

Family-based territoriality vs flocking in wintering common cranes *Grus grus*

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We describe winter territoriality in common cranes, *Grus grus*, a long-lived migrant species with long-lasting pair bonds and parental care extending throughout the winter. Cranes are territorial in the breeding season, and usually gregarious during migration and wintering. Only 2% of the families present in our study area were territorial, all other families foraged in flocks with immatures and adult pairs. Territorial pairs defended the same winter territory year after year, but only when they had offspring. They were gregarious otherwise. The average breeding success measured throughout several years was higher in territorial pairs. Winter territories were small (0.7 km² on average), but included a higher diversity of habitats than the areas visited by gregarious birds (11.7 km² on average). Adults of territorial families showed longer vigilance times, and lower food intake rates than did adults in flocks, which were compensated with a longer time spent foraging per day. The accumulated daily food intake did not differ between adults in flocks and in families. We suggest that winter territoriality is a facultative strategy, conditioned by parental experience and habitat availability.

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The coexistence of territorial and gregarious foraging behaviour in the same population has been reported for many bird species (e.g. Davies 1976, Davies and Houston 1981, Matthysen 1990, Lott 1991, Brotons 2000, Christman 2001). Group foraging is predicted when patches of food are ephemeral, unpredictable, but rich relative to the needs of a single individual, whereas territorial behaviour is favored when food resources are predictable and economically defendable (Davies and Houston 1984, Pulliam and Caraco 1984). During the non-reproductive season, flocking behaviour is usually interpreted as maximizing short-term benefits related to foraging and predator avoidance (Pulliam and Millikan 1982, Pulliam and Caraco 1984, Barnard and Thompson 1985). Long-term benefits of winter territoriality are more easily recognized in resident species, in which such behaviour may be beneficial for acquiring a breeding territory

(Ekman 1979, Smith 1984, Nilsson 1989, Matthysen 1990). Although migrant species usually obtain no such long-term payoff, winter territoriality has also been documented among migrant birds, as an either food, or an anti-predator related strategy. However, most studies deal with territoriality of single individuals (reviewed in Greenberg 1986, Matthysen 1993). Family-based winter territoriality is seldom reported in migrant bird species, hence it deserves more attention. It is common in resident, cooperatively breeding species (Brown 1987, see also Dickinson et al. 1996, Kraaijeveld and Dickinson 2001), but rare in sedentary non-cooperative breeders (Burger 1984, Gayou 1986, Veltman 1989, Strickland 1991, Ekman et al. 1994), whereby the retention of young parents at their permanent, all-purpose territories could be interpreted as representing an early stage in the evolution of cooperative breeding.

Among migratory species, family-based territoriality has only been cited in the Barrow's goldeneye *Bucephala islandica* (Savard 1988), and some species of cranes (whooping crane *Grus americana*, Allen 1952, Stehn and Johnston 1987; red-crowned crane *G. japonensis*, Masatomi and Kitagawa 1975; Siberian crane *G. leucogeranus*, Sauey 1976, and hooded crane *G. monacha*, Ohsako 1989, Eguchi et al. 1991).

Although common cranes are, like other crane species, gregarious in winter, in previous studies we have reported the presence of a small number of families foraging isolated from other cranes (Alonso et al. 1987a, Alonso and Alonso 1992, Alonso and Alonso 1993). However, family-based winter territoriality and site fidelity have not been previously reported in this species, and no study has yet addressed the economics of this strategy in relation to their more usual flocking behaviour. In this paper, we address the question whether territorial cranes used the same sites throughout eight consecutive winters, and whether they only defended a feeding territory in years when they had offspring, at one of the main wintering areas of the species in Europe (Alonso et al. 1987a, b, Bautista et al. 1992). We also ascertain some trade-offs of family winter territoriality vs flocking in cranes by comparing the habitat selection, time budget and food intake rate of marked individuals.

A major advantage of a territory with respect to the rest of the wintering habitat is that it provides the family with all necessary food elements in a small, economically defensible area (Davies and Houston 1984, Pulliam and Caraco 1984). Thus, we tested the predictions that territories should be smaller than home ranges of gregarious birds, and that they should have higher habitat diversity than feeding sites selected by flocks. Another benefit of the territorial strategy is a lower frequency of aggressive interferences with conspecifics (Myers et al. 1979a, b, Greenberg 1986, Gwinner et al. 1994). Among flocking cranes, aggressive interferences and foraging site displacements cause a significant decrease in food intake, particularly to immature, subordinate birds (Alonso et al. 1997, Bautista et al. 1998). Interference costs are particularly important for young cranes, who usually stay with their parents until the beginning of the spring migration (Alonso et al. 1984). Therefore, the absence of interferences over food should result in a significant increase in intake rate in territorial families. On the other hand, however, territorial adults should invest more time in anti-predator vigilance and territory defense than flocking birds.

