FACTORS INFLUENCING DAILY FOOD-INTAKE PATTERNS IN BIRDS: A CASE STUDY WITH WINTERING COMMON CRANES

Luis M. Bautista[1] and Juan Carlos Alonso

Department of Evolutionary Ecology, National Museum of Natural History, Consejo Superior de Investigaciones Científicas,
José Gutiérrez Abascal 2, 28006 Madrid, Spain

Abstract. Avian foraging activity during daytime peaks after dawn and before dusk. The relative importance of each period of intensive foraging on the accumulated intake varies by species, individual, and day. We studied the relative importance of each period from direct observation of radio-tagged Common Cranes (*Grus grus*) during winter at a site of stopover and wintering in Spain. After a mathematical model was fitted, accumulated intake showed a typical anti-sigmoid shape, with greatest increases of intake after dawn and before dusk. The rise of accumulated intake decelerated until 50% of the day length, when the trajectory inflected and accelerated according to the fitted model. The trajectory of accumulated intake in territorial families that foraged in small home ranges with food predictably available but the cost of vigilance high decelerated until 20% of the day length, then accelerated for the rest of the day. In flocking nonterritorial cranes the inflection point was delayed until 60% of the day length, as expected since flocking cranes foraged in larger home ranges with food less predictable and the cost of vigilance lower. The inflection point was delayed in early winter and advanced in late winter. The changes in the inflection points of the functions for accumulated food intake may be straightforwardly applied to daily foraging routines of other species whose rates of intake may be recorded.

Key words: *Common Crane, daily foraging routines, food availability,* Grus grus, *winter.*

Factores que Influencian los Patrones de Ingestión Diario de Alimentos en las Aves: Un Caso de Estudio con los Individuos Invernales de *Grus grus*

Resumen. La actividad de ingestión de alimento en aves es máxima después del amanecer y antes del atardecer. La importancia relativa de cada período de ingestión intensiva de alimento en la curva de ingestión acumulada varía entre especies, individuos y días. Estudiamos la importancia relativa de cada período en *Grus grus* en un lugar de paso e invernada en España, registrando la ingestión de alimento en individuos marcados con radio durante el invierno. La ingestión acumulada mostró la típica forma anti-sigmoidea después de ajustar un modelo matemático, con los mayores incrementos de ingestión después del amanecer y antes del atardecer. El aumento de la ingestión acumulada se deceleró hasta el 50% del período diurno, cuando la trayectoria mostró una inflexión y se aceleró de acuerdo con el modelo ajustado. La trayectoria de la ingestión acumulada de las familias territoriales que se alimentaban en pequeñas áreas de campeo con disponibilidad de alimento predecible pero elevados costos de vigilancia se frenó hasta el 20% del período diurno, mostrando una forma acelerada durante el resto del día. El punto de inflexión en los bandos de grullas no territoriales estuvo retrasado hasta el 60% del período diurno, tal y como cabía esperar porque las grullas gregarias buscaban alimento en áreas de campeo mayores con disponibilidad de alimento menos predecible pero menores costos de vigilancia. El punto de inflexión estuvo retrasado al principio del invierno y adelantado al final del invierno. Estos cambios en los puntos de inflexión de funciones ajustadas a la ingestión acumulada pueden ser aplicados directamente a las rutinas diarias de ingestión de alimento de otras especies cuyas tasas de ingestión puedan ser registradas.

INTRODUCTION

Many diurnal birds increase their foraging activity and body mass after dawn and before dusk. This bimodal pattern is prevalent among small passerines (Pravosudov and Grubb 1997, Polo and Bautista 2006a). Environmental and internal factors may change the relationship of intensity and duration of the first and second periods of body-mass gain and thus change the shape of daily trajectories of fattening (reviewed in Polo and Bautista 2006a). An early-morning body-mass gain would be promoted when food is unpredictable or interference while the bird is foraging is great, as it would when social status is low or the morning amount of nutrients stored as proteins, fat, and carbohydrates ingested from food plus fat reserves built during previous days, *nutrient stores* (Lindström and Piersma 1993, van der Meer and Piersma 1994), are low. In these circumstances the body-mass increase should decay with time of day. Alternatively, body-mass gain in late afternoon would be favored, for instance, when the morning amount of stored nutrients is high. Increased flight costs due to an increased quantity of nutrients stored in the morning may increase mass-dependent predation risk, promoting body-mass gain in the late afternoon. Abundant

and predictable food also induces body-mass gain in the late afternoon. A high social status facilitates access to food and therefore dominant birds may forage more intensively in the afternoon than do subordinate birds. There are several reasons to expect that body mass should increase exponentially during the day. The concurrent effects of environmental and internal factors result in the bimodal pattern prevalent in most passerines of small body size (McNamara et al. 1994, Macleod et al. 2005, Polo and Bautista 2006b). The same environmental and internal factors may regulate the trajectories of fattening of large birds, but in the wild continuous recording of such trajectories is not feasible in most large species. Alternatively, the foraging behavior may be recorded and the accumulated intake may be estimated. Accumulated food ingested throughout the day may be a suitable surrogate of the daily trajectory in body mass, especially for species foraging on items such as cereal seeds that can be easily quantified and are of approximately constant size. We aimed to quantify the exponential increase of continuous food intake in a large bird and to explore whether the environmental and internal factors previously described act as they do in small birds.

