How do vigilance and feeding by common cranes *Grus grus* depend on age, habitat, and flock size?

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Animals often spend less time vigilant and more time feeding when foraging in larger groups. This group-size effect does not, however, consider if larger groups differ systematically from smaller ones: Large groups could form in different habitats than small groups or be composed of a different mix of ages or classes than small groups. We examined how habitat differences and flock size and composition explain feeding and vigilance rates in common cranes *Grus grus*, wintering in holm oak *Quercus ilex* dehesas of Spain. Flock size and composition were related to habitat type in cranes: flocks formed in areas sown with cereal crops were larger than flocks formed in set aside areas. Vigilance rate depended on habitat but decreased with increasing flock size in a similar way across all habitats. Juveniles were less vigilant than adults and showed little change in vigilance with flock size. Vigilance increased and feeding time decreased over months from November through February. Our results show that vigilance is affected by habitat but that the group size effect on vigilance is not the product of differences between habitats in group size or composition.

Living in groups can help individuals to find food and avoid predators (Krause and Ruxton 2002). Numerous studies have documented that feeding rates increase and vigilance rates decrease in larger groups (Elgar 1989, Robert 1996, Beauchamp 1998, Lima 1998, Treves 2000). This correlation of group size with higher feeding and lower vigilance rates, however, fails to consider if larger groups differ systematically from smaller ones. Larger groups might, for example, form in areas of higher food concentration or lesser danger (Elgar 1989). This long-standing suggestion can be tested by measuring the feeding conditions where large and small groups form. Larger groups might also differ in composition. Not all members of groups are the same – they may even be members of different species (Randler 2004a,b). Even within one species, vigilance may differ based on age, sex, or dominance (Elgar 1989). These differences could affect the group size effect because the reduction in vigilance with group size is based on how group members share risk of attack and information about potential attacks (Bednekoff and Lima 1998). In particular, we might expect juveniles to

contribute less to the group size effect than adults. Juveniles are often less vigilant than adults, perhaps because they have greater foraging needs (Arenz and Leger 2000). Less vigilant individuals are less likely to detect attacks and therefore less likely to share information about potential attacks. Juveniles may also be less proficient at distinguishing real threats and reacting appropriately (Cheney and Seyfarth 1990), making any alarm information they do share less reliable. For these reasons, we predict that juveniles contribute less to the group size effect than do adults.

Common cranes *Grus grus* provide an opportunity to compare how age and habitat differences affect the group size effect. Cranes forage in flocks composed of adults and juveniles during winter (e.g. Alonso et al. 2004), which has allowed to explore the effects of competitor density on the level of interference among individuals in homogeneous cereal fields of the north of Spain (Stillman et al. 2002). In the crane-cereal system, Alonso and Alonso (1993) have previously shown that vigilance effort of juveniles was lower than that of adults and that parental vigilance effort was higher in family

group than in flocks. Previous research has shown that intake rates are twice as high in wooded pasturelands (dehesas) without livestock compared to dehesas with livestock (Avilés 2003). Previous studies suggest that habitat characteristics affect intake rate, flock size, and flock composition in the dehesas but have not, however, explored how variation in flock composition may affect the relationship between flock size and vigilance and how variations in habitat quality may affect the strength of the relationship between vigilance and flock size. The question is whether group size affects feeding and vigilance rates also, beyond the direct effects of habitat. We set out first to document flock size and composition in common cranes in different habitats. Having done this, we ask whether habitat differences explain feeding and vigilance by cranes, or whether they are better accounted for by flock size and composition directly.

Methods

Study system

Common cranes are a migratory Palearctic species with a wide distributional range. Cranes that use the western migratory route breed in northern latitudes and winter in North Africa, the Iberian Peninsula, and France (Sánchez et al. 1998). About 67.0% of western migratory birds winter in central and southern Iberia where wooded dehesas are the main system of land use (Sánchez et al. 1998, Avilés et al. 2002a). Wooded dehesas (hereafter dehesas) are wooded pasturelands dominated by holm *Quercus ilex* and cork *Quercus suber* oaks, with an understorey of open grassland, cereal crops or Mediterranean scrub, and with a typical savanna appearance (Díaz et al. 1997). Most cranes arrive from their breeding areas in northern latitudes in November and remain in the dehesas until the end of February. Cranes gather in flocks and feed mainly on holm oak acorns obtained under the canopy of the holm oak trees (Avilés et al. 2002b). Main natural crane predators in the dehesas of Iberia are golden eagles *Aquila chrysaetos* and Bonelli's eagles *Hieraaetus fasciatus* (Avilés et al. 1998).