Methods

Study area and species

The study area was an intensively cultivated lagoon basin of ca 54 000 ha at Gallocanta, northeast Spain (40°58'N,

1°30'W), which is regularly used by common cranes as a staging area on their way to SW Spain (Alonso et al. 1990, Bautista et al. 1992). Most cranes arriving from their breeding areas in northern Europe stage there for some days or weeks during October–December, reaching peak numbers of 30 000–50 000 birds. A variable number of cranes, 2000–10 000 birds remain there throughout the whole winter, depending on the amount of food and weather conditions (Alonso et al. 1994). A lagoon extending 1400 ha is used as a communal roost from which cranes disperse daily to forage on the surrounding cereal fields. A detailed description of the study area is given in Alonso et al. (1994), and Bautista et al. (1995).

During autumn cranes feed almost exclusively on the cereal seeds left after harvesting on stubble fields. The ploughing of stubbles and seed depletion by cranes cause a decrease of food availability on stubbles throughout the winter, and cranes shift progressively to feeding on recently sown cereal fields. A much lower amount of food is obtained from maize, sunflower, sugarbeet and potato stubbles. According to preliminary banding results, cranes mate at an age of 3–4 years and usually have long-lasting pair bonds (Alonso and Alonso 1999). Young cranes are dependent of their parents throughout their first winter, and family breakup occurs prior to departure on spring migration (Alonso et al. 1984). As a rule, cranes tend to be faithful from year to year to their nesting site (Nowald 2001), and to the sites visited on migration and during winter (Alonso and Alonso 1999, own unpubl. data).

Crane counts and habitat selection

Throughout the winters 1990–91 to 1992–93 we made fortnightly censuses of the crane population at the study area, counting all birds entering the roost at evening, from 3–4 observation points around the lagoon (for census procedure details, see Alonso et al. 1987a). Each census date we also estimated the total number of families present in the wintering population, by calculating the percentage of juveniles from samples of 5000–10 000 birds observed during daily surveys of the foraging areas, and dividing it by the mean number of offspring per family, usually one, less frequently two, as estimated from samples of over 150 families. Juveniles are easily distinguishable from adults by their head and neck plumage. Finally, to know the proportion and distribution of territorial families in the study area we carried out 12 habitat selection surveys (7 in 1990–91, 4 in 1991–92, and 1 in 1992–93) during the main foraging period in early morning, 07:00–10:00 h, by registering on a map all families seen foraging isolated from other cranes (6–26 families per survey, 151 families in the 12 surveys), and a similar sample of crane flocks

for comparison (5–10 flocks per survey, 118 flocks in total). We also located 18 isolated crane pairs without offspring, which were excluded from the analyses, because we did not see these pairs in the same locations in consecutive transects.

Behaviour of marked individuals

At the beginning of the winters 1989–90 and 1990–91, we captured 108 cranes and radiotagged 61. Most of these cranes staged in the study area only for a short period in autumn, migrating further south in mid-winter. We radiotracked 6 territorial families and 13 flocking adult cranes during 2–3 consecutive winters after capture for, respectively, 39 and 137 total days. Selective capture of families foraging gregariously was not viable, due to their small number in the wintering population (ca 11% juvenile birds on average, own unpubl. data). In our sample of 13 flocking adults, only 2 had dependent offspring, and the rest were paired adults. In an earlier study we have shown that the time budget of adults with offspring did not differ significantly from that of adults without offspring when foraging in flocks (the time spent feeding was, respectively, 61.4% and 62.5%, $t=0.48$, $P=0.63$, Alonso and Alonso 1993). Thus, in the present paper we use paired adults in flocks to compare with territorial families. We captured these birds with rocket nets or oral tranquilizers, color-banded and radio-tagged at least one member of each family or pair, and began studying their behaviour at least 1 week after having released them. The adults were sexed by sex-specific differences in the ‘unison call’, a pair display often observed in late winter that allows sexing of most crane species (Archibald 1976). The tracking method was identical for families and flocks. One observer followed each bird by car continuously during a whole day, starting at roost departure and finishing at roost entrance, and watching the marked bird with a 60–90x Questar telescope from minimum distances of 500–1000 m, to avoid disturbing the cranes. Each observation day we measured the difference in time between departure of the first crane from the roost and that of our focal marked bird. All cranes foraged on several patches per day, at distances of up to 25 km from the roost. A foraging patch was defined as a field where the crane spent some time feeding (see patch definition details in Alonso et al. 1995). At each foraging patch, we recorded the time of arrival (GMT), flock size, coordinates, substrate category (sown cereal and recently sown cereal, natural pasture, cereal stubble, corn stubble, sunflower stubble, water, sprouted cereal, track borders, ploughed fields, potatoes, sugar beet, and fallow land), and distance to the nearest crane measured in number of body-lengths. Daily home range was estimated through

the minimum convex polygon method (Mohr 1947, White and Garrot 1990).