A frequent problem in describing daytime foraging routines is setting the periods of the day when environmental and internal factors operate, because their effects usually decline or increase smoothly from dawn to dusk. Polo and Bautista (2006a) put forward a method of calculating the inflection point of daytime foraging routines by fitting body mass to time of day with a double-exponential model (also known as a *dobex* model). The inflection point defines the time of day when the trajectory of accumulated intake turns from concave to convex. The model's parameters may be statistically fitted to most trajectories of foraging routines of small birds whose foraging activity increases strongly at the start of the period, is followed by a period of reduced activity, and ends with a second increase. Polo and Bautista (2006a) tested this model with nine species of passerines, mass 9–26 g, as did Barnett and Briskie (2011) with the New Zealand Robins (*Petroica australis*; 30–44 g). Here we broaden the scope of the dobex model with a much bigger bird, the Common Crane (*Grus grus*; 4350–6350 g, Bautista et al. 1995)

Common Cranes start replenishing nutrient stores (sensu Lindström and Piersma 1993, van der Meer and Piersma 1994) spent on migration as soon as they arrive at their wintering sites in late autumn. Their foraging activity decreases progressively through the winter (Alonso and Alonso 1993). The resulting seasonal increase in nutrient stores predicts at least two changes in the foraging behavior of large migratory birds. First, a seasonal decrease in the total daily intake, already described by Alonso and Alonso (1992); second, a seasonal change in the shape of the trajectory of accumulated intake. Low nutrient stores predict a delay in the inflection point in the daily trajectory of accumulated intake (Polo and Bautista 2006a). Such a change in the trajectory has not been calculated in large birds like the Common Crane.

Another factor related to the daily foraging pattern awaiting a formal analysis is unpredictability in food availability, which is associated with the size of a species' home range

(Alonso et al. 1987, 2004). Previous studies suggest that the pattern of food intake through the day may range continuously from decelerating to accelerating (Alonso et al. 2004). Such a pattern has not been analyzed in detail and so remains to be demonstrated. We predict that for flocking cranes foraging on unpredictable cereal fields over large home ranges, the inflection point calculated with a dobex model will be delayed in comparison to that for cranes with small home ranges.

Risk of predation risk should delay the increase in body mass toward the second part of the day (Bednekoff and Houston 1994, McNamara et al. 1994); consequently Polo and Bautista (2006a) predicted and demonstrated that this risk must advance the inflection point of the body-mass trajectory instead of delaying it. Common Cranes respond to the risk of predation risk by flocking. Large flocks of hundreds of birds are routine. But some families with one or two (rarely three) young forage in isolation in winter territories; their risk of predation is greater (Alonso et al. 2004). Therefore, the inflection point should be early in cranes foraging territorially.

In small and medium-sized passerines, the timing of the inflection point is somewhat determined by the stress derived from social status (Ekman and Lilliendahl 1993, Polo and Bautista 2006a), because dominant birds have preferential access to feeding sites. One may therefore expect that the time of inflection of a crane foraging in a flock should be delayed in a subordinate bird and advanced in a dominant one, because dominant cranes may aggressively displace the nearby subordinates (Bautista et al. 1998), but this prediction has yet to be checked.

Our aim was to explore whether the daily foraging routine of a large bird may be described in the same way as for a medium-sized or small one. We therefore (1) fitted a dobex model to individual trajectories of accumulated intake recorded in radio-tagged Common Cranes, and calculated the time of the inflection point; (2) explored the effects of foraging mode (territorial vs. flocking), home-range size, and season on the inflection point's position; and (3) assessed the effect in flocking cranes of social dominance on the shape of the accumulated food-intake curve.

METHODS

STUDY AREA, FOOD AVAILABILITY, AND SPECIES

After breeding in northern Europe, most Common Cranes stage at Gallocanta, Spain (40° 58′ N, 1° 30′ W). They remain there for a period varying from a few days to the whole winter. Cranes arrive at Gallocanta from October to December, reaching peak numbers of 30 000–50 000 birds (Bautista et al. 1992, Prieta and del Moral 2009). Our study area extended over 54 000 ha of farmland (80% cereal crops of barley and wheat, with some corn, sunflower, and other minor crops) surrounding a 1400-ha shallow lake. The area has little topographical relief and almost no woody vegetation. Between 2000 and 10 000 cranes remain at this site through the winter, depending

on the amount of food and weather conditions (Alonso et al. 1994). In late February and March cranes arrive at Gallocanta from southern Iberia and Morocco. Cranes roost in the lake and continue their migration or stage for a few days, waiting for appropriate weather conditions (Alonso et al. 1990a, b). They forage little during the spring staging period.

In autumn, large amounts of waste seeds are usually available in fields of cereal and sunflower stubble. Food availability decreased through the winter as a consequence of both the plowing of stubble fields and the cranes' consumption of waste grain. This decrease was not compensated with newly sown fields. Daily intake decreased seasonally (Alonso and Alonso 1992) also because fat load increased seasonally (pers. obs.). The cranes' progressive fattening through the winter combined with the population's adjustment to the carrying capacity are probably the reasons why we do not observe a change through the winter in the cranes' foraging stress (pers. obs.).

CAPTURE AND TAGGING

We trapped and handled cranes by using devices and following protocols consistent with Swengel and Carpenter (1996). In November and December we captured 79 cranes with rocket nets (Urbanek et al. 1991) or oral tranquillizers (0.3–0.4 g α-chloralose per cup of seeds, Williams and Phillips 1973, Bishop 1991). We distributed cups of cereal seeds (25 g cup^{-1}) separated by 25 m to ensure the birds got the correct dose (one cup) or less (two or more cranes feed on the same cup of seeds) to avoid the exertional myopathy associated with excessive sedation (Hayes et al. 2003).