Study area

Data were collected from November 1994 to February 1995 in the Serena region, southwest Spain (39° 03′N, 5° 14′W). The study area covers 74,334 hectares and the winter population reaches a peak number around 17,000 birds in December (Avilés 2004). The Serena is included in the mediterranean climate region characterized by hot and dry summers and mild, wet winters, with frequent freezing days from December to February. Heavy rainfall during winter may knock acorns to the ground, making them available to cranes (Avilés et al. 2002). However, rainfall during the study year was within the normal range in the study area. Cranes have visited the Serena region since the early 20th century (reviewed in Pérez-Chiscano and Fernández-Cruz 1971), and they feed in dehesas situated in the basin of the Zújar River and roost alongside the river (for detailed description of the study area, see Sánchez et al. 1993, Avilés 2004).

Human management of dehesas leads to patches that differ in their structure and productivity and these patches may affect crane distribution (Díaz et al. 1997). In particular, farmers utilize a three-year rotation of cereal in the Serena (Avilés 2004). Cultivation is carried out 1 year, followed by a 2-year set-aside. The set-aside years are used to provide grazing and acorns for livestock (mainly sheep and cow). Therefore, the study area is characterized by a mosaic of patches of sown with cereal, stubble of cereal (1 year set-aside) and "posíos" (2-years set-aside).

Data collection

We spent five days a week collecting data (i.e. 86 d) throughout the day from when cranes flew from roost until they returned. Flocks were located during regular circuits by car. Each circuit was conducted once per week to avoid temporal dependence among the activities of cranes. Observations were made throughout the day in all the flocks that were located during the regular circuits by car. We avoided, however, time budget recording at midday because cranes typically rest and preen at this time in their winter quarters (Alonso and Alonso 1992, Avilés 1999). For each flock we recorded the number of adult and of first-winter (hereafter juveniles) cranes. Juvenile cranes are easily identifiable on the basis of their chestnut head and neck color (Alonso and Alonso 1993).

Acorn abundance on the ground is negatively correlated with livestock numbers (Díaz et al. 1996, Avilés et al. 2002b), and crane numbers are influenced by acorn abundance (Díaz et al. 1996), hence crane distribution is indirectly determined by livestock presence in the dehesas. Therefore, for each flock we recorded the ground cover classified on the basis of livestock presence as: (1) dehesas sown with cereal in which livestock are absent and do not feed on acorns and cranes can freely access them, and (2) dehesas with cereal stubble and posíos (set aside) in which livestock feed on acorns from early autumn to late spring (Avilés 2003, 2004). Because acorn availability declines throughout winter differently in sown with cereal and set aside areas (Avilés et al. 2002b) we also considered the study month (from November to February) in which observations were made. Finally, we recorded

whether flocks were under or outside the canopy of the holm oaks because vigilance and feeding rates may vary when predation is less likely, for example, when animals are closer to protective cover (e.g. Elgar 1989).

For time budget observations, cranes were randomly selected within flocks in a number proportional to flock size. Focal cranes were observed for three minutes each with a 20–60 × 60 telescope. Time spent feeding (head down below shoulders), and vigilant (head up over shoulders) were measured to the nearest second. We sampled 485 different individuals although for some flocks we could not record time budget for adults and juveniles due to movements of flocks. The number of sampled flocks was 327 and the average (range) number of adults per flock was 48.4 (1–564), while the average (range) number of juveniles per flock was 5.92 (1–50).