At each patch we tape-recorded the behaviour of the marked bird, and also that of its family members for 5 min at 30–60 min intervals. We measured the time spent in the different activities to the nearest 1 s: feeding (head down), vigilance (head up), preening, fighting, and others. We also calculated the food intake rate counting the characteristic swallowing movements of the feeding birds, which almost exactly correspond to the number of seeds ingested, according to our observations of free-living and captive cranes. We defined gross intake rate as the number of food items ingested per minute of observation multiplied by the average dry weight of the corresponding seed, as obtained from samples of 830–3000 seeds from 10–50 different fields of each type (more details in Alonso et al. 1995). The instantaneous intake rate was the number of grams ingested per minute spent feeding, i.e. head down. The total daily food intake rate (g/day) was obtained by multiplying the gross intake rate by the time spent at each feeding patch. We used the daily food intake as a short-term fitness index when comparing territorial and flocking strategies. Cranes typically drink and preen at midday, and therefore, we calculated separately the food intakes for both morning and afternoon foraging periods, to look for differences between territorial and flocking cranes in the daily foraging routines.

Relationship between average breeding success and territoriality

Between 1989 and 1998, we recorded the site fidelity of all marked cranes at our study area, and whether they had offspring or not. The average breeding success of six territorial families, measured as the mean number of young reared and survived to the winter, by the adult pair, was compared with that of 24 marked cranes of families foraging in flocks. This sample of gregarious individuals was made up by the 13 cranes radiotracked for time budget analysis in this study, plus another 11 radiotagged cranes not followed continuously but sighted at the study area during the 2–8 winters after being marked. Occasionally, some of these 11 pairs did not spend the whole winter at the study area.

Statistical analyses

Differences in daily home range between marked territorial and gregarious birds were tested with unpaired Student *t*-tests. Time budget and food intake-rate differences between flocking and territorial cranes were tested with nested ANOVA designs, with each patch or daily observation used as one data point within subjects. Birds were defined as a random factor, and nested in a

top category as territorial or flocking subjects. The F-ratio was calculated as the mean squares between treatments (flocking vs territorial, one degree of freedom), divided by the mean squares among subjects (degrees of freedom up to 19 subjects, see Underwood 1997). Other tests are specified in the sections of Results where they were applied. Two-tailed probability values are given for all analyses. Confidence intervals are reported as ± 1 SD.

We analyzed sex differences between males and females of territorial families using the non-parametric Wilcoxon matched pairs test as sample size did not allow use of a parametric test. Differences in average breeding success between territorial and gregarious birds were tested using the Mann–Whitney U-test (Siegel and Castellan 1988). Statistical differences between years, with and without offspring for territorial families, were first calculated for each family with a Fisher's exact test. Thereafter significance was calculated with a χ^2 test of combined probabilities with 2 k degrees of freedom, pooling the significance levels of individual Fisher's tests (k = number of individual tests; Sokal and Rohlf 1981). The significance level of multiple tests in habitat use and time budget analyses was adjusted with sequential Bonferroni correction (Rice 1989).

Results

Number of territorial families in the wintering population

During the surveys of the study area we recorded a relatively small number of families foraging isolated from other cranes (mean = 14.5 families, range 6–26, N = 12 surveys). Assuming that these families were territorial, as were the six families radiotracked (see below), territorial families represented a very small percentage (2% on average for the 12 surveys) of the total number of families present at the study area on each date (between 321 and 1566 families, when total wintering populations at the study area were, respectively, 4000 and 20000 cranes). Most isolated families were found at 1–3 km from the lagoon margins, while flocks usually dispersed to forage at much farther distances, up to 25 km from the lagoon.

Relationship between winter territoriality, site fidelity and breeding success

We recorded the winter site fidelity for the six marked territorial families during 2–8 years (Table 1). As a rule, these crane pairs were territorial only in years when they had offspring. Although the four pairs for which we have data, when they had no offspring, behaved gregariously, they were frequently seen in small flocks in the vicinities

of their territories of previous winters. Three of them even occasionally visited their territories of previous winters, without defending them (pairs A, B and E). Sometimes other families had taken part of their territories. All territorial families occupied the same territories year after year, and none was seen defending a different territory. Four occupied their territories throughout the whole winter season, whereas two (families D and F) abandoned the study area in late December in some years, and migrated southwards to spend the rest of the winter at other sites (Table 1). These data indicate that territorial behaviour was associated with the presence of offspring ($\chi^2 = 21.39$, $P < 0.05$, combined probability test using the six families), and show strong site fidelity among territorial families.

