

## Articles

# FOOD AVAILABILITY BUT NOT SEX DETERMINES MORNING FORAGING AREA SIZE IN THE GREAT BUSTARD *OTIS TARDA*, THE MOST SEXUALLY SIZE-DIMORPHIC BIRD SPECIES

## LA DISPONIBILIDAD DE ALIMENTO Y NO EL SEXO DETERMINA EL TAMAÑO DEL ÁREA DE FORRAJEO MATINAL EN LA AVUTARDA COMÚN *OTIS TARDA*, EL AVE CON MAYOR DIMORFISMO SEXUAL

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**SUMMARY.**—Sexual size dimorphism (SSD) may favour physiological peculiarities in diet, behaviour and home-range size both across species and within species. Sex-specific differences in diet and behaviour have been reported in several bird species but there are fewer studies of foraging area size in sexually dimorphic bird species. Foraging area size should be greater in the bigger sex according to home-range size predictions based on body mass. We tested this prediction in a winter study of foraging area size in the Great Bustard *Otis tarda*, the most sexually size-dimorphic bird species, which forages in unisexual flocks. In this species the temporal pattern of a flock's feeding intensity; the proportion of birds actively feeding (FI) and the size of the morning foraging area (MFA) of each sex are unknown. We recorded the behaviour and movements of unisexual flocks of Great Bustards during winter mornings and sampled food availability to take into account its effect on FI and MFA. FI increased and then decreased through the morning in both sexes, and was lower in males than in females. This sexual difference was greater where legume availability was smaller. Legumes were the most preferred substrate type. Consequently, MFA sizes were smaller in sites with more legume availability. We did not find sexual differences either in the size of MFA or in the selection of the two preferred substrate types: legumes and stubble fields. MFA and FI were determined to a greater extent by ecological factors such as food availability than by metabolic requirements derived from body size differences. These results obtained from a short-term study do not preclude an effect of sexual size dimorphism

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on MFA size and FI of Great Bustards over longer periods but show that the body size effect on foraging behaviour may be smaller than predicted only by SSD.

**Key words:** animal movement, body size, home range, optimal foraging, sexual size dimorphism, time-budget.

**RESUMEN.**—El dimorfismo sexual en tamaño (SSD) puede favorecer particularidades fisiológicas en la dieta, el comportamiento y el tamaño del área de campeo tanto entre especies como dentro de especies. Se han encontrado diferencias específicas en la dieta y el comportamiento en distintas especies de aves, pero hay pocos estudios sobre el área de aprovisionamiento en especies sexualmente dimórficas. El tamaño del área de aprovisionamiento debería ser mayor en el sexo más grande, de acuerdo a las predicciones sobre el área de campeo basadas en el tamaño corporal. En este trabajo comprobamos esta predicción en un estudio invernal del tamaño del área de aprovisionamiento en la avutarda euroasiática *Otis tarda*, la especie de ave con el dimorfismo sexual en tamaño más acusado y que forrajea en bandos unisexuales. En esta especie se desconoce el patrón temporal de alimentación de los bandos, la proporción de aves que están alimentándose activamente (FI) y el tamaño del área de forrajeo matutina (MFA) de cada sexo. Registramos el comportamiento y los movimientos de bandos unisexuales de avutardas durante mañanas invernales y muestreamos la disponibilidad de alimento para tener en cuenta su efecto en FI y MFA. El FI aumentó y después decreció durante la mañana en ambos sexos, fue más bajo en los machos que en las hembras. Esta diferencia sexual fue mayor donde la disponibilidad de leguminosas era más baja. Los campos de leguminosas fueron el sustrato preferido. En consecuencia, el tamaño de MFA fue más pequeño en los sitios con mayor disponibilidad de leguminosas. No encontramos diferencias sexuales ni en el tamaño del MFA ni en la selección de los dos sustratos preferidos: leguminosas y barbechos. El MFA y el FI fueron determinados más por factores ecológicos como la disponibilidad de alimento que por los requerimientos metabólicos derivados de las diferencias en el tamaño. Estos resultados obtenidos de un estudio a corto plazo no excluyen un efecto del dimorfismo sexual en tamaño sobre los tamaños de MFA y FI de las avutardas en periodos de tiempo más prolongados, pero muestran que el efecto del tamaño corporal en el comportamiento de forrajeo puede ser más pequeño que lo que se predice solamente por el SSD.