Statistical analyses

Data were transformed to comply with normality: flock size was log-transformed and percentages of time devoted to feeding and vigilance were arcsine-square root transformed preceding further analyses. To check for the association between flock size and composition and vigilance and feeding time we used General Linear Mixed Models (Mixed procedure in SAS, 1996) with normal error distribution. GLMMs were performed with vigilance time and feeding time as dependent variables respectively, and with individual age (adult versus juvenile), flock size, proportion of juveniles in the flock, habitat type (sown with cereal versus set-aside), study month (November to February) and holm oak presence (under or outside the holm oak canopy) as independent fixed variables. Time budget information was simultaneously gathered on adults and juveniles for most flocks (see above), therefore we entered flock identity as a random factor in the analysis to avoid pseudoreplication. Two-way interactions of fixed terms (except those for study month) were also entered in the full model because the main aim of this study was to see whether the relationship between flock size and vigilance or feeding time is stronger or weaker, depending on the habitat type. The hypothesis under evaluation hinges upon the habitat by group size interaction, which tests whether regression lines between number of cranes and vigilance or feeding are parallel for different kind of habitats. If those lines are parallel, then the relationship in the different habitat classes is the same, and thus the group size effect is not affected by the habitat type. If they are not parallel, we conclude that the habitat type does, in fact, alter the group size effect. Model selection was carried out by removing, one by one, the effects that were the furthest to statistical significance, starting with the highest-order interactions down to the main effects (Engqvist 2005).

Results

Flock size and composition in relation to habitat management of dehesas

GLMMs in which we controlled for the significant random effect of flock identity (flock identity: $Z > 11.95$, $P < 0.001$) showed that flocks were larger in areas sown with cereal crops than flocks formed in set aside areas ($F_{1,168} = 18.89$, $P < 0.001$, Fig. 1). The proportion of juveniles, however, did not vary with habitat type ($F_{1,162} = 1.58$, $P = 0.21$). In addition, flocks formed outside the canopy of the holm oaks were larger ($F_{1,168} = 4.16$, $P = 0.04$) and had a lower proportion of juveniles ($F_{1,162} = 54.24$, $P < 0.001$) than flocks formed under the canopy (Fig. 1).

Factors affecting vigilance and feeding in cranes

Vigilance decreased with overall group size and was higher for adults than for juveniles, and was further affected by an interaction of flock size with age (Table 1): vigilance decreased with flock size in adults but not in juvenile cranes (Fig. 2). Vigilance was not related to flock composition either directly or in interaction with other variables (Table 1).

The habitat type did not alter the group size effect on vigilance since vigilance was unrelated to flock size by interaction with habitat type (Table 1). The overall level of vigilance, however, depended on habitat and the presence of holm oaks (Table 1). In addition, there was a significant interactive effect of habitat by age on vigilance: adults devoted nearly twice the time to vigilance as juveniles when flocking in areas sown with cereal, while differences in vigilance between adult and juvenile decreased in set aside areas (Fig. 3). There was a significant interactive effect of habitat by holm oak presence on vigilance: in cereal areas cranes were much more vigilant outside of the canopy of holm oaks than under the canopy whereas cranes in set aside areas cranes showed similar levels of vigilance whether under or outside the canopy (Fig. 4). Finally, vigilance varied in relation to the study month and increased gradually from November to February (Table 1, Fig. 5).

Feeding was not strongly affected by flock size either directly or in combination with other variables (Table 1). There was as significant interactive effect of habitat by holm oak presence on feeding that showed a converse trend to vigilance (Table 1, Fig. 4): cranes showed a similar level of feeding when formed in flocks outside under the canopy of the holm oaks, however cranes formed outside the canopy devoted to feed less time when forming at the cereal than at the set aside areas (Fig. 4). Flock composition did not explain feeding rates directly but had effects in combination

Table 1. Determinants of vigilance and feeding time in common cranes as revealed by general linear mixed models involving flock size, composition, age (adult versus juvenile), holm oak presence (under versus outside the holm oak canopy), study month (November to February) and habitat type (sown of cereal versus set-aside dehesas) as fixed terms and flock identity as a random term. Significant effects at P < 0.05 are in bold. Independent fixed effects are ordered as they were removed (see Methods).