On the contrary, none of the seven families which bred successfully one or more years out of the sample of 24 marked cranes which were typically gregarious (see Methods, under 'Relationship between average breeding success and territoriality') was seen defending a winter territory in years when they had offspring.

The average breeding success was significantly higher in territorial pairs compared to gregarious pairs (respectively, 0.83 and 0.10 young per year, based on average samples of 4.6 and 3.0 years with breeding success data from the 6 territorial and 13 gregarious pairs that spent the whole winter in the study area, Mann–Whitney U test: $U = 4$, $P = 0.002$). To avoid a potentially biased sample, we skipped the first year, when all territorial pairs had offspring, and repeated the analysis. The difference was still significant ($U = 6$, $P = 0.013$; $N = 6$ territorial and 9 gregarious pairs). Including breeding success data from 1–5 winters for another 11 radiotagged gregarious pairs, some of which did not spend the whole winter at the study area in a few years, the difference between territorial and gregarious pairs was also significant ($U = 15$, $P = 0.006$, $N = 6$ and 20 respectively, skipping the first year).

Habitat use by radiotracked individuals

The mean daily home range of the six territorial families was 0.7 ± 0.8 km² (Fig. 1), much smaller than the daily home range of 13 flocking adults (11.7 ± 6.4 km², unpaired t-test: $P < 0.01$). The average distance between foraging patches used by families was smaller than in flocks (Table 2). Territorial families switched between consecutive fields walking, whereas flocks usually switched by flying. Although the mean number of different fields used per day did not differ between both groups of cranes, the home ranges of territorial families included a higher diversity of habitats than the areas visited daily by gregarious birds. All territories were close to the lagoon margins, i.e. closer to the roost than feeding sites of flocks (Table 2), including parts of

Table 1. Interannual fidelity to winter territories (T, NT: respectively, territorial and not territorial) in relation to breeding status (O, NO: respectively, with and without offspring) of the six territorial families studied. Some years these families were seen in a different wintering area (D). Empty cells mean that the family did not winter in our study area, and was not seen at other sites along the migratory route (own unpubl. data complemented with information from the European Crane Database).

Family	Number of winter seasons covered in this study since the date of capture							
	1	2	3	4	5	6	7	8
A	T, O	NT, NO	T, O					
B	T, O	T, O	NT, NO	T, O	T, O	D, NO		
C	T, O	T, O						
D	T, O	T ¹ , O						
E	T, O	NT, NO	NT, NO	NT, NO	T, O	D, NO	NT, NO	NT, NO
F	T, O	NT, NO	D, NO	T ¹ , O	T ¹ , O	NT, NO	D, NO	

¹ Territorial only during part of the winter season at the study area, left to other areas further south in December.

'cultivated marsh with mixed crops' (see Fig. 1). For example, all included a small potato or sunflower stubble (Table 3), that they used as one of their favorite feeding fields, and a water site. Territorial families frequently revisited their 1–3 favorite fields, which indicates that they did not deplete food at these sites on a single visit. Flocks did not usually revisit feeding fields on the same day, and did so only occasionally on consecutive days. Flocks rather depleted food resources at different fields as they shifted feeding sites within a main foraging zone of ca 25–50 km² during several consecutive days, and later switched to a different foraging zone of the study

area, and this pattern was repeated throughout the winter (for details see Alonso et al. 1994, 1995, 1997, Bautista et al. 1995).

Time budget and food intake rate

Adults of territorial families spent less time actively feeding (head down), almost double time vigilant, and less time flying between different feeding patches than adults in flocks (Table 4). The time spent on aggressive encounters and preening did not differ between families and flocks. However, offspring of territorial families were never involved in aggressive encounters, whereas juveniles in flocks were frequently displaced from their feeding sites by adults (see also Alonso and Alonso 1993, Alonso et al. 1997).

Adults of territorial families had not significantly lower instantaneous food intake rates than did adults in flocks after Bonferroni correction (Table 5). Territorial males ingested at a faster instantaneous rate than females, and so compensated for their higher investment in territory defense (see below). As a result, territorial males and their offspring reached the gross intake rates of adults in flocks, whereas females had slightly lower gross intake rates (Table 5).