Cranes captured with rocket nets were measured and tagged immediately. Cranes captured with sedative drugs were kept in a dark room 10–18 hr, when we measured and tagged them. We banded all captured cranes with three colors and equipped some with VHF radio transmitters (Biotrack Ltd., UK), attached with backpack harnesses or glued to the PVC bands on the legs. Radio-transmitter batteries were operative for at least 24 months. We mounted radio transmitters weighing 45 g (1 battery) on leg bands of young birds (<1% body mass, range 0.8–1.0%) because their legs were fully grown at that time. We mounted radio transmitters weighing 80 g (two batteries) as a backpack on adult birds (1% body mass, range 1.3–1.5%) to ensure that cranes were not loaded with more than 3–5% of their body mass.

We released cranes captured with sedative drugs after they were measured, tagged, and fully recovered. Cranes captured with rocket nets were released in the lake immediately after we measured and tagged them. After the birds were released we located all radio-tagged individuals for several days before starting behavioral observations, to check that birds behaved normally.

BEHAVIOR OF MARKED INDIVIDUALS

Cranes foraged on fields of cereal, corn, sunflower stubble, and newly sown cereals. These fields were patchily distributed, since plowed fields or fields of already sprouted cereals occupied most of the area. Cranes did not forage in sprouted fields. They roosted in the shallow borders of the lagoon, from which they dispersed daily to forage in the surrounding fields.

An observer followed a radio-tagged bird continuously by car between departure from the roost in the early morning and arrival at the roost in the late evening. We watched cranes with 60–90× Questar telescopes, from distances of 500–1000 m or more to avoid disturbing them. Marked cranes always foraged in flocks, but flock size and composition changed through the day. Cranes foraged on several patches per day (from 3 to more than 15), at distances of up to 25 km from the roost. We defined a foraging patch as one or a few adjacent farms where the flock including our marked bird spent some time foraging between two flights from and to another patch, drinking site, or roost. At each foraging patch we recorded the date; time (GMT) of arrival, size of the flock landing, size of the flock already foraging in the patch, time spent flying from previous patch (min), residence time in the patch (min); coordinates (with 100-m precision), type of ground (natural grassland, plowed field, stubble [cereal, corn, sunflower], unsprouted sown ground, sprouted sown ground). At each patch we tape-recorded the behavior of the marked bird for 5 min at 30- to 60-min intervals and that of 7–10 other randomly selected adults in the flock for 1 min each. We measured time spent in the various activities to the nearest 1 sec: feeding (head down), vigilance (head up), preening, and others. We also measured the rate of food intake, counting the characteristic swallowing movements, and the number of paces. Cranes walk slowly across a field, moving sideways to remove the surface earth and dig up the seeds. When they find a seed they take it and make a characteristic backward movement of their long neck, which is very apparent to the observer. Since this foraging technique forces the birds to take the seeds one by one, the number of swallowing movements is equal to the number of seeds ingested. We calculated the intake rate (g min^{-1}) multiplying the swallowing rate by the average dry weight of a seed of the corresponding crop, as obtained from samples of 830–3000 seeds from 10–50 different fields (Alonso and Alonso 1992). We defined the gross intake rate as the dry weight ingested per min of observation, the instantaneous intake rate as the dry weight ingested per min spent feeding with the head down. When we could not locate our marked bird in the flock (17% of the patches, Alonso et al. 1995) we used the flock's average intake, after testing that the means of the differences between the marked bird and the flock members were not different from zero (Alonso et al. 1995, 1997, Bautista et al. 1998). For each day we calculated the accumulated food ingested in previous patches to study the trajectory of food intake with time of day. Accumulated food intake started at zero grams when cranes left the roost at dawn, and we updated it every time the bird abandoned a patch. Total daily food intake was set when the crane flew to the roost at dusk.

We excluded days with strong wind, rain, and snowfall from all analyses. Therefore, we were able to consider food-accumulation curves only in good weather. Weather seems

an important variable to be considered in the food accumulation-models, as it affects small birds' foraging and fattening (Carey and Dawson 1999). Although a thorough study of the Common Crane's foraging routines should probably include weather, we question whether it is possible since bad weather prevents the nearly continuous (e.g., ≥85% of the daytime) recording of behavior needed to calculate the food-accumulation curve. Nonetheless, our study draws interesting parallels with other studies of small birds and also leads to important conclusions for the study of the Common Crane.

We observed the birds less than 85% of the daytime also on some other days because of logistic failures. Overall, we dropped 75 days from the sample of 226 field days.

We calculated the home-range size and dominance rank of 23 cranes, 6 foraging in territories (Alonso et al. 2004) and 17 foraging gregariously. We scored the dominance of each crane by the percentage of successes in the aggressive interactions in which it was involved. First-year birds already independent from their parents were the least dominant birds and received most aggression from their flock mates (Bautista et al. 1995, 1998).

ANALYSIS OF DAILY TRAJECTORIES OF FOOD INTAKE

Polo and Bautista (2006a, b) successfully applied a dobex model to body-mass gain of small birds, which show the typical diurnal foraging pattern with peaks in food consumption just after dawn and just before dusk. In our study we applied the model developed by Polo and Bautista (2006a), replacing body mass (y) as a function of time of day (t) by accumulated food intake (y) as a function of time of day (t). The dobex model is $y = b(e^{kt} - 1) + c(1 - e^{-kt})$, where b, c, and k are parameters statistically calculated and y and t stand for proportional food intake and time respectively. Dobex models include several improvements over previous analyses of foraging trajectories (Polo and Bautista 2006a, b). First, data points (y, t) can be distributed irregularly over time. Second, the sample size may be different for each individual trajectory, as opposed to traditional ANOVA analyses in which "period of day" is usually included in the model as a fixed or repeated factor with no empty cells. And third, the dobex model's parameters allow calculating the inflection point as $t_{inf} = \ln(c/b)/2k$. The inflection point characterizes the trajectory fairly well because it identifies a food-intake trajectory as mainly accelerated, decelerated, or mixed by locating the inflection point's coordinates (y, t) as low, high, or middle scores, respectively, in the 0–100% food-intake and time scales. The inflection point shows the relative time of day (percentage of the period of daylight, range 0–100 from dawn to dusk) when the decelerating part of the trajectory of accumulated food intake ends and the accelerating part of the trajectory starts. Further details of dobex models applied to foraging behavior are in Polo and Bautista (2006a).