Dependent variable	Independent effect	Statistic
Vigilance time	Age × holm oak presence	$F_{1,148} = 0.00$, $P = 0.95$
	Composition × holm oak presence	$F_{1,149} = 0.02$, $P = 0.89$
	Flock size × habitat type	$F_{1,149} = 0.02$, $P = 0.88$
	Composition × Age	$F_{1,149} = 0.07$, $P = 0.80$
	Flock size × holm oak presence	$F_{1,150} = 0.94$, $P = 0.33$
	Flock size × composition	$F_{1,150} = 0.96$, $P = 0.33$
	Composition × habitat type	$F_{1,151} = 2.38$, $P = 0.12$
	Composition	$F_{1,152} = 0.07$, $P = 0.79$
	Month	$F_{3,159} = 11.15$, $P < 0.001$*
	Flock size	$F_{1,159} = 4.51$, $P = 0.03$*
	Age	$F_{1,159} = 14.98$, $P < 0.001$*
	Holm oak presence	$F_{1,159} = 5.89$, $P = 0.01$*
	Habitat type	$F_{1,159} = 4.58$, $P = 0.03$*
	Flock size × age	$F_{1,159} = 5.22$, $P = 0.02$*
	Habitat type × age	$F_{1,159} = 5.88$, $P = 0.02$*
	Habitat type × holm oak presence	$F_{1,159} = 4.10$, $P = 0.04$*
	Flock identity	$Z = 3.99$, $P < 0.001$*
Feeding time	Flock size × habitat type	$F_{1,148} = 0.28$, $P = 0.60$
	Flock size × composition	$F_{1,148} = 0.30$, $P = 0.58$
	Age × holm oak presence	$F_{1,149} = 0.43$, $P = 0.51$
	Flock size × age	$F_{1,150} = 0.60$, $P = 0.44$
	Composition × holm oak presence	$F_{1,151} = 0.70$, $P = 0.42$
	Flock size × holm oak presence	$F_{1,151} = 0.71$, $P = 0.40$
	Habitat type × age	$F_{1,151} = 2.07$, $P = 0.15$
	Flock size	$F_{1,152} = 1.22$, $P = 0.27$
	Month	$F_{3,153} = 8.64$, $P < 0.001$*
	Composition	$F_{1,153} = 0.03$, $P = 0.86$*
	Age	$F_{1,153} = 4.92$, $P = 0.03$*
	Holm oak presence	$F_{1,153} = 0.15$, $P = 0.69$*
	Habitat type	$F_{1,153} = 5.86$, $P = 0.01$*
	Composition × age	$F_{1,153} = 3.77$, $P = 0.05$*
	Composition × habitat type	$F_{1,153} = 4.27$, $P = 0.04$*
	Habitat type × holm oak presence	$F_{1,153} = 4.32$, $P = 0.04$*
	Flock identity	$Z = 4.68$, $P < 0.001$*

* Variable included in the definitive model.

with age and habitat. Finally, feeding rates were affected by age and habitat (Table 1) and varied with month and showed the converse monthly pattern to vigilance from November to January, although in February feeding showed a minimal increase (Table 1, Fig. 5).

Discussion

We found that crane flocks differed systematically with habitat type during the winter. Flock size was larger on dehesas sown with cereal (where livestock do not feed on acorns) than on set aside areas (where the livestock access freely to acorns) and flocks were also larger and contained a lower proportion of juveniles outside of the canopy of holm oaks (Fig. 1). The decline in vigilance with group size, however, was not a by-product of these differences between habitats in flock size and composition.

We duplicated the finding that adult cranes were more vigilant than juveniles (Alonso and Alonso 1993, Avilés 2003). Juveniles may be less vigilant than adults because they have higher feeding requirements during development (Arenz and Leger 2000). Although the diversity of the overall winter diet in the dehesas is similar among juvenile and adult cranes, juveniles consume relatively fewer acorns and more cereal grains than their parents (Avilés et al. 2002b). Differences in the diet between adult and juvenile cranes may reflect age-differences in feeding requirements, but also could indicate non-proficiency of juveniles. Acorns require greater handling efforts than do cereal grains, however handling time of juveniles cranes exclusively feeding on acorns does not increase throughout winter (Avilés et al. 2002b).