**Palabras clave:** alimentación óptima, área de campeo, dimorfismo sexual en tamaño, movimiento animal, presupuesto de tiempo, tamaño corporal.

## INTRODUCTION

The area in which an animal lives and performs activities associated with foraging, social behaviours and resting is known as its home range (Burt, 1943). Its size has been shown to be influenced by many factors, such as food availability (Schradin *et al.*, 2010; Uzal *et al.*, 2013), body size (McNab, 1963; Jenkins *et al.*, 1981; Belovsky & Slade, 1986; Lindstedt *et al.*, 1986; Myserud *et al.*, 2001), sex (Myserud *et al.*, 2001; Dunbar & Shi, 2008; Pays & Jarman, 2008; Lees *et al.*, 2012), age (Mikesic & Drickamer, 1992; Tufto *et al.*, 1996), diet (McNab, 1963) and

brood size (Säid *et al.*, 2005). Among these factors, body size and food availability have been identified as the main determinants of home range size, which correlates positively with body size and inversely with food availability (McNab, 1963; Schoener, 1968; Peters, 1983; Jetz *et al.*, 2004; Tamburello *et al.*, 2015), both between species (Haskell *et al.*, 2002) and within species (e.g., Cederlund & Sand, 1994; Palomares, 1994). It is unknown whether both determinants of home range size also limit the foraging area size during the morning, a short but important period for daytime survival. For instance, time-energy budgets of diurnal species show

that many species forage intensely during the morning (Aschoff, 1966; Bednekoff & Houston, 1994; Polo & Bautista, 2006).

Body size affects all aspects of individual morphology, physiology and ecology (Peters, 1983). Since metabolic rate is closely tied to body mass, much interspecific variation in foraging behaviour may be directly related to body size variation among species (Maurer, 1996). In many bird species, males and females differ considerably in body size, but in spite of the extensive literature on the evolution of sexual size dimorphism (Székely *et al.*, 2007; Fairbairn, 2013), little is known about the influence of dimorphism on bird physiology and ecology (Carey, 1996; Lees *et al.*, 2012). Sexual differences in body mass and thus in energy expenditure and intake, may be associated with differences in diet and time-energy budgets and therefore may be an important factor causing sexual segregation (Selander, 1966; Ruckstuhl & Neuhaus, 2006; Wearmouth & Sims, 2008). Where foraging rate and resource encounter rate are functions of body size (Bryant & Westerterp, 1980), the main factor influencing the size of a foraging area is the density and distribution of resources (Haskell *et al.*, 2002). According to this hypothesis, the larger sex would show a greater foraging area because a larger area should offer more food. How much greater? According to optimal foraging theory (MacArthur & Pianka, 1966; Schoener, 1971; Maurer, 1996), it should be at least large enough to yield an adequate food supply to satisfy the body needs during a given period (Andersson, 1978; Schoener, 1983; Seidel & Boyce, 2016). Thus, it must be greater in the sex with bigger body size according to terrestrial movement energetics and its application to the optimising animal (Halsey, 2016).

In this study we recorded the behaviour and movements of unisexual flocks of Great Bustards, the most sexually size-dimorphic bird species, on winter mornings and sampled the food availability in their foraging areas. We

aimed to test whether (1) the morning foraging area (MFA, hereinafter) size was larger for males than for females; (2) flock feeding intensity (FI), the proportion of birds in a flock that were actively feeding, was higher in male flocks than in female flocks; and (3) these two variables showed any correlation with legume and overall food availability for one or both sexes. Sexual size dimorphism could be associated with sexual differences in the size of foraging areas and feeding behaviour but this possibility has not yet been explored. Home range size variation across herbivorous cursorial birds (Tamburello *et al.*, 2015) suggests that the foraging areas of male Great Bustards could be about 60% greater than those of females if a scaling of body size similar to that prevailing between species is applied within species. We predict a larger MFA in the bigger sex, whatever the exact magnitude. To our knowledge, this prediction has not been tested in herbivorous cursorial birds.