Although territorial families left the roost marginally later than adults in flocks (respectively, 13.1 and 8.9 min after departure of the first crane, $P=0.09$), the time of arrival at the foraging areas was almost identical (respectively, 19.4 and 21.1 min after departure of the first crane, $P=0.99$), because territories were closer to the roost than foraging sites of flocks (see Table 2). Families spent 18% more time foraging per day than the adults in flocks (Table 6). This compensated for their lower gross intake rate, and so the accumulated daily food intake did not differ between the birds in families and the adults in flocks (Table 7). Even juveniles of families reached similar intake values than adults in flocks. The daily pattern of intake, however, clearly differed between territorial families and flocks. Families ingested less food in the morning and more in the

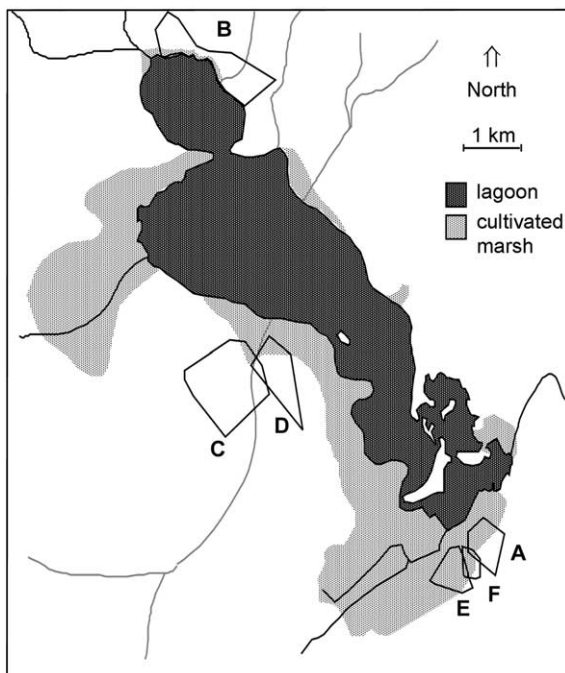


Fig. 1. Map of the study area showing the territories of the six families radiotracked. The cultivated marsh includes farmland mixed with a high proportion of pastureland and other minor crops. The territories are the minimum convex polygons calculated with 90% locations. Territory of family B was not convex because the lagoon on the south and the town of Gallocanta on the north limited it.

Table 2. Differences in home range parameters between territorial families and flocks. Values are daily means of radiotracked cranes (6 territorial families, 13 adults in flocks).

	Families	Flocks	F _{1,17}	P
No. of habitat types used	4.1 ± 1.0	3.0 ± 0.5	9.42	0.007 ¹
Diversity (Shannon's H')	1.2 ± 0.2	0.9 ± 0.2	8.71	0.009 ¹
No. of different fields used	6.7 ± 1.9	6.6 ± 1.9	0.03	0.866 ¹
Maximum no. of fields	9.7 ± 3.6	7.0 ± 2.1	4.98	0.039 ¹
No. visits to the favorite field	2.6 ± 1.0	1.3 ± 0.3	17.91	0.001
Distance between consecutive patches (km)	0.6 ± 0.2	2.6 ± 1.3	34.44	<0.001
Distance to roost (km)	2.2 ± 0.9	9.3 ± 3.6	17.07	0.001

¹ Significant P-values after sequential Bonferroni correction (Rice 1989) for these related variables are shown in bold.

afternoon than did flocking adults ($P < 0.01$, ANOVA test of the interaction between time of day, morning and afternoon, and behaviour, territorial families and flocks, see Table 7). Since water sources were scarce in our study area, flocks always had to fly relatively long distances at midday to drink and preen. Furthermore, most cranes usually gathered at the 1–2 largest drinking sites of the study area, which they used as secondary roosts during almost 2 h. In contrast, territories always included smaller streams or ponds that were exclusively used by the territory owners. The midday pause at drinking sites was longer in flocks than in families (Table 3).

Sex differences in territorial families

Males and females of territorial families did not differ in their time budget at foraging patches. Sex differences in time spent feeding, alert, and preening were not significant (ANOVA tests: respectively, $P = 0.84$, $P = 0.97$, and $P = 0.22$). However, accumulated daily food intake was higher in males than in females (Table 7; $F_{5,33} = 19.6$, $P < 0.001$ for the daily total).

Territorial males spent more time than females defending the territory from intruders. In all territorial families studied, males expelled intruders from the

territory or its surroundings with much higher frequency than females (1.64 attacks to intruders per day in males, 0.67 in females; $N = 6$ families; Wilcoxon matched pairs test: $T = 0$, $P = 0.05$). Most attacks occurred at territory borders between neighbor families. Thus the number of attacks launched by territorial families was not different from those received from neighbors ($T = 1$, $P > 0.05$). Intruders never repelled these attacks. Young cranes of territorial families were closer to their mother than to their father (respectively, 3.1 ± 1.6 SD, and 4.6 ± 3.2 SD body-lengths, $N = 6$ families; $T = 0$, $P = 0.05$).