In a novel finding, vigilance declined with group size for adult cranes but not for juveniles (Fig. 2). This may
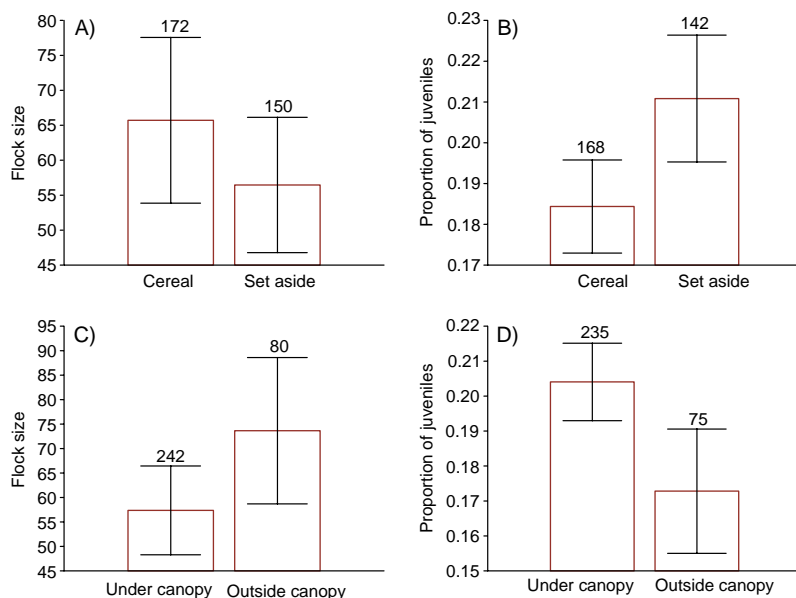
Fig. 1. Flock size and composition (mean $\pm$ SE) in relation to habitat type (A, B; sown of cereal, set aside), and holm oak presence (C, D; outside the canopy, under the canopy). Shown values are untransformed, although statistical analysis was based on log-transformed flock size and arcsine transformed percentage of juveniles, respectively.

be a by-product of higher feeding requirements for juveniles, so that they feed at high rates in both large and small flocks. Alternatively, juveniles are likely less proficient at detecting real threats, simply because juveniles have not previously experienced the threats they will face in the dehesas. Indeed the golden eagle

and Bonelli's eagle, which are the most common natural predators in dehesas of Spain during the winter (Avilés et al. 1998), are absent of crane breeding areas in north of Europe and therefore unfamiliar to juveniles. Juveniles generally forage with their parents and may rely on their parents to detect predators. Finally, large
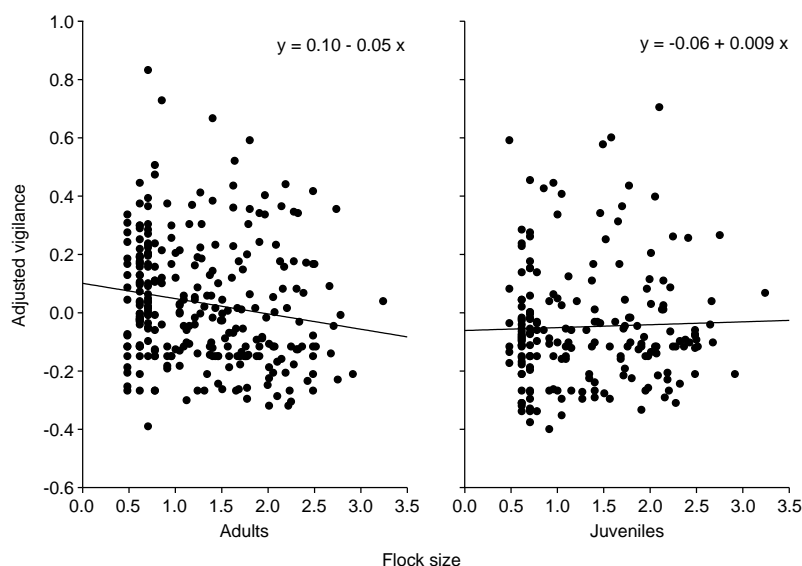

Fig. 2. Relationship between adjusted vigilance and log-transformed flock size according to age (adults versus juveniles). The y-axis represents the residuals from the general linear mixed model performed controlling for the effect of study month as a fixed term and flock identity as a random factor on vigilance. The solid line corresponds to the fit estimated from the univariate relationship between log-transformed flock size and adjusted vigilance estimated for each age class.
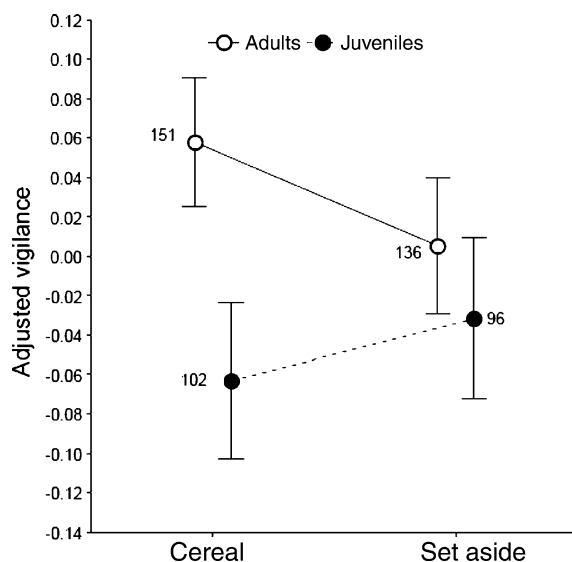
Fig. 3. Adjusted vigilance (mean ± SE) in relation to habitat type (sown with cereal, set aside) and age (adults versus juveniles). The y-axis represents the residuals from the general linear mixed model performed controlling for the effect of study month and flock size as a fixed terms and flock identity as a random factor on arcsine-square root transformed vigilance.