The proportion of feeding birds in a flock does not only vary with daytime, but is also determined by food availability (ducks: Maxson & Oring, 1980; shorebirds: Sedinger & Raveling, 1988; Common Cranes: Alonso *et al.*, 1997; Bautista & Alonso, 2013). Food availability also determines the size of the foraging area (Schoener, 1968; Brown & Orians, 1970). An optimal forager should minimise its foraging area according to food availability: the greater the food availability, the smaller the foraging area and the smaller the feeding intensity of a Great Bustard flock. Determining to what extent Great Bustards forage optimally was not one of the aims of this study but changes in habitat selection patterns of Great Bustards generally parallel changes in estimated food availability (Moreira *et al.*, 2004). Thus, we predict FI and MFA sizes of Great Bustards flocks should be negatively correlated to overall food availability and specifically to legume availability, since Great Bustards seek the optimal feeding conditions provided by legume fields,

legumes (vetch *Vicia sativa*) being their preferred winter food (Lane *et al.*, 1999).

## MATERIAL AND METHODS

### *Study area*

The study was conducted between November and February of 2007 to 2009 in Madrid province, where a population of c. 1,150 Great Bustards has been intensively studied through two decades (Martín *et al.*, 2012). We selected ten sites (coordinates provided in Supplementary material, Table S1) with enough observatories and absence of human disturbance to allow us to observe undisturbed birds from dawn until noon. Although anthropogenic disturbances can occasionally frighten the birds, in our study area less than 0.3% of the morning time-budget of Great Bustards is spent responding to disturbances and most disturbance occurs at weekends (Sastre *et al.*, 2009), when we did not collect data.

The study area is flat to slightly undulating, which enabled an unobstructed view of flocks using 60-90x telescopes over long periods. Winter is a pertinent season to check for sexual differences in the sizes of foraging areas and feeding intensity routines because then most of the daytime period is spent foraging (Martínez, 2000), the daytime period is short and the air temperature is low.

Great Bustards live in flat, agro-steppe landscapes mainly cultivated with non-irrigated cereal (> 80% wheat and barley), grown in Madrid on a traditional two-year rotation system, where fields are left as stubble during the year following harvest (Martínez, 2000; Alonso & Palacín, 2009). A few fields are sometimes left fallow for two or more years, while elsewhere irrigation systems have been introduced to allow annual crops. Ploughed, sown and stubble fields comprise a mosaic throughout the region. This farming system is

complemented with minor crops (legumes, olives, sunflowers and vineyards). In our study area, the most nutritious food and preferred food type of Great Bustards is legumes, mainly vetch *Vicia sativa* (Bravo *et al.*, 2016 and references therein).

### *Species*

In Spain adult males weigh 7-13 kg, while females weigh 3-5 kg (Alonso *et al.*, 2009). This marked body-size dimorphism determines sexual differences in many life history parameters, such as delayed sexual maturity and shorter lifespan in males, a female-skewed sex ratio, differences in breeding strategies, and low overlap in diet (Morales & Martín, 2002; Alonso, 2014; Bravo *et al.*, 2016). Great Bustards move mostly by walking, reluctantly flying when necessary (Martínez, 2000). Males and females live year-round in sexually segregated flocks with no niche segregation (Traba *et al.*, 2015), which provides an excellent framework to infer that potential sexual differences in foraging areas could be mainly due to body size dimorphism.

Both sexes are mostly herbivorous, preferring broad-leaved plants, and in some seasons also insects, seeds and fruits (Lane *et al.*, 1999; Gooch *et al.*, 2015; Bravo *et al.*, 2016). However, males and females show small but significant differences in the composition of their diet when they are juveniles (Bravo *et al.*, 2012; Gooch *et al.*, 2015) and adults (Bravo *et al.*, 2016). These differences result in a mean dietary overlap between adult males and females of 70%, one of the smallest known values among birds (Bravo *et al.*, 2016). Although dietary differences could account for SSD to some extent, a sex bias in mobility as a consequence of SSD cannot be ruled out until field data on morning foraging area sizes were recorded.

The daily activity of Great Bustard flocks depends on sex: in winter males feed longer

and rest less than females (Martínez, 2000). Great Bustards rest at midday (Morales & Martín, 2002), but it is unknown whether flocks of males feed more intensively than flocks of females before and after midday. The foraging routines of diurnal birds show a typical bimodal pattern with two periods of maximum activity, respectively in the early morning and late evening, with a resting period at midday when activity is reduced (e.g., Polo & Bautista, 2006; Bonter *et al.*, 2013).

