

## DAILY ACTIVITY PATTERNS OF GREAT BUSTARDS *OTIS TARDA*

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**SUMMARY.**—*Daily activity patterns of Great Bustards* *Otis tarda*. The daily activity patterns of the Great Bustard *Otis tarda* were investigated at Villafáfila, NW Spain. This is the first published description of the time budget of this species. Time budgets were analysed according to sex, season and time of day, habitat and size and sex composition of flocks. Females spent more time feeding and resting, and less time preening than males. Feeding was the most frequent behaviour throughout the year, except in spring. Time allocated to different activities was affected by the time of day, being also related to the season of the year. Activity budgets differed among land uses, being influenced by the sex of individuals and the season of the year. The proportion of feeding was highest in pasture and lowest in ploughed land. Daily activity was also affected by the size and composition of flocks. Solitary individuals devoted less time to feeding and more time to scanning than individuals in flocks. Feeding time was longer in family flocks and shorter in male flocks. Time budget differences are interpreted as a response to individual requirements and social factors.

**Key words:** Activity, flock size and composition, habitat, *Otis tarda*, season, sex, time of day.

**RESUMEN.**—*Patrones de actividad diaria en la Avutarda Común* *Otis tarda*. Se han estudiado los patrones diarios de actividad de la Avutarda Común *Otis tarda* en Villafáfila, NW España, describiendo por primera vez estos patrones y su variabilidad. Los patrones diarios observados fueron analizados en función del sexo, estación, hora del día, hábitat y tamaño y composición de los bandos. Las hembras emplearon más tiempo que los machos en la alimentación y el descanso, y menos en el cuidado del plumaje. La alimentación fue la actividad más frecuente a lo largo del año, excepto en primavera. El tiempo dedicado a las diferentes actividades se vio influido por la hora del día, estando también relacionado con la estación. La proporción de tiempo dedicado a alimentarse fue mayor en pastizales y menor en terrenos labrados. La actividad diaria también se vio afectada por el tamaño y composición de los bandos. Los individuos solitarios dedicaron menos tiempo a alimentarse y más tiempo a vigilar que los individuos en bandos. El tiempo dedicado a la alimentación fue mayor en los grupos familiares y menor en los bandos de machos. Las diferencias en el porcentaje de tiempo dedicado a cada actividad son interpretadas como respuesta a requerimientos individuales y factores sociales.

**Palabras clave:** Actividad, estación, hábitat, hora del día, *Otis tarda*, sexo, tamaño y composición de los bandos.

### INTRODUCTION

The sequential organization of behaviour is expected to be oriented to maximize the fitness of individuals (Sibly & McFarland, 1976; Caraco, 1980; McNamara *et al.*, 1987), as the time spent on one behaviour limits the time available for other behaviours. Time allocation to different activities could be affected by several factors such as sex and age (Beveridge & Deag, 1987; Sullivan, 1988), season and time of day (Frederick & Klaas, 1982; Pietz, 1986), habitat (Barnard, 1980; Eberhardt *et al.*, 1989; Morton *et al.*, 1989; Rave & Baldassarre, 1989) and social organization (Pulliam, 1973; Caraco, 1979), among others.

The Great Bustard *Otis tarda* is a steppe bird widely distributed in agricultural areas of the Iberian Peninsula, whose habitat is characterized by the fluctuation of the types of land uses available throughout the year. Bustards are polygynous and show a pronounced sexual size dimorphism, males being three times larger than females (Cramp & Simmons, 1980). It is a gregarious species that forms flocks of up to almost two hundred birds in winter (Martínez, 1988). The aim of this paper is to describe the variation in time budgets of the Great Bustard according to sex, season and time of day, habitat, and size and sex composition of flocks. In spite of a considerable research effort on this species (Alonso & Alonso, 1990; Hidalgo de Trucios & Carran-

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za, 1990; Martínez, 1991, 1992; Alonso *et al.*, 1998, 2000; Lane *et al.*, 1999; among others), this is the first published description of the time budget of Great Bustards.

## METHODS

Field work was carried out between June 1985 and March 1987 at the Lagunas de Villafáfila National Wildlife Reserve (32682 ha) in northwestern Spain. This Reserve probably holds the world's densest Great Bustard population: more than 2000 birds in winter (Alonso *et al.*, 1996). The terrain is treeless and gently undulated, occupied by cereal cultivations (more than 80%), alfalfa and pasture lands.

Monthly visits were made and on each visit the area was surveyed from dawn to dusk, in such a way that there was equal observation effort over the whole area. Focal birds were randomly selected during the surveys of the study area and their behaviour was tape-recorded during 3 minutes. The duration of the sample session was established to obtain an unbiased estimate of the duration of each behaviour as well as to record even the more occasional behaviours (Altmann, 1974). Because bustards were not marked, repeated observations of the same individual cannot be excluded. However, since the study area is very large and has a high density of Great Bustards, if a bird was observed more than once, it was on different dates, at different places or in different flocks. From a total sample of 2498 records, 1934 of them were randomly selected in order to obtain an evenly distributed sample of males and females (Males = 840, Females = 814, Juveniles = 40 and Unsexed = 240).

The following behaviours were considered: feeding (head down, eating or searching for food), scanning (head up, looking around), moving (walking from one location to another), preening (including all comfort behaviours such as wing flapping, stretching and scratching), resting (lying on the ground) and courtship behaviour (including aggressive interactions; see Hidalgo de Trucios & Carranza, 1990). The proportion of time devoted to each activity and the mean duration of activity bouts (in seconds) were calculated, taking each three-minute observation session as a replicate.

The analysis of temporal variation was made

at two scales: seasonal and daily. Time of day was classified into five periods: 5:00-8:00, 8:00-11:00, 11:00-14:00, 14:00-17:00 and 17:00-20:00 hours GMT. To determine the influence of the habitat on the activity patterns, five types of land uses were recorded: cereal crop, alfalfa, ploughed land, cereal stubble and pasture. In order to analyze time budget variation in relation to size and sex composition of flocks, four types of flocks were defined: 1) mixed flocks, 2) male flocks, 3) female flocks and 4) family flocks (flocks with juveniles) (Martínez, 1988). According to their size, flocks were divided into five categories: solitary individuals, 2-5 birds, 6-15 birds, 16-50 birds, and more than 50 birds.