flocks feeding on acorns have high levels of aggressive interactions (Avilés 2003) that may be more costly to juveniles than to adults. We cannot discriminate among the possible mechanisms for explaining age-related differences in the effects of group size in cranes.

Previous research found that acorn availability changes throughout winter differently in dehesas with and without livestock (Díaz et al. 1996, Avilés et al. 2002b). Acorns are depleted where livestock are present (i.e. set aside areas) and their availability is very low and unpredictable compared to that in dehesas without livestock (i.e. those sown with cereal; Avilés et al. 2002b). Cranes could, therefore, feed more continuously in areas of high acorn availability and flocks increase their size by local enhancement (Fig. 1). Because feeding and vigilance are mutually exclusive behaviors in common cranes (Avilés 2003), local enhancement due to acorn availability may, at least theoretically (Elgar 1989), have lead to a relationship between vigilance and flock size. On the other hand, the effect of acorn availability on feeding would be presumably lower at the set aside areas where acorn availability is low. Our results, however, do not support an effect of habitat on the relationship between vigilance and flock size (Table 1).

The habitat type affected differently the time that adult and juvenile cranes devoted to vigilance (Table 1); adult cranes were more vigilant when formed in flocks in dehesas sown with cereal than adult cranes flocking
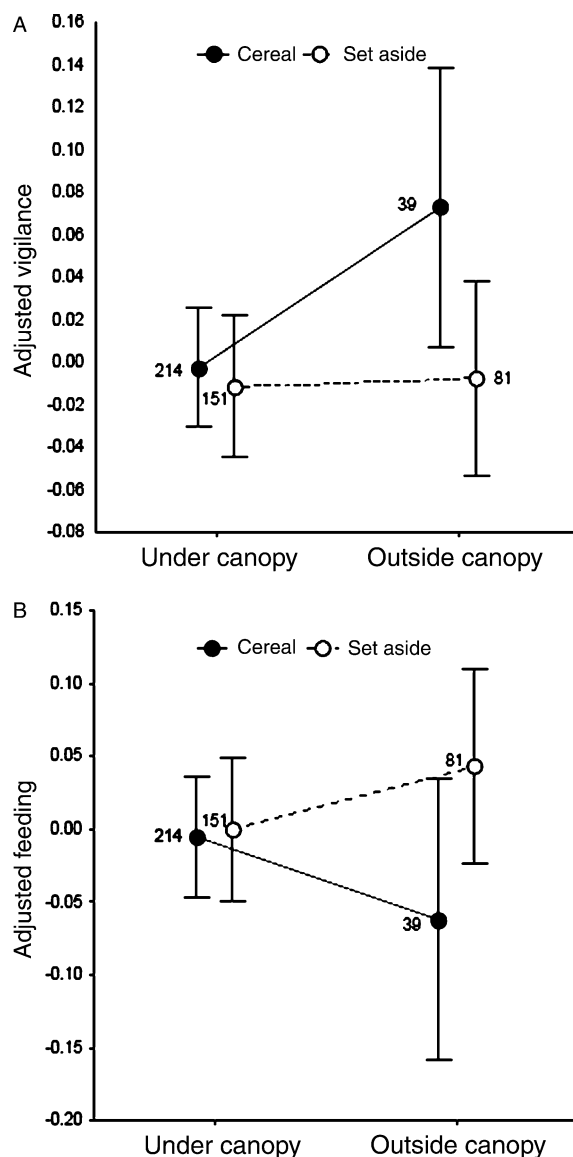