Discussion

Characteristics of winter territories

We showed that territories were small, but included a higher variety of substrates than home ranges of flocking adults. All territories contained a water site, and a small potato or sunflower field, which families revisited daily as one of their favorite feeding grounds. In contrast, cranes foraging in flocks did not usually revisit feeding fields on the same day. Flocks foraged on a field until their average feeding rate decreased below that needed to meet daily energy requirements, and then switched to

Table 3. Differences in habitat selection between territorial families and flocks. Results are mean percentages of time spent on each habitat by radiotracked cranes (6 territorial families, 13 adults in flocks). In sown cereal fields all seeds were buried, whereas in recently sown cereal a variable number of seeds were on the surface.

	Families	Flocks	t	P ¹
Sown cereal	49.3	53.5	-0.48	0.640
Cereal stubble	8.8	12.5	-0.54	0.600
Drinking sites	6.7	13.7	-2.30	0.034
Pasture	9.6	4.6	1.79	0.092
Sown cereal with seeds on surface	1.3	7.9	-2.07	0.054
Sprouted cereal	5.8	1.8	1.65	0.118
Track borders	7.6	0.0	2.85	0.011
Ploughed sunflower field	4.1	0.0	1.53	0.146
Maize stubble	0.0	3.8	-1.16	0.263
Sunflower stubble	2.8	0.2	1.59	0.131
Potatoes	2.1	0.0	3.52	0.003
Sugarbeet	0.5	0.8	-0.29	0.775
Ploughed cereal field	0.7	0.3	0.84	0.414
Sunflower	0.8	0.0	1.53	0.146
Other crops	0.0	0.7	-1.30	0.211
Fallow land	0.0	0.2	-0.76	0.456

¹ Significant P-values after sequential Bonferroni correction (Rice 1989) at the tablewide level are shown in bold.

Table 4. Differences in time budget at foraging patches between adults of territorial families and adults in flocks. Results of nested ANOVA analyses of foraging patches of 6 territorial families vs 13 adults in flocks. Values are means \pm SD. Sample sizes changed for each variable considered (range 764–1212 foraging patches).

	Families	Flocks	F _{1,17}	P ¹
Time feeding (seconds head down per min)	41.9 \pm 2.6	47.7 \pm 4.1	10.51	0.005
Time alert (seconds head up per min)	15.8 \pm 2.8	8.8 \pm 3.2	19.23	<0.001
Time preening (seconds per min)	2.1 \pm 1.2	1.8 \pm 2.5	0.71	0.412
Time fighting (seconds per min)	0.07 \pm 0.08	0.15 \pm 0.12	2.15	0.161
No. vigilance bouts per min	1.8 \pm 0.3	1.0 \pm 0.2	30.28	<0.001
No. steps per min	12.8 \pm 4.2	12.1 \pm 2.9	0.15	0.706
Time flying between patches (min)	0.9 \pm 0.5	5.1 \pm 2.0	39.49	<0.001

¹ Significant P-values after sequential Bonferroni correction (Rice 1989) at the tablewide level are shown in bold.

another field, depleting more or less uniformly all foraging zones found in the study area (see Alonso et al. 1995). As for the pattern of daily food intake, cranes in flocks ingested most of their daily food intake during the morning, whereas territorial families ingested similar quantities during morning and afternoon, in a manner consistent with the predictability and defendability of their food resources. These differences between territorial and gregarious cranes suggest that winter territories fulfilled the main requisites of economic territory defendability, namely the predictability and spatial concentration of food resources (Brown 1964, Brown and Orians 1970, see our first prediction in introduction).

However, the extent of land showing these characteristics, small and varied fields, and abundant drinkable water sites, is practically reduced in our study area to a strip of land of ca 2 km around the lagoon, because the rest of the area is intensively cultivated (Fig. 1, and Alonso et al. 1984, 1987b). This could explain why only 2% of the families present were territorial, and why most territories were found at 1–2 km from the lagoon, whereas flocks foraged at up to 25 km from it. Agricultural intensification has favored the increased staging and wintering of cranes at Gallocanta (Bautista et al. 1992, Alonso et al. 1994), but some effects of this new farming system, like the decrease in habitat diversity, increase in average field size, and suppression of small streams and ponds, may make it difficult to find

defendable territories. The small percentage of families foraging isolated in our study area (13% of 934 flocks, Alonso et al. 1987a, Alonso and Alonso 1992), contrasted with that observed in holm-oak habitat in southwestern Spain (44% of 822 flocks, Avilés 1999), where habitat diversity is much higher and the farming system is extensive and still traditional (Alonso and Alonso 1990, Díaz et al. 1996, Avilés 1999). We suggest that recent agricultural intensification in Gallocanta has favored the gregarious behaviour of cranes, probably setting an ecological constraint to winter territoriality. Similar increases favored by agricultural resources have occurred during the last decade at some staging areas in France (Génard et al. 1992, Salvi et al. 1996, Avignon and Loubeyres 2003, Le Roy and Moinnet 2003).