Because all behaviours defined were not always performed by focal birds within observation period, the distributions of most activities were skewed or had a large number of zero scores. As for this type of distributions there is not an available transformation, data were analysed by non-parametric methods (Mann-Whitney U test or Kruskal-Wallis test, and Spearman correlations).

## RESULTS

Feeding was the most important activity (mean  $\pm$  SE: 32.8%  $\pm$  0.8), followed by scanning (21.8%  $\pm$  0.6). The 45% of the diurnal activity budget was accounted for by resting (17.2%  $\pm$  0.8), moving (14.6%  $\pm$  0.5) and preening (12.7%  $\pm$  0.6). Courtship behaviour only represented 1.0%  $\pm$  0.2 of diurnal activity. The behaviours of the longest duration were resting (136.4  $\pm$  3.3 s) and courtship (62.8  $\pm$  8.9 s), followed by feeding (32.0  $\pm$  1.2 s), scanning (20.2  $\pm$  1.1 s), moving (19.0  $\pm$  0.9 s) and preening (12.6  $\pm$  0.7 s). Females spent more time feeding and resting than males (Appendix 1). Preening was significantly less frequent in females, while courtship behaviour was restricted to males. There were no significant differences in the mean duration of the different behaviours between males and females, except in preening (Appendix 1).

### *Temporal variation*

Activity patterns showed significant seasonal differences (Appendix 2). Feeding was the pre-

valent behaviour throughout the year with the exception of spring. Seasonal time budgets differed according to sex (Fig. 1). Females showed striking differences in the time allocated to feeding and preening. They spent nearly 50% of their diurnal time feeding in summer and

autumn, while time devoted to preening in summer was 3.6% versus 17.3% in males. The highest similarity in the activity of males and females corresponded to spring, with the exception of courtship behaviour which accounted for 8.2% of activity of males.

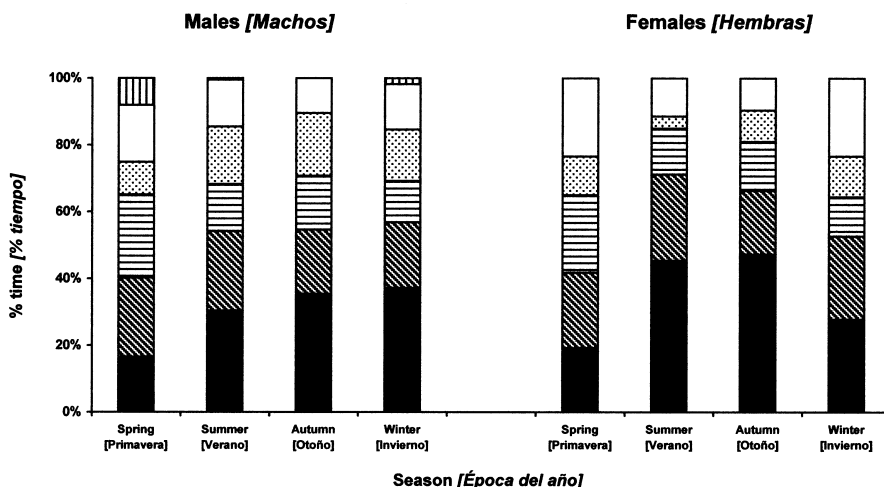


FIG. 1.—Seasonal variation in the percentage of time spent on different activities by males and females of Great Bustard. Sample size: spring (169 males and 126 females), summer (224 males and 170 females), autumn (158 males and 181 females) and winter (289 males and 337 females). Feeding (closed), scanning (crossed), moving (horizontally striped), preening (pointed), resting (open) and courtship (vertically striped).

[Variación estacional en el porcentaje de tiempo dedicado a diferentes actividades por los machos y hembras de Avutarda Común. Tamaño de muestra: primavera (169 machos y 126 hembras), verano (224 machos y 170 hembras), otoño (158 machos y 181 hembras) e invierno (289 machos y 337 hembras). Alimentación (negro), vigilancia (rayado cruzado), movimiento (rayado horizontal), cuidado del plumaje (punteado), descanso (blanco) y cortejo (rayado vertical).]

There was a strong relationship between time allocated to each activity and time of day (Appendix 2). Daily activity patterns were also affected by the season of the year (Fig. 2). Feeding showed a bimodal pattern in summer that contrasts with the daily changes of this behaviour in winter, when it increased throughout the day. The daily pattern of moving also differed among seasons being minimal at midday in spring and summer, while it reached a maximum in the same period in autumn. Kruskal-Wallis tests performed for each season by hour and for each hour by season supported these statements.

#### Variation in relation to land use

Time allocated to different activities varied significantly according to the type of land use (Appendix 3). Percentage of time spent on feeding and feeding bouts were highest in pasture and lowest in ploughed land. Time budget according to land uses showed a different pattern depending on the sex of the individuals (Fig. 3). Major differences corresponded to cereal crops and pasture lands. The most frequent activity of males in cereal crops was feeding, while females preferentially used them for resting. Pasture lands were the most common fee-