### Field observations

In this study we did field observations during the morning foraging period, which is usually the longest and most intensive one in diurnal birds (Polo & Bautista, 2006 and references therein; Bautista & Alonso, 2013). Our results therefore apply to this short period of the day; longer periods might deliver different results. Bird behaviour was classified as feeding (head down) or non-feeding (alert, walking, preening and resting). Great Bustards may rest lying down or standing. Standing birds observed at dawn or early morning were defined as resting when their head was leant on the back. We defined a bird as feeding when its head was below the main body horizontal axis, a posture clearly indicating a search for food or food intake. In most cases the Great Bustards alternated steps with the head down and steps with the head up. The flock's feeding intensity FI was defined as the number of birds feeding divided by the total number of birds in a flock. Flocks rather than individuals were used in data analyses because individuals of the same flock cannot be regarded as independent of one another when foraging together. Feeding is dependent on other behaviours such as vigilance, which in turn is dependent on the number of birds in the flock (Wang *et al.*, 2015). That is, feeding time (flock as well as individual) or feeding intensity (FI) can be re-

lated to flock size. Nonetheless mean flock sizes (min.-max.) in our study were 21 (2-76) females and 17 (3-29) males (Table 1), above the range for which a significant effect of flock size on vigilance and feeding has been reported in Great Bustards (< 5 birds, Martínez, 2000; < 11 birds, Wang *et al.*, 2015) and other species (Pulliam, 1973; Roberts, 1996).

Flocks of Great Bustards walk slowly while foraging and rest on the same fields where they feed, allowing the observer to record the position and activity of more than one flock per morning. Flocks isolated for at least 50% of the morning were included in the statistical analyses. We recorded the location (UTM coordinates) of isolated flocks, their flock size and feeding intensity (percentage of birds with the head down) every hour from dawn to noon (c. 0700 to 1300 hours). Flocks were easily sexed by body size and plumage (Alonso *et al.*, 2005). Locations were plotted on a 1:12,000 map showing field boundaries. The size of the morning foraging area (MFA) was defined as the minimum convex polygon (MCP) that included 95% of a flock's locations (UTM coordinates). The MCP was calculated with locations recorded every hour, using the Ranges 7 program (South *et al.*, 2005). Visits were repeated opportunistically on  $6 \pm 2$  mornings (mean  $\pm$  IC95%, N = 10 sites) to enhance the reliability of MCPs of Great Bustards in each site. In each MFA we used ArcGIS 9.3 (ESRI, Redlands, California, USA) to calculate the extent of the main field types: legume, stubble, cereal sown, ploughed and olive. The proportional availability of each substrate was calculated as a percentage of the total surface within the MCP. The Great Bustard is a polygynous lekking species, with a sex ratio of 2.4 females per male in the study area (Martín *et al.*, 2007). Flocks of males were less frequent than female flocks: males were only found at six sites, whereas female flocks were present at all sites. The total number of birds did not change during a winter nor did

TABLE 1

Morning foraging areas (MFA, ha) of Great Bustard flocks at 10 sites in central Spain. There were no male flocks at several sites because the sex ratio in this population was female-biased: 0.41 males per female (Alonso *et al.*, 2003). Statistics are means  $\pm$  SD, except days (N).  
 [Áreas de alimentación matutinas (MFA, ha) de bandos de avutardas en 10 sitios del centro de España. No hubo bandos de machos en cada sitio por- que la proporción de sexos en esta población estaba sesgada a favor de las hembras: 0.41 machos por cada hembra (Alonso *et al.*, 2003). Los valores son medias  $\pm$  SD, excepto en los días (N).]

