The mean dry weights of seeds were significantly different between cereal stubble fields (0.027 g, n = 935 seeds from 50 different fields), cereal sown fields (0.033 g, n = 3000 seeds from 10 different fields), and sunflower stubble fields (0.064 g, n = 836 seeds from 10 different fields). Therefore, we estimated food intake rate as the product of the number of seeds ingested per minute by the mean dry weight of the corresponding seed sample. We defined net intake rate as the dry weight ingested per minute spent actually feeding, i.e. head down, and absolute intake rate as the dry weight ingested per minute of observation. We analysed the daily variation and age differences in per cent time devoted to each activity, mean duration of activity bouts in seconds, number of paces per minute, and net and absolute intake rates in grams ingested per minute, taking each one- or three-minute observation period as a data point. Later, we grouped data into hourly periods. Because foraging bouts frequently lasted more than one minute, we only used the sample of three-minute observation periods to calculate the mean foraging bout. We also calculated the accumulated daily food consumption multiplying each hourly value of absolute intake rate per minute by 60. Since onset and termination of cranes’ daily activity did not coincide with entire clock hours, in the first and last hourly periods the per minute rate values were multiplied by a mean fraction of those hourly periods, calculated for each month independently as follows. We recorded the difference
between the mean roost departure and arrival times on 112 days evenly distributed throughout the six winter seasons, and subtracted 15 minutes to account for the flying time from the roost to the first morning feeding sites, where we began observations, plus 5 minutes for the flying time between the last evening feeding sites and the roost, estimated from data on individual radiotracking (own obs.). For a detailed description of roosting flight counts see Alonso et al. (1985).

Sample sizes were, respectively for 1980-81 through 1985-86, 427, 407, 48, 1659 and 1297 focal birds. There were no interannual differences in daily or seasonal patterns of behaviour or intake rate. Thus, we combined the data from all six winter seasons to simplify the presentation of the results, a total of 3837 minutes for adults (2639 birds), and 1765 minutes for juveniles (1199 birds).

Since all activities defined were not always performed by focal birds within the observation period, many distributions were skewed or had a relatively large number of zero scores. No suitable transformation was available for distributions like these (see also Goss-Custard & Durell 1987). Therefore we analysed data by non-parametric methods (Mann-Whitney U-test or Kruskal-Wallis test). To further assess reliability of these results, subsets of these variables excluding zero scores (which were analysed separately) were also subjected to equivalent parametric tests (t-test and ANOVA) after logarithmic (bouts and intake rates) or arcsin transformation (per cent times). Two-tailed probability values are given for all analyses.

RESULTS

Time budget

The daily pattern of feeding activity showed two peaks both in adults and juveniles (Fig. 1; Kruskall-Wallis test, *H* = 250 in adults, *H* = 71.6, in juveniles, both *df* = 10, *P* < 0.001). The pattern was similar in all months considered independently (November-March), but more pronounced later in the season due to a more marked and prolonged through between both peaks. In adults, the two-peak pattern was still highly significant when each month was considered separately. In juveniles, the decrease in per cent time feeding at midday was not significant in November (*H* = 11.4, *df* = 9, 189 observed birds, *P* = 0.252), almost significant in December and January (*H* = 16.3, *df* = 9, 269 birds, *P* = 0.060, and *H* = 16.7, *df* = 9, 216 birds, *P* = 0.054 respectively), and highly significant in February and March (*P* < 0.001). In adult birds, the evening peak was higher than the morning peak in the whole winter sample and in the monthly samples of February and March.

Per cent time devoted to vigilance, preening and other activities increased throughout the morn-
feeding bout

vigilance bout

Fig. 2. Daily variation in mean duration of feeding bout (top, \( n = 468 \)) and vigilance bout (bottom, \( n = 1386 \)) in adults. Vertical lines indicate 95\% confidence intervals.

Intake rate and pacing rate

The net food intake rate, i.e. intake rate while feeding, was relatively high and constant during the morning, decreased between midday and early afternoon, and later increased again to a second peak in late evening, the pattern being very similar in both age groups (Fig. 3; \( F_{9,1450} = 3.18, P < 0.001 \) in adults, and \( F_{9,726} = 2.29, P = 0.015 \) in juveniles).

The daily pattern of absolute food intake rate was very similar to that of per cent time feeding in both adults and juveniles (Fig. 3; Kruskall-Wallis test, \( H = 170, 1996 \) adult birds and \( H = 49.6, 898 \) juveniles, both \( df = 10, P < 0.001 \)).

The pattern of accumulated food ingested throughout the day increased almost linearly in November, reaching 350 g cereal in adults and 299 g in juveniles at the end of the day. The slope of the curve decreased progressively until March, when total food ingested was only 96 g in adults and 104 g in juveniles (Fig. 4).