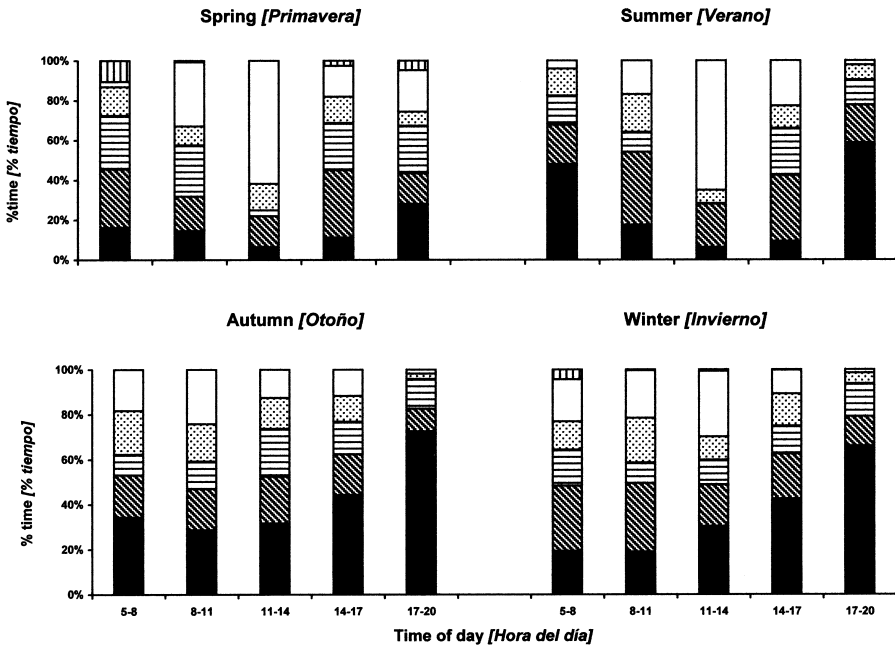


FIG. 2.—Seasonal variation in the percentage of time spent on different activities by Great Bustard according to time of day. Sample size: spring (5-8: 78; 8-11: 79; 11-14: 28; 14-17: 58 and 17-20: 72), summer (5-8: 132; 8-11: 75; 11-14: 28; 14-17: 77 and 17-20: 144), autumn (5-8: 75; 8-11: 134; 11-14: 79; 14-17: 124 and 17-20: 54) and winter (5-8: 53; 8-11: 157; 11-14: 239; 14-17: 200 and 17-20: 48). Feeding (closed), scanning (crossed), moving (horizontally striped), preening (pointed), resting (open) and courtship (vertically striped). [Variación estacional en el porcentaje de tiempo dedicado a diferentes actividades por la Avutarda Común según la hora del día. Tamaño de muestra: primavera (5-8: 78; 8-11: 79; 11-14: 28; 14-17: 58 y 17-20: 72), verano (5-8: 132; 8-11: 75; 11-14: 28; 14-17: 77 y 17-20: 144), otoño (5-8: 75; 8-11: 134; 11-14: 79; 14-17: 124 y 17-20: 54) e invierno (5-8: 53; 8-11: 157; 11-14: 239; 14-17: 200 y 17-20: 48). Alimentación (negro), vigilancia (rayado cruzado), movimiento (rayado horizontal), cuidado del plumaje (punteado), descanso (blanco) y cortejo (rayado vertical).]

ding grounds for females, which practically did not use them for comfort behaviour, while the time devoted to preening in this land use by males was higher than 16%.

The activity of bustards in the different land uses changed seasonally (Fig. 4). The predominant activity in cereal crops was feeding in autumn and resting in spring. In alfalfa, the prevalent behaviour throughout the year was feeding, conversely to ploughed land in which predominated scanning. In summer, more than 60% of time that bustards spent in cereal stubble was devoted to feeding, which also was the most frequent activity in pasture, where it reached a maximum in summer and autumn. Kruskal-Wallis tests supported these statements.

#### Variation in relation to size and sex composition of flocks

There were no significant correlations between percent time spent feeding and scanning and flock size. However, solitary individuals allocated less time to feeding, preening ( $r = 0,097$ ,  $P < 0,001$ ) and resting, and more time to scanning, walking and courtship behaviour, although the latter was only performed by males (Appendix 1). Feeding bout duration reached a minimum in solitary individuals and a maximum in small flocks, gradually decreasing in larger flocks. Mean scan duration was significantly longer in solitary individuals than in flocks of more than 50 birds (Appendix 1).

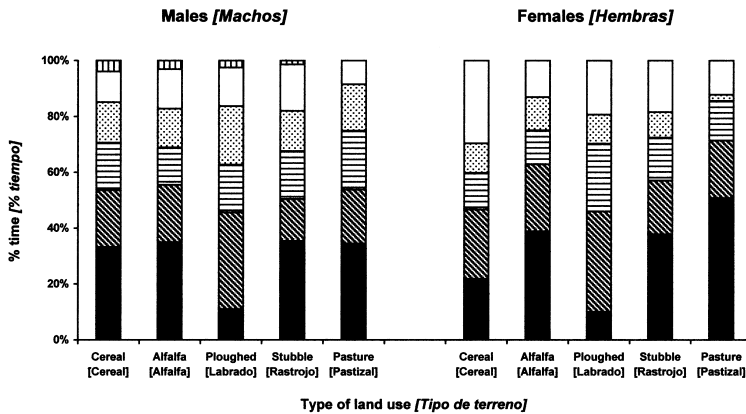


FIG. 3.—Sexual variation in the percentage of time spent on different activities by Great Bustard according to type of land use. Sample size: males (cereal: 81; alfalfa: 357; ploughed land: 133; stubble: 170 and pasture: 94) and females (cereal: 114; alfalfa: 291; ploughed land: 78; stubble: 245 and pasture: 79). Feeding (closed), scanning (crossed), moving (horizontally striped), preening (pointed), resting (open) and courtship (vertically striped).

[Variación sexual en el porcentaje de tiempo dedicado a diferentes actividades por la Avutarda Común según el tipo de terreno. Tamaño de muestra: machos (cereal: 81; alfalfa: 357; labrado: 133; rastrojo: 170 y pastizal: 94) y hembras (cereal: 114; alfalfa: 291; labrado: 78; rastrojo: 245 y pastizal: 79). Alimentación (negro), vigilancia (rayado cruzado), movimiento (rayado horizontal), cuidado del plumaje (punteado), descanso (blanco) y cortejo (rayado vertical).]

Time budgets of bustards differed according to type of flock (Appendix 1). Feeding reached a maximum in family flocks and a minimum in male flocks. A similar pattern was observed in the duration of feeding bouts.

## DISCUSSION

Feeding was the most time-consuming activity for Great Bustards, so that it is expected that changes in patterns of foraging will have an adaptive value. Although energetic requirements are the key factor in the time allocated to feeding, other factors could change the time budget, especially breeding activity. The latter appears to be the reason for the sharp decrease in feeding during spring. It remains unclear which factors may be responsible for the lesser time devoted to feeding by males, whose body size is three times larger than females. Although information about diet composition according to sex is lacking, maybe the quality and quantity of food differs between sexes. On the other hand, and although the percentage of

time feeding does not necessarily measure ingestion rate, males devoted to feeding a percentage of time much higher than females in winter when the availability of trophic resources is lower. The higher feeding rates of females in summer and autumn would be related to their presence in family flocks, which had the highest food intake.