Site	Females <sup>a</sup>					Males <sup>a</sup>				
	MFA	days	No. flocks	flock size	No. birds	MFA	days	No. flocks	flock size	No. birds
A	12.6 $\pm$ 8.8	6	2.2 $\pm$ 1.0	15 $\pm$ 9	33 $\pm$ 23			0		
B	23.2 $\pm$ 19.1	11	2.5 $\pm$ 0.9	21 $\pm$ 15	50 $\pm$ 37	19.3 $\pm$ 16.4	8	1.0 $\pm$ 0.0	25 $\pm$ 13	25 $\pm$ 13
C	11.8	1	1.0	11	11	33.9 $\pm$ 32.4	2	1.0 $\pm$ 0.0	9 $\pm$ 2	9 $\pm$ 2
D	11.2 $\pm$ 4.3	3	2.0 $\pm$ 1.0	16 $\pm$ 10	27 $\pm$ 4			0		
E	26.9 $\pm$ 15.2	6	2.3 $\pm$ 1.2	25 $\pm$ 15	45 $\pm$ 10	40.8 $\pm$ 60.1	8	1.0 $\pm$ 0.0	25 $\pm$ 6	25 $\pm$ 6
F	14.5 $\pm$ 11.2	4	2.0 $\pm$ 0.8	32 $\pm$ 10	60 $\pm$ 17	10.4 $\pm$ 6.2	3	1.7 $\pm$ 0.6	15 $\pm$ 4	23 $\pm$ 6
G	31.9 $\pm$ 73.7	10	1.5 $\pm$ 0.8	19 $\pm$ 13	22 $\pm$ 11	21.5 $\pm$ 25.5	10	1.1 $\pm$ 0.3	20 $\pm$ 5	21 $\pm$ 6
H	9.4 $\pm$ 9.9	11	1.8 $\pm$ 0.9	29 $\pm$ 17	44 $\pm$ 21			0		
I	34.5 $\pm$ 20.8	10	2.2 $\pm$ 0.9	18 $\pm$ 7	42 $\pm$ 22			0		
J	12.1 $\pm$ 7.6	7	2.3 $\pm$ 1.1	22 $\pm$ 12	45 $\pm$ 24	11.8	1	1.0	8	8
All <sup>b</sup>	19.0 $\pm$ 9.1		2.0 $\pm$ 1.0	21 $\pm$ 7	38 $\pm$ 15	23.3 $\pm$ 12.3		1.1 $\pm$ 0.3	17 $\pm$ 8	19 $\pm$ 8

(a) Number of flocks, flock size and MFA were averaged first within days in each site, and the result then averaged between days. Numbers of birds observed at each site were first calculated as the sum of flock sizes within morning and site, and the result was averaged across mornings within site. Males were grouped in a single flock most of the time, and so the mean male flock size and the accumulated number of birds did not differ.

(b) Calculations of all sites were computed across sites (females: 10 sites; males: 6 sites) as simple means (number of flocks, flock size, birds) or a weighted mean (MFA), with the number of birds in each site defined as the weighting variable.

Great Bustards move between sites, according to winter censuses and surveys of tagged birds (Alonso *et al.* unpub. data).

### Data analyses

Sex differences in MFAs were analysed with generalized linear mixed models (GLMM), assuming a Poisson error distribution. Flock sex was included as fixed factor, legume availability as covariable and site as random factor. Flock size was included as a weighting variable of MFA to suppress the under-contribution of big flocks and the over-contribution of small flocks in the statistical analyses (Krause & Ruxton, 2002; Majolo *et al.*, 2008; Reiczigel *et al.*, 2008). Sex differences in flock feeding intensity FI were analysed with generalized linear mixed models (GLMM), assuming a binomial error distribution of FI (proportion of birds actively feeding). Sex was included as fixed factor, legume availability as covariable and time and time-squared were included as independent variables (repeated measures) to test non-linear changes in feeding intensity during the morning. The effect of flock identity, nested within each of the ten studied sites, was defined as a random factor.

Following Zuur *et al.* (2007) we built beyond optimal models (i.e. the most complex models, with all factors and their plausible interactions) with different random error structure (i.e. only site and flock nested in site) using the restricted maximum likelihood estimation procedure. Once random structure had been defined, fixed effects structure was defined using the maximum likelihood ratio-test. Models were compared with the Akaike's information criterion to determine the best predictive model. Being conservative, the best model was the one with the lowest AICc value with a difference  $> 2$  from the second best model, which is considered a substantial support for a real difference between the

models (Burnham & Anderson, 2002; p. 271 in Burnham & Anderson, 2004). To evaluate the variance explained we calculated  $R^2$  values of the models using the methods of Nakagawa and Schielzeth (2013). We calculated the marginal  $R^2$  ( $R_m^2$ ), which describes the variance explained by the fixed factors, and conditional  $R^2$  ( $R_c^2$ ), which is concerned with the variance explained by both the fixed and random factors (Nakagawa & Schielzeth, 2013). Residuals from the GLMM tests were normally distributed and residual variances were homogeneous. All analyses above were calculated with 'lme4' package (Bates *et al.*, 2015) in R 3.2 (R Development Core Team, 2016).