We transformed accumulated food intake (AFI) and time of day (t) to percentages as $y = 100 \cdot AFI_t / AFI_{dusk}$ and $t = 100 \cdot (t - t_{dawn})/(t_{dusk} - t_{dawn})$ before the calculation of the dobex regression model. Dimensionless intake and time are suitable for comparison of the shape of trajectories by species and experimental condition (Polo and Bautista 2006a), but the inflection time may be calculated with dimensional quantities also (Polo and Bautista 2006b). We look for shape differences in dimensionless routines because the duration of the Common Crane's morning and evening foraging periods do not vary as winter progresses (Alonso and Alonso 1992).

STATISTICAL ANALYSES

We fitted the dobex function to the accumulated food intake (0–100%) as a function of time (0–100%) with the simplex–quasi-Newton method (Nocedal and Wright 2006). We performed analyses with the procedure Non-linear Estimation available in Statistica 6.0 (StatSoft 2001). A few trajectories ($n = 15$ days) were sigmoid, a pattern unsuitable for fitting by a dobex model (Polo and Bautista 2006a), and we excluded them from further analyses. Our sample of trajectories analyzed consisted of 136 days. With this sample, we calculated individual means ($n = 23$ birds, 8 ± 5 days per bird, mean $\pm$ SD) of the time of the inflection point (t_{inf}). We calculated the date as the number of days since 1 August, the approximate start of migration from the breeding range. Although most cranes arrived at Gallocanta lagoon in late autumn, migration may be observed as early as 1 September (Bautista et al. 1992, Prieta and del Moral 2009).

We calculated the statistical significance of differences between foraging modes (territorial vs. nonterritorial) in the inflection times with ANOVA ($n = 23$ individual means). We explored bivariate relationships between individual means of inflection times, home-range size, and day of year with Pearson correlation and linear regression ($n = 23$ individual means). We explored simultaneous relationships between the daily inflection time ($n = 136$ days) and other variables with ANOVAs. Before parametric tests we transformed variables that did not meet the assumptions of such tests. Independent variables are (1) foraging mode (territorial vs. nonterritorial), defined as a fixed factor, (2) subject, defined as a random factor and nested within foraging mode, (3) extent of the home range, ln-transformed and defined as a co-variable, and (4) day of year, defined as a co-variable. We tentatively included in the model an interaction term between home range (ln-transformed) and day of year but removed because it did not reach statistical significance ($F_{1, 108} = 0.3$, $P = 0.56$). We calculate the statistical significance of the difference in the inflection times of dominant ($n = 7$ birds) and subordinate ($n = 6$ birds) with the Wilcoxon signed-rank test z. Notice that we excluded from this test nonflocking cranes that forage in winter territories because their dominance rank was scored mostly with interactions with neighbors at territorial boundaries, not from interference with other cranes foraging within the same flock. Values under Results are means $\pm$ SD.

RESULTS

Between early November 1988 and early March 1993 we radio-tracked 24 individuals for periods ranging from 2 to 25 whole days (mean 9, total 227 days). Twenty birds were adults, two were first-year birds already independent of their parents, and two were young still dependent on their parents. One of the birds was not involved in any aggressive interaction so we cannot calculate its dominance rank and excluded it from the analyses ($n = 23$ birds).

Food-intake rate was greater at the start and end of the day than at midday, so the trajectories of accumulated food intake followed the characteristic curvilinear patterns (Fig. 1) that may be fitted with a dobex model. This typical bimodal pattern was observed in most days (Fig. 2), with the inflection point located slightly later than the middle of the day when the
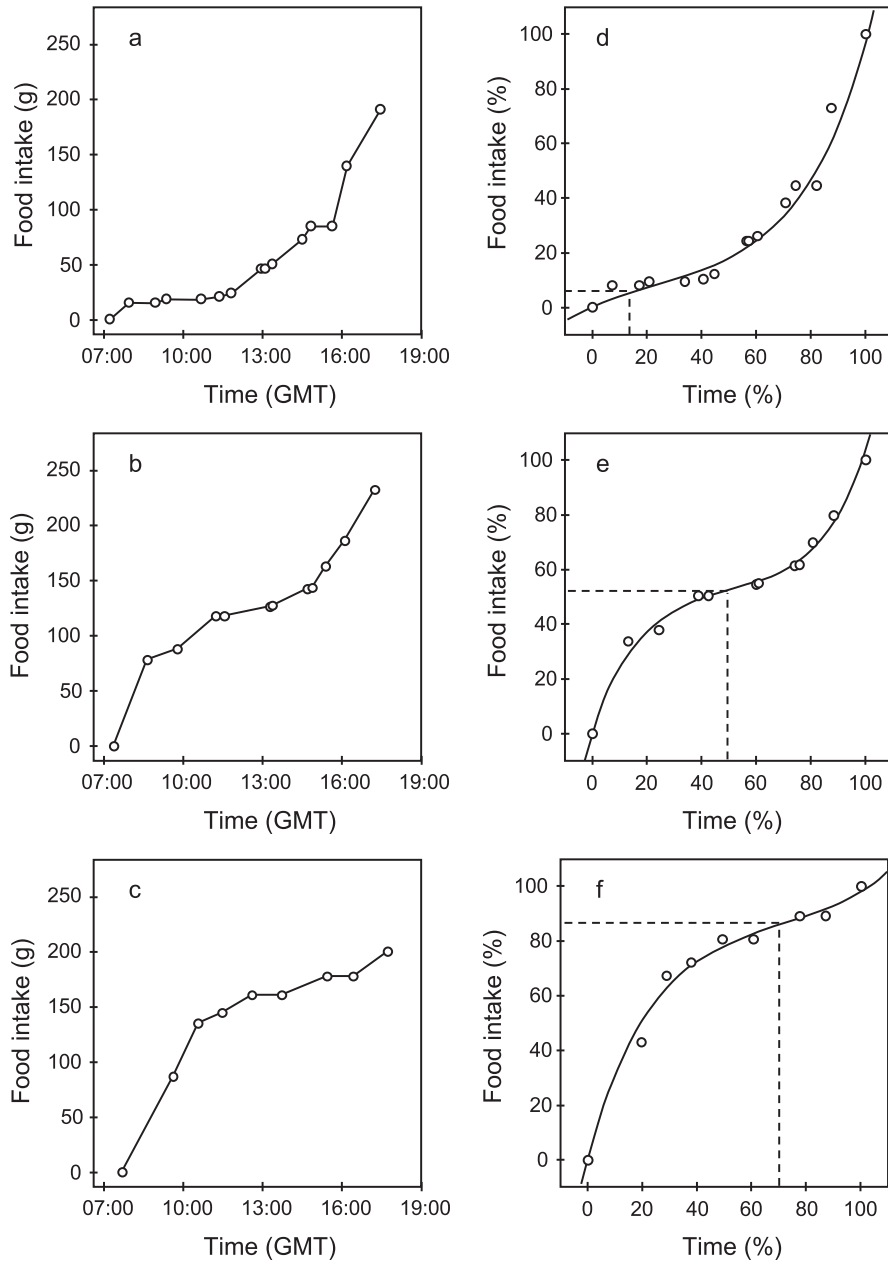