The seasonal pattern of moving is quite similar in both sexes, showing a peak in spring which is in accordance with the mobility pattern reported by Martínez (1989). In winter, due to cold temperatures, it could be expected that birds devote less time to activities with a high energetic cost, such as moving, for the benefit of others with a low cost, such as resting. Decreasing moving and increasing resting in winter is consistent with this hypothesis. The seasonal change in the diet composition (Palacios *et al.*, 1975; Lane *et al.*, 1999) could also explain a lesser time devoted to moving in winter. At this time, food is basically composed of plant material and it is more concentrated, which determines that birds could remain for longer in feeding patches without moving. Du-

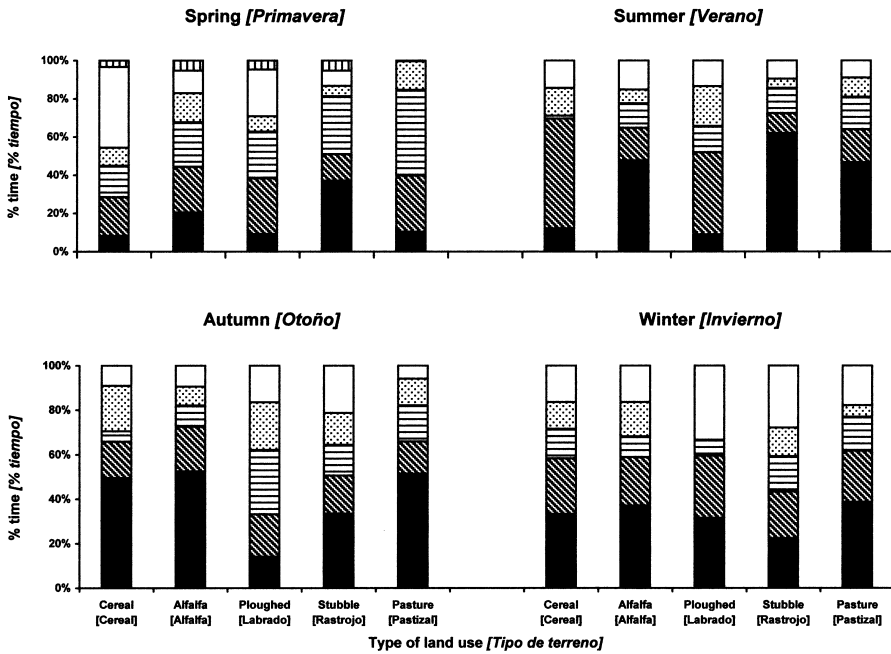


FIG. 4.—Seasonal variation in the percentage of time spent on different activities by Great Bustard according to type of land use. Sample size: spring (cereal: 95; alfalfa: 123; ploughed land: 45 stubble: 37 and pasture: 12), summer (cereal: 7; alfalfa: 112; ploughed land: 148; stubble: 97 and pasture: 89), autumn (cereal: 22; alfalfa: 126; ploughed land: 47; stubble: 221 and pasture: 50) and winter (cereal: 103; alfalfa: 388; ploughed land: 3; stubble: 154 and pasture: 43). Feeding (closed), scanning (crossed), moving (horizontally striped), preening (pointed), resting (open) and courtship (vertically striped).

[Variación estacional en el porcentaje de tiempo dedicado a diferentes actividades por la Avutarda Común según el tipo de terreno. Tamaño de muestra: primavera (cereal: 95; alfalfa: 123; labrado: 45; rastrojo: 37 y pastizal: 12), verano (cereal: 7; alfalfa: 112; labrado: 148; rastrojo: 97 y pastizal: 89), otoño (cereal: 22; alfalfa: 126; labrado: 47; rastrojo: 221 y pastizal: 50) e invierno (cereal: 103; alfalfa: 388; labrado: 3; rastrojo: 154 y pastizal: 43). Alimentación (negro), vigilancia (rayado cruzado), movimiento (rayado horizontal), cuidado del plumaje (punteado), descanso (blanco) y cortejo (rayado vertical).]

ring winter and early spring, Great Bustards devoted about a fifth part of daytime to resting, probably due to cold weather.

The foraging pattern changed daily. The lower food intake in early morning in spring and winter, and the peak in late evening, has been reported for other bird species and has been interpreted as an adaptation to reduce energy losses during the cold morning temperatures (Gjerde & Wegge, 1987). The greater food digestibility with high temperatures (Morrison *et al.*, 1990) could also explain the peak in the food intake in the evening, when temperature is higher. Courtship behaviour showed a bimodal pattern with a much more marked peak in

early morning, which coincides with the data reported by Gewalt (1959).

Given that the different types of land use vary greatly with respect to species composition and spatial distribution of food resources, it could be expected that the time spent feeding changes among habitat types. The high use of alfalfa lands as feeding grounds is consistent with the predominance of this legume in the diet of Great Bustards (Lucio, 1985; Lane *et al.*, 1999), as well as with the presence of the largest flocks in these crops (Martínez, 1992). The short time devoted to feeding in ploughed land, and conversely the long time allocated to scanning, identical in males and females, is

consistent with the low availability of trophic resources in these land uses (Martínez, 1998). The peak of feeding in cereal stubble in summer could be explained by the high availability of both cereal grain and insects at this time, while cereal crops were preferentially used to feed in autumn, when the recent sowings are especially attractive to Bustards. The high density of insects, especially grasshoppers, in pastures in summer and autumn could explain the peak in the food intake in this type of land use at this time of year (Hidalgo de Trucios & Carranza, 1990). Differences in locomotion patterns among land uses most likely stem from differences in food searching behaviour depending on the nature and density of food (Puttick, 1979; Hafner *et al.*, 1982; Pienkowski, 1983; Eberhardt *et al.*, 1989). When feeding on pastures, Bustards mainly feed on insects (pers. obs.), which have a patchy distribution. This explains why individuals moved further there than when they feed on alfalfa grounds, where the distribution of food, basically alfalfa plants, is much more uniform. Sexual differences in habitat use could be attributed to different requirements and roles of both sexes. Males fed in cereal crops in a larger proportion than females, this land use being the most frequently used for courtship. More than 50% of daytime that females spent in pasture lands was devoted to feeding, which can be attributed to the basically insectivorous diet of juveniles, as most of these females formed family flocks.