Habitat selection was examined with Compositional Analysis (Aebischer *et al.*, 1993; Smith, 2010), which examines habitat use in relation to availability, taking the log-ratio differences of used and available field types. Proportional availability of the main field types within MCP was compared with proportional use. Null proportions were replaced by 0.01 (Aebischer *et al.*, 1993). The value of  $t$ , a statistic that measures the significance of the deviation in the use of each field type relative to random in compositional analysis, was also calculated for each field type by randomisation with 1,000 iterations, as recommended by Aebischer *et al.* (1993). The positive log-ratio differences calculated with the compositional analyses were ranked, the most positive log-ratio difference receiving the highest rank as the most preferred field type. From the log-ratios matrix, the sexual effect on rank preferences was analysed with a general linear model where dependent variables were the log-ratios matrix and sex was defined as a fixed factor. We verified the normal distribution of the model residuals visually by checking normal probability plots and with the Shapiro-Wilk's test, and the homogeneity of variances and goodness of fit by plotting residuals versus fitted values.

## RESULTS

Each morning we recorded the position and behaviour of  $2.0 \pm 1.0$  flocks of females and  $1.1 \pm 0.3$  flocks of males per site (mean  $\pm$  SD, Table 1). The mean size of the morning foraging area MFA was  $19.0 \pm 9.1$  ha for female flocks ( $N = 10$  sites) and  $23.3 \pm 12.3$  ha for male flocks ( $N = 6$  sites). Gender did not contribute to explaining the MFA difference, because the best model obtained for MFA included legume availability as the only significant predictive factor (Table 2 and Supplementary material, Table S2). The MFA significantly decreased with increasing legume availability ( $-0.06 \pm 0.02$ ; estimate  $\pm$  SE, Table 2) in both sexes.

The mean flock feeding intensity FI measured over the morning was  $31.4 \pm 0.9\%$ . According to the best model, male flocks foraged less intensively than female flocks ( $-0.55 \pm 0.16$ ; estimate  $\pm$  SE, Table 2). FI increased early in the morning, followed by a decrease (Figure 1). The best model to explain FI included sex, legume, time and squared time as predictive factors (Table 2). This model outcompeted simpler models with fewer variables (statistics available in Supplementary material, Table S1). Great Bustard flocks foraged more intensively where legume availability was greater. In addition, FI in male flocks was smaller than in female flocks ( $-0.55 \pm 0.16$ ; estimate  $\pm$  SE of sex=males), but the sex difference decreased in sites with

TABLE 2

Parameters ( $\pm$  SE) and statistical significance of variables included in final generalized linear mixed models for morning foraging area size (MFA) and feeding intensity (FI) of Great Bustard flocks.

[Parámetros ( $\pm$  SE) y significación estadística de las variables incluidas en los modelos lineales generalizados mixtos finales para el tamaño del área matutina (MFA) y la intensidad de alimentación (FI) de los bandos de avutardas.]

		Estimate	Z	P
MFA <sup>a</sup>	Intercept	$2.81 \pm 0.12$	24.21	< 0.001
	Legume abundance	$-0.06 \pm 0.02$	-2.87	0.004
FI <sup>b</sup>	Intercept	$-17.53 \pm 0.43$	-40.88	< 0.001
	Sex <sup>c</sup>	$-0.55 \pm 0.16$	-3.48	0.001
	Legume abundance	$0.14 \pm 0.07$	2.13	0.034
	Time of day	$80.39 \pm 1.77$	45.37	< 0.001
	(Time of day) <sup>2</sup>	$-97.25 \pm 2.14$	-45.37	< 0.001
	Sex $\times$ Legume abundance	$0.14 \pm 0.05$	2.94	0.003

(a) The estimated standard deviation for the random effect Site was 0.18 (residual variance = 0.42).

(b) The estimated standard deviation for the random effect Flock was 1.48 (residual variance = 2.19).