FIGURE 1. Accumulated daily food intake of Common Cranes illustrated with three examples. Three cranes (a, b, and c) left the roost and started foraging at slightly different times. The accumulated daily food intake was 200–250 g of cereal seeds. Their food intake and time of day are transformed to percentages (d, e, and f) highlight the differences in the shape of the trajectories of accumulated food intake. The continuous lines show the dobex fits to the trajectories (see text for details of the calculation). The discontinuous lines show the times and accumulated food intake at the inflection points derived from the dobex fits.
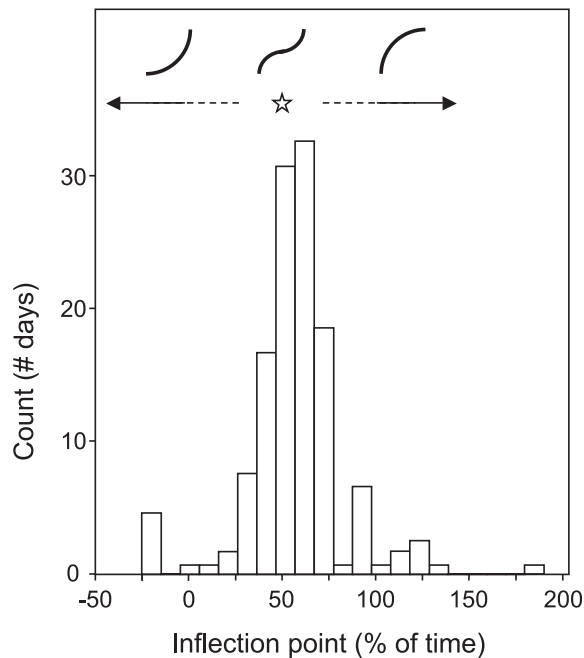
FIGURE 2. The frequency distribution of inflection times shows that on most days the cranes ingested food faster after dawn and before dusk than in the middle of the day, since many inflection times were located around noon (50% of the daytime, top star). Early food intake was negligible when the inflection time was located on the left of the distribution (accelerated shape, left top line). Late food intake was negligible when the inflection time was located on the right side of the distribution (decelerated shape, right top line). Negative inflection points were located before dawn, and inflection points greater than 100 were situated after dusk.

inflection times of all days were plotted together. The mean time of individual inflection points calculated with a dobex model was $50 \pm 26\%$ ($n = 23$ birds, Table 1). The inflection point came earlier for territorial cranes ($t_{inf} = 20 \pm 34\%$, $n = 6$ birds) than for cranes foraging in nonterritorial flocks ($t_{inf} = 60 \pm 11\%$, $n = 17$ birds; ANOVA: $F_{1,21} = 20.1$, $P < 0.001$). For nonterritorial, flocking cranes the mean time of individual inflection points for dominant ($t_{inf} = 63 \pm 4\%$, $n = 7$ birds) and subordinate ($t_{inf} = 65 \pm 4\%$, $n = 6$ birds) cranes did not differ (Wilcoxon signed-rank test $z = 0.8$, $n = 13$, $P = 0.43$).

The mean inflection times of individual birds increased with the size of their home range (Fig. 3a, $t_{inf} = 34 + 10.9$ ln[home range area], $F_{1,21} = 37.0$, $P < 0.001$). The mean inflection time of individual birds was not correlated with the individual mean date (Fig. 3b).

The inflection point for territorial cranes was significantly earlier than for cranes foraging in flocks, as it was when other factors were included in the analyses (Table 2). A multivariate model of the concurrent effects of foraging mode (territorial families vs. non-territorial flocks), individual, home-range size, and date in the inflection-point schedule was statistically significant ($R^2_{adj} = 21.4$, $F_{24, 109} = 2.5$, $P < 0.001$, ANOVA

model). Increasing home-range size delayed the inflection point (parameter estimate $= 13.18 \pm 6.48$, $t_{133} = 2.0$, $P = 0.04$, t-test), and date of year advanced the inflection point (parameter estimate $= -0.419 \pm 0.176$, $t_{133} = -2.4$, $P = 0.02$, t-test).