The pacing rate was studied excluding samples with feeding rate equal to zero, since it was intended to represent an estimate of the feeding costs. In both age groups it was intermediate in early morning, increasing until mid-morning and decreasing...
later to minimum values in late evening (Fig. 5; Kruskall-Wallis $H = 38.4$, in adults and 39.6 in juveniles, both $df = 10$, $P < 0.001$).

**Distance to roost, foraging ground and intake rate**

The mean distance between foraging flocks and the roost decreased regularly throughout the day (Fig. 6; $F_{10,825} = 20.33$, $P < 0.001$). Cranes used cereal stubble and sown fields as their main feeding grounds. Use of sunflower stubbles was only residual (2.1% of 513 foraging flocks, and restricted to November and December) (see also Alonso et al. 1984). The type of foraging ground changed significantly throughout the day: cranes preferred grounds with food on surface during the morning and sown grounds, in spite of having to dig up the seeds, in the evening (Fig. 7; $\chi^2 = 324.6$, $df = 9$, $P < 0.001$).

The flock feeding effort increased with the distance to roost ($F_{12,434} = 3.78$, $P < 0.001$). It was higher on sown grounds with no seeds on surface (85.2%, $SE = 1.8$, $n = 125$) than on grounds with food on surface (stubble fields plus sown grounds with seeds on surface, 76.5%, $SE = 1.6$, $n = 236$; $t = 3.45$, $P < 0.001$).

**Flock size and interindividual distance**

The mean flock size increased during the morning, reaching a peak during midday, at drinking-
resting sites. Later, flocks decreased during early afternoon and increased again to reach highest values in late evening (Fig. 8a). Mean interindividual distance within flocks decreased throughout the day, following an inverse pattern to that of flock size (Fig. 8b).

**DISCUSSION**

The main activity of cranes during winter was feeding, to which they devoted 62% of their daily time budget. The daily patterns of percentage time spent feeding, feeding bout length, and food intake rate showed two peaks, in early morning and late evening. These double-peak patterns of feeding effort have probably evolved as an adaptation to compensate for the prolonged fasting imposed by winter nights and is now endogenous in many bird species (Beer 1961, Aschoff 1966, 1967, Meier & Russo 1985). Like in these species, hungry cranes filled their empty crops as soon as possible in early morning, and in late evening they refilled them to anticipate fasting during night.

Water needs may have also been important in determining a double-peaked daily pattern in feeding activity. Recent studies of water economy in granivorous birds have shown that even during winter a period of negative water balance usually occurs during midday (MacMillen 1990). In fact, the double-peaked average pattern observed resulted from most cranes stopping to feed on cereal fields at midday for some time, which they devoted to drinking, bathing and preening. Frequently they had to fly a considerable distance to reach one of the few drinking sites available in our study area (see Alonso et al. 1984).

We think that the lower feeding effort around midday was not due to a digestive bottleneck as proposed for some birds (e.g. Kenward & Sibly 1978, Zwarts & Dirksen 1990), since cranes were able to continue feeding at high rates during midday in November and December (see Fig. 4).

Several authors have discussed the significance of the 'bigruminus' versus 'alternans' patterns, i.e. respectively with a more pronounced morning or evening peak. Some species living in northern latitudes show a higher feeding activity peak in eve-
ning, which has been interpreted as an adaptation to reduce energy losses during the extremely cold morning temperatures (Gjerde & Wegge 1987, and references therein). These cases are probably exceptions, since most birds show higher morning activity peaks (Aschoff 1966, 1967). Wintering cranes had similar feeding efforts during the morning and evening periods, excepting in February and March. The differing pattern in these two months was probably determined by the arrival of large numbers of migrating cranes during the afternoon. After landing, cranes foraged intensively to compensate for the time they had spent flying, increasing the average evening feeding peak.

However, in spite of a globally greater feeding effort during the evening, net and absolute intake rates were higher during the morning. The main reason for the higher morning net intake rate was probably the higher average quality of the morning foraging grounds (stubble and sown grounds with food on surface) with respect to the evening foraging grounds (when the use of sown grounds with buried seeds increased). Comparison of daily curves of net and absolute intake rates suggests that birds maintained the net intake rate (i.e. when searching food, head down), probably as high as possible, with the only constraint of the availability of food on the ground. On the evening sown grounds, although cranes spent less energy walking, they had to dig up the cereal seeds from the earth, and thus spent more time and probably also more energy than during morning foraging. One benefit of these afternoon flocks was a reduced individual vigilance time due to the large flock size, and thus an increased time head down, searching food. But this compensated only in part for the lower accessibility of buried seeds on sown grounds.