(c) Sex estimates were fitted to males ( $H_0$ : females = 0).

greater legume availability ( $0.14 \pm 0.05$ ; estimate  $\pm$  SE of sex  $\times$  legume interaction).

The study sites were mainly stubbles ( $44.4 \pm 21.1\%$ , mean  $\pm$  SD), sown cereal fields ( $21.7 \pm 20.6\%$ ), ploughed fields ( $19.0 \pm 22.4\%$ ), legume fields ( $3.0 \pm 3.6\%$ ), and olive groves ( $2.9 \pm 3.5\%$ ). Great Bustard flocks were observed mainly in stubbles ( $35.5 \pm 33.3\%$  of the morning time), sown cereal fields ( $21.6 \pm 36.9\%$ ), ploughed fields ( $9.6 \pm 25.2\%$ ), legume fields ( $23.6 \pm 32.0\%$ ), and olive groves ( $3.3 \pm 5.9\%$ ). Compositional analysis showed that legumes and stubbles were the substrate types preferred by Great Bustards (Table 3). Legumes were significantly preferred over stubble ( $t_{4,7} = -15.84$ ,  $P = 0.004$ ) and ploughs ( $t_{4,7} = -7.55$ ,  $P = 0.017$ ; Table 3). There were

no significant differences in habitat selection between flocks of males and flocks of females ( $F_{1,4} = 2.31$ ,  $P = 0.203$ ).

## DISCUSSION

Our results did not support our main hypothesis that the bigger males should move significantly more than the smaller females, regardless of the extreme sexual size dimorphism of Great Bustards and their sexual segregation in unisexual flocks. This lack of support would be explained by the magnitude of the sexual difference that was smaller than the scale at which some of the predictions arise (Haskell *et al.*, 2002; Rosten *et al.*, 2016), although the data sets available need more representation for several animal groups (e.g. large terrestrial birds, Nagy, 1987). Also, bioenergetic patterns associated with body mass could differ within and between species (e.g. Figure 3 in Tinbergen & Dietz, 1994). Although the hypothesis of a body-size-determined food encounter rate (Haskell *et al.*, 2002) applies to differences between species, it could also be applied to body size differences within species (Cederlund & Sand, 1994; Palomares, 1994). The underlying logic linking body size and food encounter rate is the need to meet short-term energy requirements in a fixed period. Optimal foraging theory applied to energetics of avian foraging predicts birds would behave efficiently based on a cost-benefit trade-off (Maurer, 1996), which means an optimising animal adjusts terrestrial movement seeking short-term optimality (Halsey, 2016). Thus, we predicted that the larger the body mass, the greater the MFA size of Great Bustards. Our results did not support this prediction and therefore Great Bustards seemed not to behave as optimal foragers. But perhaps they did behave as optimal foragers if their MFA sizes minimised energy expenditure. Short-term optimality can be achieved by maximising energy intake, minimising the

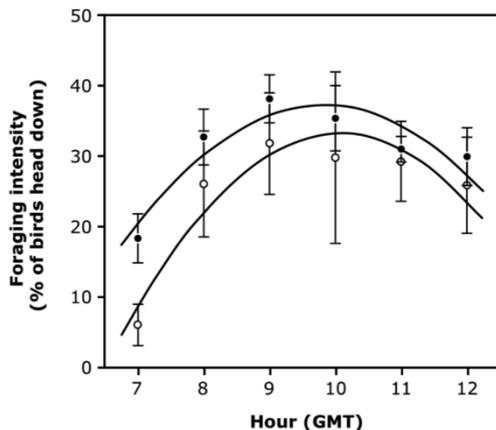


FIG. 1.—Morning feeding intensity (mean  $\pm$  SE) in unisexual flocks of Great Bustards during winter (black dots: female flocks; open dots: male flocks). Feeding intensity was scored as the percentage of birds in a flock that were actively foraging with the head down.