Fig. 4. Adjusted vigilance (A) and feeding (B; mean ± SE) in relation to habitat type (sown with cereal, set aside) and holm oak presence age (under the canopy vs outside the canopy). The y-axis represents the residuals from the general linear mixed model performed controlling for the effect of study month and flock size as a fixed terms and flock identity as a random factor on arcsine-square root transformed vigilance and feeding respectively.

in set aside areas (Fig. 3). This result may reflect the twofold function of vigilance in prevention of attacks by aerial predators and of aggressive encounters with other individuals. Flocks are larger in cereal fields (Fig. 1) where adults are exposed to a higher level of encounters (Avilés 2003). We also detected an interactive effect of the presence of protective cover and habitat type on
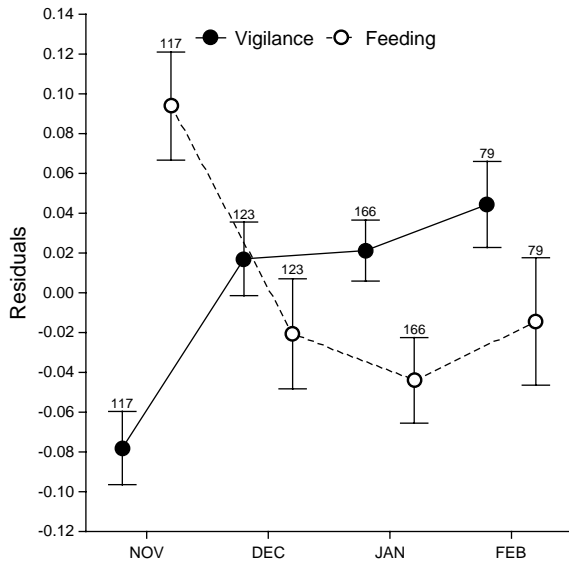
Fig. 5. Adjusted vigilance and feeding (mean ± SE) in relation to study month. The y-axis represents the residuals from the general linear mixed model performed controlling for the effect of flock identity as a random factor on arcsine-square root transformed vigilance and feeding respectively.

vigilance and feeding (Table 1). This effect was due to cranes grouped in cereal fields and outside the holm oak canopy being more vigilant. Perhaps when cranes feed far from protective covers and at high densities (i.e. cereal fields, Fig. 1) vigilance may serve to avoid predators but also to avoid intra-specific aggressions. A possible role of vigilance in avoiding aggressive interactions is supported by the absence of differences in vigilance between cranes grouped under and outside the canopy at the set aside areas (Fig. 4).

Time devoted to vigilance increased and to feeding decreased throughout winter in the dehesas (Fig. 5). Monthly patterns of activity in the dehesas paralleled previous findings in the crane-cereal system in the north of Spain (Alonso and Alonso 1993). Autumn migration imposes severe costs to long distance migratory birds, and changes in body mass and composition have been reported in birds at arrival to their wintering quarters (Jenni and Jenni-Eiermann 1998, Battley et al. 2001). Thus, the high feeding rate in autumn could reflect the need of recuperate the energy spent during the migration.

Elgar (1989) emphasized that because of the lack of adequate control on possible confounding variables most of the field studies with social birds and mammals fail to demonstrate an unambiguous negative relationship between vigilance behavior and flock size. Here we found that the relationship between group size and vigilance in social wintering common cranes did not vary with habitat type and flock composition. Future

field studies aiming to address how vigilance behavior covaries with group size should at least statistically control for the effect of habitat and age to ensure that individual in the groups alter their scanning rates as a direct consequence of changes in flock size.

References

Alonso, J. C. and Alonso, J. A. 1992. Daily activity and intake rate patterns of wintering common cranes *Grus grus*. – Ardea 80: 343–351.

Alonso, J. A. and Alonso, J. C. 1993. Age-related differences in time budgets and parental care in wintering common cranes *Grus grus*. – Auk 110: 78–88.

Alonso, J. C., Bautista, L. M. and Alonso, J. A. 2004. Family-based territoriality vs flocking in wintering common cranes *Grus grus*. – J. Avian Biol. 35: 434–444.

Arenz, C. L. and Leger, D. W. 2000. Antipredator vigilance of juvenile and adult thirteen-lined ground squirrels and the role of nutritional need. – Anim. Behav. 59: 535–541.

Avilés, J. M. 1999. Dieta y patrones de actividad de la grulla común *Grus grus* en dehesas del centro de la Península Ibérica. – PhD. Thesis, Universidad de Extremadura, Badajoz, 131 pp.