The daily changes in time allocation decisions were therefore related with those about feeding patch and flock size, and altogether with the pattern of daily intake rate. During the morning cranes showed a higher locomotor activity, foraging in smaller flocks, at longer distances from the roost, on grounds with higher food availability, in which cereal seeds were easily obtained from the surface. On the contrary, during the afternoon, birds showed lower locomotor activity, aggregated in larger flocks, foraged closer to the roost and used more frequently sown grounds, which offered a lower but less variable food availability. These results suggest that the increasing degree of satiation with advancing daytime relaxed the dispersal trend of the birds, which foraged progressively closer to the roost and formed larger flocks on grounds with lower but more constant food availability, thus reducing other possible non-foraging risks. This daily shift from a more risky but higher rewarding foraging behaviour in the morning to a less risky and less rewarding one in the evening, as birds become satiated, agree with the predictions of risk-sensitive foraging models (Caraco et al. 1980, Stephens 1981, Stephens & Krebs 1986).

These results also show how individual cranes can obtain similar food intake rates in two situations differing in time budget, flock size, foraging ground type and distance to the dispersal center, i.e. during morning and evening feeding periods. This is relevant when studying the relationships between intake rate and flock size or other social and behavioural variables, which are often assumed to be unimodal by simple foraging models (see Stephens & Krebs 1986).

Finally, there was a steep seasonal decrease in feeding effort and daily food intake. Since the diet composition did not change throughout the season, we interpret this as a consequence of the increased energetic demands of birds recently arrived on migration from the north. Cranes showed then a hyperphagia similar to that observed in most migratory birds just before migration departure (e.g. King & Farner 1965). Data (own obs.) on seasonal changes in body weight (lowest during autumn and reaching highest values already in January) support the idea that cranes acquire fat reserves as soon as possible over the winter period and later they just feed to maintain appropriate intake levels. The existence metabolism (EM) of a crane, considering 5000 g as its average weight (W), 0°C mean temperature, and a 10-hour photoperiod, is $EM = 17.73W^{0.5316}$ (Wiens & Dyer 1977) which is equal to 1.64 MJ bird$^{-1}$ day$^{-1}$. Assuming a caloric value of 18.2 kJ g$^{-1}$ for cereal seeds (Cummins & Wuy-
check 1971) and 77.7% assimilation efficiency (Castro et al. 1989), a crane is expected to ingest around 116 g per day. This figure is much smaller than our field estimation of 350 g in November, and only somewhat higher than the estimated 96 g in March. This result also suggests that cranes progressively decrease fat deposition from highest values in November to a minimum in March.

The progressive fattening throughout the winter is probably the reason that we did not observe a premigratory increase in food intake such as that observed in many other species. The alternative explanation that the observed pattern could be due to seasonal food depletion is indeed excluded by the high percentage time spent in non-feeding activities in February and March (respectively 47.1 and 43.3%, compared to 27.1, 31.4 and 42.7% in November, December and January).

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REFERENCES

SAMENVATTING

In Gallocanta, noordoostelijk Spanje, werden overwinterende Kraanvogels bestudeerd. Dit artikel gaat over de dagelijkse activiteitspatronen van Kraanvogels in relatie tot kenmerken van de fourageerplaats, de afstand tot de slaapplaats en de groepsgrootte. De hoeveelheid tijd besteed aan voedselzoeken, de duur van 'vlagen' van voedselzoek-gedrag en de voedselopname-snelheid vertoonden twee pieken per dag: één in de vroege ochtend en een tweede in de late namiddag (Figs 1-3). De tijd besteed aan waken, poetsen en andere activiteiten vertoonde één piek rond het middaguur (Figs 1 & 2), wanneer de vogels zich gewoonlijk ophielden bij de drinkplaatsen. Het patroon van deze activiteiten was dus tegengesteld aan dat van het patroon van de fourageerge­dragingen.

De mobiliteit van de kraanvogels was vooral 's ochtends hoog (Fig. 5). Er werd dan ver weg van de roestplaats (Fig. 6) gefourageerd op plaatsen met een hoog voedselaanbod (Fig. 7) in betrekkelijk kleine groepen (Fig. 8). In de late namiddag was het beeld omgekeerd. De opnamesnelheid verandert daarbij nauwelijks. Dit patroon werd beschouwd als een verschuiving van ris­kante naar minder riskante fourageerstrategieën in de loop van de dag, naarmate de honger afneemt. De waar­genomen sterke afname in de totale voedselopname per vogel per dag van november tot maart (Fig. 4) werd toe­geschreven aan de zeer grote voedselbehoeftte van pas aangekomen migranten die in een zo vroeg mogelijk sta­dium reserves proberen op te bouwen.