Finally, the fact that new families occupied the territories that were left vacant by pairs that had defended them in previous winters, suggests that the amount of appropriate habitat was a limiting factor in Gallocanta. In other crane species, some pairs failed to establish winter territories and joined subadult birds as the number of cranes increased in the wintering area. Also, the average territory size became smaller as more pairs established their territories. The authors concluded that intraspecific aggressive interactions limited the size and the number of territories (Stehn and Johnson 1987, Eguchi et al. 1991). Removal experiments have also shown intense competition for winter territories in

Table 5. Differences in instantaneous and gross intake rates at foraging patches between cranes in territorial families and flocks. Results of nested ANOVA analyses of cranes of 6 families vs 13 adults in flocks. Instantaneous and gross intake rates are defined as grams per minute feeding, i.e. head down, and per minute on foraging patches, respectively.

	Mean \pm SD	Difference with respect to adults in flocks [†]	
		F _{1,17}	P ¹
Instantaneous intake rate:	0.52 \pm 0.26 [†]		
Adult males in families	0.57 \pm 0.25	0.13	0.720
Adult females in families	0.41 \pm 0.17	0.80	0.383
Juveniles in families	0.43 \pm 0.10		
Gross intake rate:	0.39 \pm 0.13 [†]		
Adult males in families	0.36 \pm 0.13	0.30	0.589
Adult females in families	0.28 \pm 0.11	3.08	0.097
Juveniles in families	0.34 \pm 0.09		

¹ There were no significant P-values after Bonferroni correction (Rice 1989).

Table 6. Daily foraging timetable (mean \pm SD in minutes) of adults in territorial families and adults in flocks. Differences in foraging time were tested with nested ANOVA analyses. The mean number of days used in the analyses was 131 (range 90–160 days).

	Families	Flocks	F(df)	P ¹
Flying between roost and foraging area	8 \pm 6	35 \pm 9	24.42 (1,13)	<0.001
Time foraging during the day	529 \pm 24	450 \pm 44	7.70 (1,13)	0.016
Time at drinking sites at midday	52 \pm 20	102 \pm 58	2.06 (1,13)	0.175
Time at pre-roosting sites	7 \pm 8	12 \pm 12	1.32 (1,14)	0.252

¹ Significant P-values after sequential Bonferroni correction (Rice 1989) at the tablewide level are shown in bold.

several passerine species (Brown 1969, Smith 1978, Stutchbury 1994).

Costs and benefits of winter territoriality

A major benefit of territories is that they offer the opportunity to administrate food resources in a predictable way (Davies and Houston 1984). Since food resources of cranes wintering in our study area (stubble or sown fields) are not renewable, it may pay defending enough resources to ensure survival throughout the winter season. For example, in some species it has been shown that birds unable to obtain winter territories suffer higher mortality through starvation than territory owners (Winker et al. 1990, Johnson et al. 2001). Territorial cranes also benefited from lower energy expenditure due to the shorter distance between their feeding sites and the roost (see Terrill 1990). Gregarious cranes may compensate for these advantages of territories by foraging benefits derived from flocking, such as intake rate maximization and starvation risk minimization mechanisms (see details in Alonso et al. 1995, 1997, Bautista et al. 1998). Our results showed that territorial adults spent more time vigilant between feeding bouts, and needed more time to actively forage during the day to fulfill their daily energy requirements. They achieved this by reducing the time spent resting at midday roosts,

and starting the afternoon foraging period earlier. As a result, even their offspring reached similar daily food intakes as gregarious adults. Adult females, however, could not reach the total daily food intake as that of their mates. Although they were smaller than males (own unpubl. data), we do not think the sex difference in food intake corresponds entirely to the size difference. We believe that the lower intake may reflect a maternal care cost related to their higher investment in the raising of offspring as compared to fathers. Indeed, mothers frequently showed their offspring where and how to feed, shared the food they found with them, and sometimes even fed them directly. We think the higher proximity of the offspring to the mother may reflect such a maternal care cost. Adult males, in contrast, invested more time and energy in territory defense.