Results show that flocking enabled Bustards to devote more time to feeding and to enhance feeding rate through a decrease in the time spent alert. This is in accordance with the hypothesis that flocking increases foraging efficiency (Ward & Zahavi, 1973; Caraco, 1979; Pulliam & Milikan, 1982). In flocks of more than 50 individuals, a small loss in feeding time was observed, probably due to aggressive interactions among members of the flock (Caraco, 1979; Benkman, 1988; Saino, 1994). Foraging differences within types of flock are related to both flock size and individual requirements of its members. In family flocks, the high percentage of time spent feeding and the reduction in preening and resting, could not be attributed to their small size, but to the higher energy requirements of juveniles.

High values for percentage of alert behaviour and scanning bouts in solitary individuals

agree with the vigilance patterns of many birds (Bertram, 1980; Knight & Knight, 1986; Carrascal *et al.*, 1990; Saino, 1994; Beauchamp & Livoreil, 1997; Reboreda & Fernández, 1997). The lack of correlation between percent time scanning and flock size has been also reported in other bird species (Elgar & Catterall, 1981; Catterall *et al.*, 1992; Reboreda & Fernández, 1997), and has been attributed to multiple factors such as flock geometry (Bekoff, 1995), position in the flock (Jennings & Evans, 1980; Inglis & Lazarus, 1981), distance to nearest neighbour (Pöysä, 1994), habitat visibility (Metcalf, 1984; Glück, 1986) and the limits to collective detection marked by the visual and spatial separation between flock members (Lima & Zollner, 1996), among others (see Elgar, 1989). Sharing vigilance among more individuals, as occurs in larger flocks, also allows individuals to devote more time to preening and resting. The longer time spent preening with increasing flock size could also be explained by the synchronization of behaviour in flocking birds in response to the stimuli elicited by the activity of other individuals (Evans & Paterson, 1971; Bruggers & Jackson, 1977). Courtship behaviour is closely related to flock size. The peak of this behaviour in solitary males is congruent with the isolationist tendencies in the breeding males during the courtship display (Cramp & Simmons, 1980).

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#### BIBLIOGRAPHY

- ALONSO, J. A. & ALONSO, J. C. (Eds.) 1990. *Parámetros demográficos, selección de hábitat y distribución de la Avutarda (Otis tarda) en tres regiones españolas*. Colección técnica, ICONA. Madrid.
- ALONSO, J. C., MORALES, M. B. & ALONSO, J. A. 2000. Partial migration, lek fidelity and nesting area fidelity in females great bustards *Otis tarda*. *Condor*, 00: 000-000.
- ALONSO, J. C., ALONSO, J. A., MORALES, M. & MARTÍN, E. 1996. Seasonal and interannual population dynamics of the Great Bustard (*Otis tarda*) at Vi-

- llafáfila Reserve, NW Spain. In, J. Fernández Gutiérrez & J. Sanz-Zuasti (Eds.): *Conservación de las Aves Esteparias y su Hábitat*, pp. 191-200. Junta de Castilla y León. Valladolid.
- ALONSO, J. C., ALONSO, J. A., MARTÍN, E. & MORALES, M. B. 1998. Proximate and ultimate causes of natal dispersal in the Great Bustard. *Behavioral Ecology*, 9: 243-252.
- ALTMANN, J. 1974. Observational study of behavior: sampling methods. *Behaviour*, 49: 227-267.
- BARNARD, C. J. 1980. Flock feeding and time budgets in the house sparrow (*Passer domesticus* L.). *Animal Behaviour*, 28: 295-309.
- BEAUCHAMP, G. & LIVOREIL, B. 1997. The effect of group size on vigilance and feeding rate in spice finches (*Lonchura punctulata*). *Canadian Journal of Zoology*, 75: 1526-1531.
- BEKOFF, M. 1995. Vigilance, flock size, and flock geometry: information gathering by western evening grosbeaks (Aves, Fringillidae). *Ethology*, 99: 150-161.
- BENKMAN, C. W. 1988. Flock size, food dispersion, and the feeding behavior of crossbills. *Behavioral Ecology and Sociobiology*, 23: 167-175.
- BERTRAM, B. C. R. 1980. Vigilance and group size in ostriches. *Animal Behaviour*, 28: 278-286.
- BEVERIDGE, F. M. & DEAG, J. M. 1987. The effects of sex, temperature and companions on looking-up and feeding in single and mixed species flocks of house sparrows (*Passer domesticus*), chaffinches (*Fringilla coelebs*) and starlings (*Sturnus vulgaris*). *Behaviour*, 100: 303-320.
- BRUGGERS, R. L. & JACKSON, W. B. 1977. Time budgets of mandarin ducks under semi-natural conditions. *Wildfowl*, 28: 87-93.
- CARACO, T. 1979. Time budgeting and group size: a test of theory. *Ecology*, 60: 618-627.
- CARACO, T. 1980. On foraging time allocation in a stochastic environment. *Ecology*, 61: 119-128.
- CARRASCAL, L. M., ALONSO, J. C. & ALONSO, J. A. 1990. Aggregation size and foraging behaviour of white storks *Ciconia ciconia* during the breeding season. *Ardea*, 78: 399-404.
- CATTERALL, C. P., ELGAR, M. A. & KIKKAWA, J. 1992. Vigilance does not covary with group size in an island population of silvereyes (*Zosterops lateralis*). *Behavioural Ecology*, 3: 207-210.
- CRAMP, S. & SIMMONS, K. E. L. (Eds.). 1980. *The Birds of the Western Palearctic*, vol. II. Oxford University Press. Oxford.
- EBERHARDT, L. E., BOOKS, G. G., ANTHONY, R. E. & RICKARD, W. H. 1989. Activity budgets of Canada geese during brood rearing. *Auk*, 106: 218-224.
- ELGAR, M. A. 1989. Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biological Reviews*, 64: 13-33.
- ELGAR, M. A. & CATTERALL, C. P. 1981. Flocking and predator surveillance in house sparrows: test of an hypothesis. *Animal Behaviour*, 29: 868-872.
- EVANS, S. M. & PATTERSON, G. R. 1971. The synchronization of behaviour in flocks of estrildine finches. *Animal Behaviour*, 19: 429-438.
- FREDERICK, R. B. & KLAAS, E. E. 1982. Resource use and behavior of migrating snow geese. *Journal of Wildlife Management*, 46: 601-614.
- GEWALT, W. 1959. *Die Grosstrappe*. Neue Brehm-Bücherei. Wittenberg Lutherstadt
- GJERDE, I. & WEGGE, P. 1987. Activity patterns of Capercaille, *Tetrao urogallus*, during winter. *Holarctic Ecology*, 10: 286-293.
- GLÜCK, E. 1986. Flock size and habitat-dependent food and energy intake of foraging Goldfinches. *Oecologia*, 71: 149-155.
- HAFNER, H., BOY, V. & GORY, G. 1982. Feeding methods, flock size and feeding success in the little egret *Egretta garzetta* and the squacco heron *Ardeola ralloides* in Camargue, Southern France. *Ardea*, 70: 45-54.
- HIDALGO DE TRUCIOS, S. J. & CARRANZA, J. 1990. *Ecología y Comportamiento de la Avutarda* (*Otis tarda* L.). Servicio de Publicaciones de la Universidad de Extremadura. Cáceres.
- INGLIS, I. R. & LAZARUS, J. 1981. Vigilance and flock size in brent geese: the edge effect. *Zeitschrift für Tierpsychologie*, 57: 193-200.
- JENNINGS, T. & EVANS, S. M. 1980. Influence of position in the flock and flock size on vigilance in the starling *Sturnus vulgaris*. *Animal Behaviour*, 28: 634-635.
- KNIGHT, S. K. & KNIGHT, R. L. 1986. Vigilance patterns of bald eagles feeding in groups. *Auk*, 103: 263-272.
- LANE, S. J., ALONSO, J. C., ALONSO, J. A. & NAVESO, M. A. 1999. Seasonal changes in diet and diet selection of great bustards (*Otis t. tarda*) in north-west Spain. *Journal of Zoology, London*, 247: 201-214.
- LIMA, S. L. & ZOLLNER, P. A. 1996. Antipredatory vigilance and the limits to collective detection: visual and spatial separation between foragers. *Behavioral Ecology and Sociobiology*, 38: 355-363.
- LUCIO, A. 1985. Datos sobre la alimentación de la avutarda (*Otis tarda* L., 1758) en la cuenca del Duero. *Alytes*, 3: 69-86.
- MARTÍNEZ, C. 1988. Size and sex composition of Great Bustard (*Otis tarda*) flocks in Villafáfila, northwest Spain. *Ardeola*, 35: 125-133.
- MARTÍNEZ, C. 1989. *Organización social y relaciones espacio-temporales en una población de avutarda* (*Otis tarda*). Tesis doctoral. Universidad Autónoma de Madrid. Madrid.
- MARTÍNEZ, C. 1991. Patterns of distribution and habitat selection of a Great Bustard (*Otis tarda*) population in northwestern Spain. *Ardeola*, 38: 137-147.
- MARTÍNEZ, C. 1992. Variación del tamaño y tipo de los bandos de avutarda (*Otis tarda*) en función del hábitat. *Miscel-lània Zoològica*, 16: 161-170.