DISCUSSION

Common Cranes foraged in a pattern similar to that of smaller birds, i.e., with accumulated intake decelerating during the first half of the day and accelerating during the second half of the day. This simple pattern comprised a full continuum of shapes, which varied from some entirely accelerating to others entirely decelerating. That continuum was determined by three factors known to affect foraging routines. First, foraging of territorial cranes was more accelerating than that of flocking cranes, whose foraging mostly followed a bimodal shape. Second, an increase in home range was associated with decelerating foraging. And third, we found decelerating foraging to be more frequent in early winter, accelerating foraging more frequent in late winter.

It was interesting that the Common Crane's pattern of foraging resembles that of smaller birds. In winter in the Northern Hemisphere, small birds feeding on seeds eat about 30% of their morning body mass and increase that mass between 7 and 15% (Metcalfe and Ure 1995, Crocker et al. 2002). Such relatively large daily percentages are rare in larger birds. Because of their large surface-to-volume ratio, small birds lose relatively more heat than do large birds and therefore need relatively more food at both ends of the day, perhaps to recover from and to prepare for the nocturnal expenditure of energy. However, small birds avoid feeding as much as possible after dawn, which may be a way to avoid increasing predation risk due to early mass gain. Besides, they may forage intensively at the end of the day when the risk of diurnal predation is diminishing. Therefore, it was interesting that the crane, a large species with a smaller surface-to-volume ratio, a much lower mass-dependent risk of predation, and daily intakes representing in winter in our study area about 5% of their morning body mass, also showed a bimodal pattern of accumulated food intake typical of small birds, and that this pattern, like that of small passerines, could also be fitted to a dobex model (Polo and Bautista 2006a). Consequently, the Common Crane's daily foraging routines in winter may be explained to some extent by the same factors reported for small birds: quick recovering from a night of fasting and a delayed body-mass gain in late afternoon to minimize the effect of body-mass gain on predation risk.

Foraging in an uncertain environment predicts that the inflection point should be a delayed in comparison to that in a situation where foraging conditions are predictable, because in the former situation most of the intake accumulates early in the day, but in the latter situation the late-afternoon foraging period is or may be the prominent (Polo and Bautista 2006a and references therein). In early morning, flocking cranes foraged on fields with abundant food where cereal seeds were easily

TABLE 1.   Parameters (mean ± SD) of the double exponential regression model (Polo and Bautista 2006a): accumulated intake $= b(e^{kt} - 1) + c(1 - e^{-kt})$, inflection time of the trajectory $[t_{inf} = ln(c/b)/2k]$, and percentage of variance explained (R^2) by the dobex model. Each day was fitted independently.

Bird[a]	Days	b	c	k	t_{inf}	R^2
ABV123	14	3.02 ± 3.47	55.6 ± 25.8	0.036 ± 0.012	49.8 ± 19.0	0.987 ± 0.012
ANR080	3	0.75 ± 0.37	67.0 ± 11.0	0.038 ± 0.005	60.3 ± 6.5	0.980 ± 0.015
ANV504	3	2.53 ± 2.35	43.3 ± 4.9	0.050 ± 0.038	44.9 ± 3.1	0.988 ± 0.006
AVR923	7	1.60 ± 1.65	65.6 ± 22.1	0.039 ± 0.014	65.4 ± 30.3	0.984 ± 0.012
AZR460	6	−2.90 ± 34.24	104.1 ± 151.4	0.027 ± 0.020	60.3 ± 68.5	0.987 ± 0.011
AZV144	10	0.55 ± 1.39	76.0 ± 23.0	0.055 ± 0.027	73.2 ± 41.5	0.982 ± 0.013
BAV433	9	2.19 ± 3.37	72.6 ± 20.1	0.074 ± 0.102	60.5 ± 17.4	0.984 ± 0.020
BNV883	2	6.18 ± 2.37	44.5 ± 2.5	0.024 ± 0.004	41.5 ± 0.2	0.978 ± 0.016
BRV523	9	0.19 ± 0.55	80.9 ± 18.2	0.110 ± 0.081	65.5 ± 19.5	0.994 ± 0.007
BRZ360	4	1.15 ± 2.23	73.0 ± 27.1	0.050 ± 0.025	69.1 ± 35.8	0.985 ± 0.010
BVA684	9	2.89 ± 2.80	64.3 ± 25.2	0.038 ± 0.023	59.7 ± 19.2	0.985 ± 0.014
BVR901	2	7.23 ± 1.74	47.4 ± 2.9	0.022 ± 0.002	42.7 ± 1.1	0.990 ± 0.008
BZB020	15	1.62 ± 2.37	68.7 ± 20.9	0.048 ± 0.026	59.4 ± 10.8	0.987 ± 0.009
RAB459	1	0.32	53.2	0.049	51.1	0.999
RBV170	2	0.29 ± 0.38	62.9 ± 10.7	0.057 ± 0.018	53.9 ± 2.6	0.997 ± 0.003
RBZ414	12	0.53 ± 1.72	79.8 ± 31.1	0.069 ± 0.041	71.9 ± 27.9	0.976 ± 0.015
RNR555	1	0.005	60.6	0.090	52.4	0.999
RVB260	1	5.80	−2.1	0.028	−17.0	0.982
RVZ013	10	1.28 ± 2.76	66.7 ± 22.5	0.045 ± 0.018	59.7 ± 16.1	0.979 ± 0.013
RZR130	7	2.77 ± 7.15	53.7 ± 38.6	0.056 ± 0.019	46.9 ± 31.7	0.973 ± 0.022
VBR053	2	0.53 ± 0.68	98.5 ± 2.1	0.035 ± 0.012	85.9 ± 0.3	0.987 ± 0.004
ZAV243	2	18.90 ± 0.00	10.0 ± 0.0	0.018 ± 0.000	−17.0 ± 0.5	0.980 ± 0.011
ZBZ383	3	11.39 ± 7.35	14.0 ± 3.4	0.023 ± 0.005	4.5 ± 19.5	0.986 ± 0.018
All cranes[b]		3.00 ± 4.59	59.2 ± 25.5	0.047 ± 0.022	49.8 ± 26.1	0.986 ± 0.006