In an earlier study with non-marked birds we have shown that the instantaneous intake rate of juveniles, included in flocks, decreased due to interference from flock mates, resulting in lower gross intake rates than their parents (Alonso and Alonso 1993). We concluded that flocking was disadvantageous for them, while it did not affect the parents in terms of gross food intake. In that study, we were not able to calculate total daily food intake, since cranes were not individually marked and we could not follow them throughout the whole day. However, gregarious juveniles were surely not able to reach the total food intake of territorial juveniles, since

Table 7. Differences in total daily food intake (mean \pm SD in g) between territorial families and adults in flocks. Results of nested ANOVA analyses of six families vs 13 adults in flocks (total number of days = 137).

	Food intake	Difference with respect to adults in flocks [†]	
		F _{1,17}	P ¹
Daily total:	189 \pm 45 [†]		
Adult males in families	182 \pm 55	0.52	0.482
Adult females in families	153 \pm 45	1.37	0.258
Juveniles in families	176 \pm 39		
Morning:	125 \pm 44 [†]		
Adult males in families	86 \pm 37	4.89	0.041
Adult females in families	76 \pm 30	6.82	0.018
Juveniles in families	89 \pm 40		
Afternoon:	62 \pm 24 [†]		
Adult males in families	96 \pm 31	3.61	0.075
Adult females in families	77 \pm 20	2.11	0.165
Juveniles in families	87 \pm 14		

[†] The significance of the P-values in morning food intake of males and females in families compared to adults in flocks disappeared after sequential Bonferroni correction (Rice 1989) at the tablewide level.

they were included in flocks that devoted less time per day to foraging than did territorial cranes. Indeed, in the present study, territorial adults compensated for the time spent on vigilance and territory defense, with a longer total time devoted to feeding per day.

Apart from food intake, other short- and long-term costs and benefits that are more difficult to quantify should also be considered when comparing the two strategies. For example, those related to obtaining some kind of site-related advantage, or maintaining pair bonds across seasons (Matthysen 1993). Some results suggest that the main long-term benefit of territoriality might indeed be related to winter site philopatry. We observed that pairs that were territorial when they had offspring did not defend their territory in years when they had no offspring. Winter territoriality is probably a facultative behavioural strategy that is costly for the parents, but brings some benefit to the offspring. However, some territorial pairs did not completely shift to gregarious behaviour, even when they had no dependent young. Pairs A, B and E were frequently sighted in small flocks close to their territories in winters in which they had no offspring, and they even visited their territories occasionally. Although they did not defend them, monitoring their winter territories from previous years probably rendered some long-term benefit. An exception was pair F, whose adults were seen separated from each other and integrated in large flocks, up to 10 km away from the territory, one year after defending their territory. Possibly these pairs broke up their pair bond. The suppression of winter territory philopatry due to a change of mate, and the prevalence of the new mate's site has been recorded in geese and swans (Raveling 1979, Rees 1987). Finally, during our habitat transects we saw only eighteen pairs without offspring. We suggest that these pairs were visiting their territories like pairs A, B and E (see above). In the two other crane species in which winter territorial behaviour has been described, it has also been interpreted as being advantageous for rearing juveniles (Tacha 1988, Eguchi et al. 1991). However, these studies lack a detailed comparison of costs and benefits of territorial vs gregarious strategies.

As for the short-term advantages of territoriality, we could identify one benefit and one cost that are not directly related to food intake. The benefit was that the offspring of territorial pairs were never involved in aggressive behaviour with other cranes, and thus ran no risk of being injured, whereas offspring of families included in flocks were often victims of such attacks, and the attack frequency increased with flock size (Alonso and Alonso 1993, Alonso et al. 1995, 1997). The most evident cost of territorial behaviour is a higher predation risk, whereas shared vigilance and the dilution effect in the flock are two major advantages of flocking (Pulliam

and Caraco 1984). However, the only natural predators of cranes in our study area are currently golden eagles *Aquila chrysaetos*, which are relatively scarce (Muñoz-Pulido et al. 1992).

Conclusion

In summary, the costs of territorial behaviour (longer foraging time, higher vigilance rate) were apparently compensated by the benefits that accrued to territorial adults and their offspring (familiarity with food resources in their territories, predictability of these resources, and shorter time spent flying). Combining the results of the present study with those of a previous one on non-marked birds (Alonso and Alonso 1993), we conclude that while territoriality is beneficial to the offspring, it may incur costs to the parents, in terms of time invested in vigilance, territory defense, and additional foraging to satisfy the daily food requirements. However, territorial adults were able to obtain the same daily food intake as flocking adults.

We hypothesize that since territories benefit offspring, many pairs may try to become territorial, but as the territorial strategy is more costly for the parents than flocking in terms of anti-predator vigilance, territorial defense, and daily foraging time, only experienced or more dominant pairs probably can afford it. This hypothesis is supported by the higher average breeding success observed in pairs that were able to defend territories as compared to pairs that were always gregarious.

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