- MARTÍNEZ, C. 1998. Selección de microhábitat del sitio *Tetrax tetrax* durante la estación reproductora. *Ardeola*, 45: 73-76.
- MCNAMARA, J. M., MACE, R. H. & HOUSTON, A. I. 1987. Optimal daily routines of singing and foraging in a bird singing to attract a mate. *Behavioral Ecology and Sociobiology*, 20: 399-405.
- METCALFE, N. B. 1984. The effects of habitat on the vigilance of shorebirds: is visibility important?. *Animal Behaviour*, 32: 981-985.
- MORRISON, M. L., RALPH, C. J., VERNER, J. & JEHL, J. R. 1990. *Avian Foraging: Theory, Methodology, and applications*. Studies in Avian Biology n° 13. Cooper Ornithological Society. Los Angeles.
- MORTON, J. M., FOWLER, A. C. & KIRKPATRICK, R. L. 1989. Time and energy budgets of American black ducks in winter. *Journal of Wildlife Management*, 53: 401-410.
- PALACIOS, F., GARZÓN, J. & CASTROVIEJO, J. 1975. La alimentación de la avutarda (*Otis tarda*) en España, especialmente en primavera. *Ardeola*, 21: 347-406.
- PIENKOWSKI, M. W. 1983. Changes in the foraging pattern of plovers in relation to environmental factors. *Animal Behaviour*, 31: 244-264.
- PIETZ, P. J. 1986. Daily activity patterns of South polar and brown skuas near Palmer station, Antarctica. *Auk*, 103: 726-736.
- PÖYSA, H. 1994. Group foraging, distance to cover and vigilance in the teal, *Anas crecca*. *Animal Behaviour*, 48: 921-928.
- PULLIAM, H. R. 1973. On the advantages of flocking. *Journal of Theoretical Biology*, 38: 419-422.
- PULLIAM, H. R. & MILLIKAN, G. C. 1982. Social organization in the non-reproductive season. In, J. R. Krebs & N. B. Davies (Eds.): *Behavioural Ecology: an Evolutionary Approach*, pp. 122-147. Blackwell Scientific Publications. Oxford.
- PUTTICK, G. M. 1979. Foraging behaviour and activity budgets of curlew sandpipers. *Ardea*, 67: 111-122.
- RAVE, D. P. & BALDASSARRE, G. A. 1989. Activity budget of green-winged teal wintering in coastal wetlands of Louisiana. *Journal of Wildlife Management*, 53: 753-759.
- REBOREDA, J. C. & FERNÁNDEZ, G. J. 1997. Sexual, seasonal and group size differences in the allocation of time between vigilance and feeding in the greater rhea *Rhea americana*. *Ethology*, 103: 198-207.
- SAINO, N. 1994. Time budget variation in relation to flock size in carrion crows, *Corvus corone corone*. *Animal Behaviour*, 47: 1189-1196.
- SIBLY, R. M. & MCFARLAND, D. J. 1976. The fitness of behaviour sequences. *American Naturalist*, 110: 601-617.
- SULLIVAN, K. A. 1988. Ontogeny of time budgets in yellow-eyed juncos: adaptation to ecological constraints. *Ecology*, 69: 118-124.
- WARD, P. & ZAHAVI, A. 1973. The importance of certain assemblages of birds as «information centres» for food finding. *Ibis*, 115: 517-534.