[a]Bird code shows the three-color combination initials in Spanish (A: yellow, B: white, N: black, R: red, V: green, Z: blue) followed by the last three digits of the radio frequencies (148.001–148.999 kHz).
[b]Means (± SD) calculated from 23 individual means.

obtained from the surface. These fields were far from the roosting sites, and their exact location has to be sampled day by day, increasing the risk of sampling failure. In the afternoon flocking cranes foraged closer to the roost on fields that offered less food but with less variability (Alonso et al. 1987, 1995, Alonso and Alonso 1993). The shift from a more risky and perhaps more rewarding foraging behavior in the morning to a less risky but less rewarding one in the evening is compatible with the predictions of risk-sensitive foraging theory (Stephens and Krebs 1986, Kacelnik and Bateson 1996), which predicts a preference shift from more variable resources toward the less variable resources when the need of nutrient stores may be certainly fulfilled in the less variable resource.

Territorial cranes experienced the least uncertainty in foraging. They had prior knowledge of food availability in their foraging territories, foraged much closer to the roost than did flocking cranes, and had home ranges smaller than those of flocking cranes (Alonso et al. 2004). Instead of trying to maximize accumulated intake in the early morning, the daily foraging behavior of territorial cranes was likely aimed at minimizing predation risk, since all territorial birds were families with at least one offspring to look after (Alonso et al. 2004).

In small birds, the inflection point is predicted to fall earlier in the day if predation risk is a decisive factor regulating foraging behavior (Polo and Bautista 2006a and references therein). It is plausible that territorial cranes' foraging routines with an accelerating trajectory and the inflection time advanced satisfied their nutritional requirements and minimized the risk of predation of their young, whereas flocking cranes maximized daily food intake by foraging early in the day with unpredictable success. Although the total accumulated intake was similar under both strategies (Alonso et al. 2004), in this study we show that the daily curve of accumulated intake clearly differed.

Common Cranes acquired nutrient stores as soon as possible upon arrival in Gallocanta, accumulated fat reserves through the first months of the winter, and had less demanding foraging behavior in late winter (Alonso and Alonso 1993). In the Palearctic, this is a pattern common to many species of migrants (Lindström and Piersma 1993, Piersma and Jukema 2002). This seasonal increase in nutrient stores predicted a seasonal change in the shape of the curve of accumulated daily intake. This change was inferred from pooled data from nontagged birds (Alonso and Alonso 1992) and formally calculated with
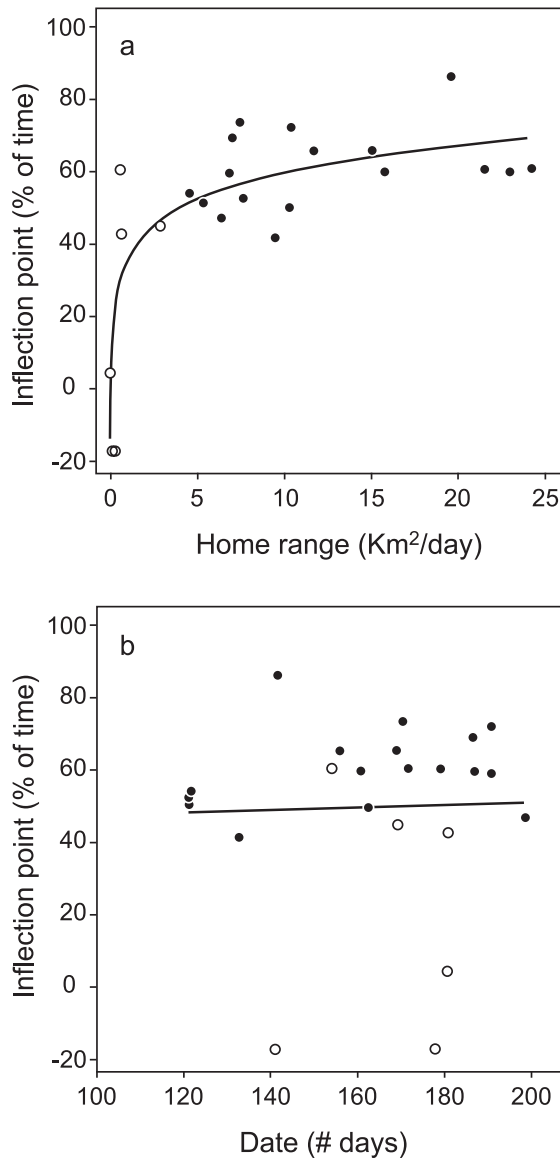
TABLE 2.   Results of the ANOVA for the inflection time and selected independent variables. The inflection time of the accumulated food intake depends on foraging mode (territorial vs. gregarious) and home-range area (km^2 day^{-1}), besides a random individual factor. The latter was nested within foraging mode because each bird foraged either territorially or gregariously throughout the study.

Source	Factor type	F	df	P
Foraging mode	Fixed	7.1	1, 85	0.009
Bird[a]	Random	1.7	21,109	0.039
Home range	Covariates	4.1	1,109	0.044
Date	Covariates	5.7	1,109	0.019

[a]Bird was nested within foraging mode (territorial family or nonterritorial flock).