Avilés, J. M. 2003. Time budget and habitat use of the common crane wintering in dehesas of southwestern Spain. – Can. J. Zool. 81: 1233–1238.

Avilés, J. M. 2004. Common cranes G*rus grus* and habitat management in holm oak dehesas of Spain. – Biodivers. Conserv. 13: 2015–2025.

Avilés, J. M., Sánchez, J. M. and Medina, F. J. 1998. Response of the crane *Grus grus* to potential predators in traditional wintering areas. – Vogelwarte 39: 202–203.

Avilés, J. M., Medina, F. J., Sánchez, J. M. and Parejo, D. 2002a. Does temporal variability of winter common cranes in the dehesas depend on farming practices? – Waterbirds 25: 86–92.

Avilés, J. M., Sánchez, J. M. and Parejo, D. 2002b. Food selection of wintering common cranes (*Grus grus*) in holm oak (*Quercus ilex*) dehesas of Southwest of Spain in a rainy season. – J. Zool. 256: 71–79.

Battley, P. F., Dekinga, A., Dietz, M. W., Piersma, T., Tang, S. and Hulsman, K. 2001. Basal metabolic rate declines during long-distance migratory flight in great knots. – Condor 103: 838–845.

Bednekoff, P. A. and Lima, S. L. 1998. Re-examining safety in numbers: interactions between risk dilution and

collective detection depend upon predator targeting behaviour. – Proc. R. Soc. B 265: 2021–2026.

Beauchamp, G. 1998. The effect of group size on mean food intake rate in birds. – Biol. Rev. 73: 449–472.

Cheney, D. and Seyfarth, R. 1990. Attending to behavior versus attending to knowledge: examining monkeys attribution of mental status. – Anim. Behav. 40: 742–753.

Díaz, M., Campos, P. and Pulido, F. 1997. The Spanish dehesas: a diversity in landuse and wildlife. – In: Pain, D. J. and Pienkowski, M. W (eds). Farming and birds in Europe: the common agricultural policy and its implications for bird conservation. Academic Press, London.

Díaz, M., González, E., Muñoz-Pulido, R. and Naveso, M. A. 1996. Habitat selection patterns of common cranes *Grus grus* wintering in holm oak *Quercus ilex* dehesas of central Spain: effect of human management. – Biol. Conserv. 75: 119–123.

Elgar, M. A. 1989. Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. – Biol. Rev. 64: 13–33.

Engqvist, L. 2005. The mistreatment of covariate interaction terms in linear model analyses of behavioural and evolutionary ecology studies. – Anim. Behav. 70: 967–971.

Jenni, L. and Jenni-Eiermann, S. 1998. Fuel supply and metabolic constraints in migrating birds. – J. Avian Biol 29: 521–528.

Krause, J. and Ruxton, G. D. 2002. Living in Groups. – Oxford University Press, Oxford.

Lima, S. L. 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. – Adv. Stud. Behav 27: 215–290.

Pérez-Chiscano, J. L. and Férnandez-Cruz, M. 1971. Sobre *Grus grus* y *Circus pygargus* en Extremadura. – Ardeola 21: 509–574.

Randler, C. 2004a. Vigilance of mallards in the presence of greylag geese. – J. Field Ornithol. 75: 404–408.

Randler, C. 2004b. Coot benefit from feeding in close proximity to geese. – Waterbirds 27: 240–244.

Roberts, G. 1996. Why individual vigilance declines as group size increases. – Anim. Behav. 51: 1077–1086.

SAS. 1996. SAS/STAT software changes and enhancements through release 6.11. –SAS Institute, Cary.

Sánchez, J. M., Avilés, J. M. and Medina, F. J. 1998. Status and trends of the common crane *Grus grus* in the western route. – Bird Conserv. Int. 8: 269–279.

Sánchez, J. M., Sánchez, A., Fernández, A. and Muñoz, A. 1993. La Grulla común (*Grus grus*) en Extremadura. Status y relación con el uso del suelo. – University of Extremadura, Spain.

Stillman, R. A., Bautista, L. M., Alonso, J. C. and Alonso, J. A. 2002. Modelling state-dependent interference in common cranes. – J. Anim. Ecol. 71: 874–882.

Treves, A. 2000. Theory and method in studies of vigilance and aggregation. – Anim. Behav. 60: 711–722.