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## APPENDIX I

Percentage of time (mean±SE) spent on different activities by Great Bustards and mean (±SE) duration (sec) of different activity bouts of Great Bustards according to sex (sample size: males: 840 and females: 814), flock size (sample size: 1: 64; 2-5: 361; 6-15: 734; 16-50: 695 and >50: 76) and type of flock (sample size: mixed flocks: 941; male flocks: 525; female flocks: 289 and family flocks: 95).

[Porcentaje de tiempo (media±ES) dedicado a diferentes actividades por la Avutarda Común y duración media (±ES) en seg. de las diferentes actividades según el sexo (tamaño de muestra: machos: 840 y hembras: 814), tamaño de bando (tamaño de muestra: 1: 64; 2-5: 361; 6-15: 734; 16-50: 695 y >50: 76) y tipo de bando (tamaño de muestra: bandos mixtos: 941; bandos de machos: 525; bandos de hembras: 289 y bandos familiares: 95).]

	Sex [Sexo]		Flock size [Tamaño de bando]							Type of flock [Tipo de bando]				$\chi^2$	P		
	Males [Machos]	Females [Hembras]	Z	P	1	2-5	6-15	16-50	>50	$\chi^2$	P	Mixed Flocks [Bandos de mixtos]	Male flocks [Bandos de machos]			Female flocks [Bandos de hembras]	Family flocks [Bandos familiares]
Feeding [Alimentación]	30.0±12%	34.4±1.3%	-1.92	0.055	14.7±3.4%	35.9±1.9%	31.7±1.3%	34.4±1.4%	3.1±4.1%	18.55	0.001	33.6±0.7%	27.5±1.5%	35.9±2.3%	47.3±4.2%	25.13	
Scanning [Vigilancia]	27.8±16%	30.4±1.8%	-0.23	0.818	10.7±2.2%	34.5±3.3%	32.6±2.0%	32.1±1.9%	27.3±4.7%	36.70	0.000	31.0±1.6%	26.8±2.1%	36.1±3.8%	53.7±7.7%	1324	
Moving [Desplazamiento]	21.5±0.9%	23.5±0.9%	-0.77	0.444	40.8±5.1%	21.5±1.4%	21.7±0.9%	20.4±0.9%	21.2±2.3%	10.77	0.029	21.5±0.8%	22.4±1.2%	22.9±1.7%	18.0±2.9%	8.07	
Preening [Cortijo]	17.7±1.4%	21.2±1.7%	-1.32	0.186	62.6±10.9%	20.7±2.7%	20.3±1.7%	16.9±1.5%	9.9±1.3%	18.60	0.001	16.3±1.2%	21.4±2.1%	26.5±3.6%	27.8±7.3%	4.75	
Resting [Descanso]	16.1±0.8%	14.6±0.8%	-1.02	0.307	18.8±3.6%	19.4±1.5%	12.8±0.8%	14.3±0.8%	8.6±1.8%	9.94	0.029	13.7±0.7%	16.8±1.1%	12.4±1.3%	26.2±3.8%	13.33	
Courship [Cortijo]	17.4±1.1%	17.9±1.4%	-0.02	0.988	17.5±2.6%	27.6±3.4%	17.4±1.4%	16.5±1.1%	16.1±3.9%	6.79	0.147	17.4±1.2%	18.4±1.4%	14.2±1.7%	5.11±9.2%	14.50	
	15.4±0.9%	9.7±0.7%	-3.92	0.000	5.5±1.9%	8.5±1.0%	13.2±0.0%	14.8±1.0%	14.3±2.6%	19.59	0.001	14.2±0.8%	13.2±1.1%	8.1±1.1%	3.7±1.4%	28.72	
	13.5±1.1%	10.9±0.8%	-3.08	0.002	8.7±1.1%	10.4±0.5%	13.3±1.1%	13.5±1.3%	9.7±0.7%	3.83	0.430	12.5±0.9%	12.7±1.3%	9.8±1.1%	20.6±10.7%	10.73	
	13.8±1.1%	17.8±1.3%	-2.47	0.013	12.5±4.2%	13.9±1.8%	19.8±1.4%	15.1±1.3%	24.8±4.7%	16.72	0.002	16.2±1.1%	17.8±1.6%	20.7±2.3%	4.8±2.1%	13.44	
	136.3±5.6%	133.0±4%	-0.63	0.532	180.0±0.8%	155.4±7.1%	144.0±4.6%	116.6±6.2%	131.5±14.9%	24.43	0.000	124.5±5.0%	144.5±6.0%	153.1±6.7%	135.8±28.3%	13.26	
	2.4±0.4%	0.0±0.0%	-6.03	0.000	7.7±3.3%	0.7±0.4%	0.8±0.2%	0.9±0.2%	0.5±0.3%	12.27	0.016	0.7±0.2%	2.5±0.2%	0.0±0.0%	0.0±0.0%	19.78	
	70.5±9.4%	2.5±0.3%	-3.16	0.000	176.4±2.5%	112.5±42.6%	57.8±13.7%	40.1±9.5%	16.8±8.7%	13.41	0.009	54.8±13.5%	77.3±13.5%	2.7±0.3%	0.0±0.0%	9.35	

## APPENDIX 2

Percentage of time (mean±SE) spent on different activities by Great Bustards and mean (±SE) duration (sec) of different activity bouts of Great Bustards according to season (sample size: spring: 315; summer: 456; autumn: 466 and winter: 697) and time of day (sample size: 5-8: 338; 8-11: 445; 11-14: 374; 14-17: 459 and 17-20: 318).  
 [Porcentaje de tiempo (media±ES) dedicado a diferentes actividades por la Avitarda Común y duración media (±ES) en seg. de las diferentes actividades según la estación (tamaño de muestra: primavera: 315; verano: 456; otoño: 466 e invierno: 697) y la hora del día (tamaño de muestra: 5-8: 338; 8-11: 445; 11-14: 374; 14-17: 459 y 17-20: 318).]