FIGURE 3.   Inflection time of the foraging trajectory in 23 Common Cranes as a function of home-range size (a) and the number of days since 1 August (b). Cranes foraged as isolated families (up to four birds per family) in small winter territories (empty symbols) or in nonterritorial flocks (up to 500 birds per flock, filled symbols). The inflection time was delayed as the home range increased, but there was no significant correlation with the mean date.

a dobex regression model fitted to individual trajectories of accumulated intake (this study). The suitability of a dobex model to study the accumulated intake may be emphasized applying it to pooled data from nontagged cranes (figure 4 in Alonso and Alonso 1992). The inflection time calculated after the dobex regression model was fitted to those trajectories built with pooled data from nontagged birds advanced from 59% of the daytime in November and December through 56% in January, 46% in

February, and 46% in March. These times calculated from untagged cranes cannot be compared to those calculated for radio-tracked cranes because the former data were pooled and calculated for hourly periods (Alonso and Alonso 1992), while the latter were raw individual data. Nonetheless, both datasets showed the same result: the inflection time of the daily intake curve advanced through the winter. It could be argued that a seasonal advance in the inflection time is not biologically relevant but trivial, due to the seasonal increase in absolute duration of daylight. Cranes may have delayed their daily food intake as the winter progressed, decreasing their absolute intake early in the day more than that late in the day, but this was not observed: cranes eat less food at each time of day as winter progresses (Alonso and Alonso 1992). Therefore the seasonal advance in the inflection time calculated for Common Cranes is not due to an increase of the period of light in which they can forage. The effects of day length on the temporal shift of the inflection time has to be explored in the laboratory to ensure that nutrient stores do not co-vary with day length.

Common Cranes may not strictly need to fit their energy gain on daily basis since their ability to fast is greater than that of small birds, given their greater capacity to store energy and more favorable surface-to-volume ratio. One might expect that the Common Crane's food-accumulation curve is to some extent affected by foraging on days before the observation day and that the birds can deal with large changes in foraging conditions from day to day and modify their behavior accordingly (Alonso et al. 1994, 1997). We know the base-level condition in large birds like the Common Crane less well than we do in small or medium-sized birds (van der Meer and Piersma 1994, Piersma 2002, Reneerkens et al. 2002, Wiersma and Tinbergen 2003). In other words, the timing of the inflection point highlights how much foraging stress a bird experiences, but it does not explain the causes. A definitive understanding of birds' foraging strategies requires approaches more comprehensive (Mangel and Clark 1988) than the calculation of an inflection time, although the inflection time is useful for characterizing foraging stress.

Dominant birds are most likely to take advantage of their priority in food access (Ekman and Lilliendahl 1993, Krams 2000, Pravosudov and Lucas 2000), suffering less stress when foraging in flocks than do subordinate birds. Daily intake routines may thus differ according to dominance rank, with inflection time in subordinate birds being delayed in comparison to that in dominant birds (Polo and Bautista 2006a). However, dominant and subordinate flocking cranes did not differ significantly in the mean time of individual inflection points. The absence of a dominance-related difference in the timing of inflection in flocking cranes may have two explanations. First, gregarious cranes are to some extent forced to follow patterns similar to those of their flock mates if they remain attached to the same flock through most of the day, which was the rule in our study area, as it is in other flocking birds (Folmer et al. 2010, 2012). The main factor accounting for variability in intake rate within a flock was the quality of a foraging patch (i.e., the amount of food available in a field), which had an effect on intake rate greater than that of dominance rank (Alonso et al. 1995). The second, not mutually exclusive, explanation for the absence of a dominance-related difference in the inflection timing in flocking cranes is that the daily dispersal of cranes on the agricultural fields (~27 000 ha) around the Gallocanta lagoon was compatible with a truncated phenotype-limited distribution (Parker and Sutherland 1986) with greater concentrations of dominant cranes in the foraging areas with more food in mid-winter (Bautista et al. 1995). This spatial adjustment between foragers and resources would have reduced the social stress and its effect on the shape of trajectory of accumulated intake. Nonetheless, we do not discount that daily intake routines may differ according to dominance rank because interference has been found in foraging of flocking nonterritorial cranes (Stillman et al. 2002). A perfect test of the effect of dominance rank on the inflection point would require pairs of dominant and subordinate radio-tagged birds foraging in the same flock all day, but this situation has never been recorded in our study area.

Our study makes use of an equation that allows identification of an inflection point in the curve of daily food accumulation, in cases when intensive foraging is concentrated in the early morning, late afternoon, or both. This is a useful feature of the model because it helps in the interpretation of birds' foraging strategies between short periods (morning vs. afternoon) and individual traits (territorial vs. nonterritorial, home-range size). Therefore the delay of the inflection point may reveal an elusive environmental stress that may be not detected by the observer. This and other advantages of a dobex model in the study of daily foraging behavior (Polo and Bautista 2006a) do not replace but complement other well-established analytical techniques of behavioral routines. For instance, dynamic optimization models (Houston et al. 1988, Mangel and Clark 1988) of short-term, diurnal energy management for birds in which only short winter days are considered have shown that the predicted increase of fat reserves is consistent with field data from small birds (Pravosudov and Lucas 2001).

Common Cranes are large birds that, during winter in Gallocanta, feed on cereal seeds. Through intensive radio-tracking, we could record the accumulated food intake of marked individuals, a situation unusual in other studies. We acknowledge that the main obstacle in the study of daily foraging routines in species with large home ranges is not the analytical technique but the recording of the intake rate from dawn to dusk. With enough field data, dobex regression models may show the degree of stress in foraging routines in other species of birds and other study areas.

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