	Season [Epoca del año]				Time of day [Hora del día]							$\chi^2$	P
	Spring [Primavera]	Summer [Verano]	Autumn [Otoño]	Winter [Invierno]	5-8	8-11	11-14	14-17	17-20				
Feeding [Alimentación]	16.6±1.4%	37.1±1.9%	39.3±1.7%	32.9±1.4%	33.0±2.0%	20.8±1.4%	27.1±1.8%	33.5±1.7%	54.9±2.2%	168.09	0.000		
	12.0±0.88	48.3±3.5s	32.7±2.3s	28.9±1.7s	30.6±3.0s	24.6±2.3s	25.6±1.9s	24.4±1.6s	52.7±3.8s	55.88	0.000		
Scanning [Vigilancia]	22.8±1.6%	24.6±1.5%	17.8±1.0%	22.1±0.9%	23.3±1.4%	25.5±1.3%	19.0±1.3%	23.4±1.2%	15.7±1.3s	42.15	0.000		
	23.5±2.9s	30.0±3.1s	12.8±1.6s	17.0±1.5s	16.4±2.0s	24.8±2.5s	20.9±2.5s	20.9±2.3s	15.9±2.4s	27.81	0.000		
Moving [Desplazamiento]	23.2±1.7%	13.8±1.2%	14.0±1.1%	11.6±0.7%	16.5±1.4%	13.2±1.1±	11.7±1.1%	16.3±1.2%	15.4±1.4%	10.66	0.031		
	23.5±2.5s	26.2±3.1s	18.3±1.8s	13.7±0.9s	20.0±2.4s	20.0±2.1s	14.2±1.3s	20.7±2.1s	19.2±2.5s	10.72	0.030		
Preening [Confort]	11.2±1.2%	11.7±1.1%	13.5±1.2%	13.4±0.9%	14.8±1.5%	16.9±1.3%	11.0±1.2%	12.9±1.1%	6.1±1.0%	47.63	0.000		
	10.5±0.6s	15.0±2.3s	13.1±1.3s	12.0±0.9s	10.9±0.6s	12.6±1.1s	15.7±2.3s	11.3±1.1s	14.1±3.5s	11.90	0.018		
Resting [Descanso]	21.8±2.3%	12.5±1.5%	15.3±1.6%	19.3±1.4%	9.1±1.5%	23.3±1.9%	30.8±2.3%	13.5±1.5%	6.3±1.3%	129.50	0.000		
	149.3±6.7s	153.4±7.3s	135.1±7.2s	125.1±5.2s	129.6±10.6s	138.5±5.6s	138.7±8.2s	128.2±8.2s	150.9±12.7s	2.97	0.564		
Courtnship [Cortejo]	4.4±1.0%	0.3±0.2%	0.0±0.0s	0.7±0.2%	3.2±0.8%	0.3±0.1%	0.4±0.2%	0.4±0.2%	1.5±0.6%	17.96	0.001		
	88.7±14.0s	32.6±16.9s	3.0±0.0s	38.3±9.6s	88.1±15.9s	21.8±7.8s	31.9±12.1s	49.9±23.8s	78.5±23.1s	6.48	0.166		

## APPENDIX 3

Percentage of time (mean $\pm$ SE) spent on different activities by Great Bustards and mean ( $\pm$ SE) duration (sec) of different activity bouts of Great Bustards according to type of land use (sample size: cereal: 227; alfalfa: 749; ploughed land: 243; stubble: 509 and pasture: 194).

[Porcentaje de tiempo (media $\pm$ ES) dedicado a diferentes actividades por la Avutarda Común y duración media ( $\pm$ ES) en seg. de las diferentes actividades según el tipo de terreno (tamaño de muestra: cereal: 227; alfalfa: 749; labrado: 243; rastrojo: 509 y pastizal: 194).]

	Type of land use [Tipo de terreno]					$\chi^2$	P
	Cereal [Cereal]	Alfalfa [Alfalfa]	Ploughed land [Labrado]	Stubble [Rastrojo]	Pasture [Pastizal]		
Feeding [Alimentación]	23.8 $\pm$ 2.1% 24.9 $\pm$ 3.2s	38.3 $\pm$ 1.4% 31.5 $\pm$ 1.8s	10.3 $\pm$ 1.2% 10.6 $\pm$ 1.0s	35.7 $\pm$ 1.7% 34.4 $\pm$ 2.3s	43.9 $\pm$ 2.9% 50.2 $\pm$ 5.2s	132.42 94.05	0.000 0.000
Scanning [Vigilancia]	23.3 $\pm$ 1.9% 25.4 $\pm$ 3.8s	21.0 $\pm$ 0.9% 14.6 $\pm$ 1.2s	35.3 $\pm$ 2.2% 43.7 $\pm$ 4.7s	16.8 $\pm$ 1.0% 14.0 $\pm$ 1.5s	18.6 $\pm$ 1.8% 20.4 $\pm$ 3.9s	54.544 47.58	0.000 0.000
Moving [Desplazamiento]	13.4 $\pm$ 1.5% 18.4 $\pm$ 2.6s	12.1 $\pm$ 0.7% 14.2 $\pm$ 1.2s	18.5 $\pm$ 1.7% 22.9 $\pm$ 2.1s	15.5 $\pm$ 1.1% 22.42.3s	18.1 $\pm$ 2.0% 25.0 $\pm$ 3.8s	3.33 44.75	0.505 0.000
Preening [Confort]	11.9 $\pm$ 1.6% 11.7 $\pm$ 1.2s	12.9 $\pm$ 0.9% 11.2 $\pm$ 0.5s	18.2 $\pm$ 1.8% 16.3 $\pm$ 2.8s	11.4 $\pm$ 1.1% 12.0 $\pm$ 1.2s	9.7 $\pm$ 1.6% 16.4 $\pm$ 4.5s	18.13 3.34	0.001 0.503
Resting [Descanso]	26.5 $\pm$ 2.8% 142.6 $\pm$ 7.2s	14.2 $\pm$ 1.2% 130.5 $\pm$ 6.1s	16.2 $\pm$ 2.3% 137.8 $\pm$ 9.6s	20.0 $\pm$ 1.7% 136.3 $\pm$ 5.8s	9.6 $\pm$ 2.1% 155.6 $\pm$ 13.6s	31.29 1.82	0.000 0.768
Courtship [Cortejo]	1.4 $\pm$ 0.8% 97.0 $\pm$ 37.4s	1.5 $\pm$ 0.3% 52.5 $\pm$ 9.7s	1.4 $\pm$ 0.6% 78.0 $\pm$ 26.2s	0.5 $\pm$ 0.3% 68.9 $\pm$ 30.6s	0.0 $\pm$ 0.0% 0.0 $\pm$ 0.0s	19.04 1.33	0.001 0.722