[Intensidad de alimentación matutina (media  $\pm$  SE) en bandos unisexuales de avutardas durante el invierno (puntos negros: bandos de hembras; puntos vacíos: bandos de machos). La intensidad de alimentación se registró como el porcentaje de aves en un bando que estaban forrajeando activamente con la cabeza hacia abajo.]

energy expenditure or both. In fact, there are some indications that in size-dimorphic terrestrial species, the larger sex could reduce the total costs of locomotion by foraging in a smaller MFA (Maurer, 1996; Alonso *et al.*, 2016; Halsey, 2016). Particularly among cursorial birds, body mass may determine most of the daily energy expenditure since the cost of walking is higher than other activities (i.e. Desert Gambel's Quail *Callipepla gambelii*, Goldstein & Nagy, 1985; Halsey, 2016). Incidentally, in summer Great Bustard males reduce their energy expenditure on thermoregulation by walking shorter distances than females between their activity and resting locations (Alonso *et al.*, 2016). Given enough food availability the MFA size of males could be lower than that of the smaller sex. Although we would probably require a greater sample size to detect differences in MFA size between sexes, a larger sample could not be enough to discriminate between the two hypotheses (i.e., food intake maximisation and

energy expenditure minimisation), because both hypotheses set contradictory predictions that could offset each other. This possibility cannot be ruled out in the present study and deserves further research.

Another explanation for the absence of sex differences in the size of the foraging area could be a high availability of the preferred substrate type (legume, Table 3), which could relax the energy link between sexual dimorphism and movement. That is, our main hypothesis would not apply above a saturation threshold of legume availability, making it unnecessary to optimise foraging behaviour (Stephens & Krebs, 1986). Such a threshold is unknown to date. In our study case we reject this explanation because we found a significant negative effect of the surface covered with legume fields on the MFA size. Thus, there must be an energy link between sexual size dimorphism and movement in our study even though we did not find a sexual effect in MFA size.

TABLE 3

Results of the compositional analysis rank matrix of substrate types used by Great Bustard flocks in central Spain based on the comparison of habitat relative availability with frequency of use in the study sites. Significance levels (\* :  $P < 0.05$ ) and ranks are shown according to randomisation results.

[Resultados del análisis composicional de la matriz de rangos de los tipos de sustratos utilizados por bandos de avutardas en el centro de España basados en la comparación de la disponibilidad relativa del hábitat con respecto a la frecuencia de uso en los sitios de estudio. Los niveles de significación (\* :  $p < 0,05$ ) y los rangos se muestran de acuerdo con una aleatorización de los resultados.]

Used	Available					Rank
	Stubble	Sown	Plough	Legume	Olive	
Stubble		+	+	-*	+	3
Sown	-		+	-	-	1
Plough	-	-		-*	-	0
Legume	+*	+	+*		+	4
Olive	-	+	+	-		2

Legume crops were the substrate type most preferred by both sexes (Table 3), as reported in previous studies of foraging behaviour of Great Bustards (Lane *et al.*, 1999; Gooch *et al.*, 2015). Accordingly, the foraging area size decreased with legume availability in both sexes. A decrease in foraging area as food availability increases has been found in other species (Schradin *et al.*, 2010; Uzal *et al.*, 2013). Besides the legume availability effect on the size of morning foraging area, there could be a food distribution effect on animal mobility. Where food is patchily distributed the individual would have to move between more patches and thus increases its foraging area (Tufto *et al.*, 1996; Haskell *et al.*, 2002; Säid *et al.*, 2005; Seidel & Boyce, 2016). Here we did not evaluate the effect of spatial distribution of legume fields on MFA sizes because legume fields were aggregated according to an agri-environmental scheme (Ponce *et al.*, 2014 and own unpub. data), which was not aimed at exploring the correlation between the distributions of legume fields and Great Bustard morning distributions.

A complex web of functional and hierarchical relationships underlies the ecology of home range, where food availability is the primary determinant of home range ecology in birds (Rolando, 2002). Perhaps a sexual effect on foraging area size could be found over longer periods than mornings, although this possibility is contrary to the well-known fact that for birds the morning is the most important part of the day for feeding during the Palearctic winter. Home-range area sizes calculated with individual monitoring of Great Bustards from dawn to dusk would solve this uncertainty.

Feeding intensity (FI) increased and then decreased over the morning in both sexes. The early morning increase responded to the common need of diurnal species to fill their empty guts after a long fast during the night. The decreasing feeding intensity towards noon could result from progressive satiation, and

the consequent need to spend time digesting food (i.e. a digestive bottleneck, Sedinger & Raveling, 1988; Van Gils *et al.*, 2005). The foraging behaviour described for another Great Bustard population (Martínez, 2000) could not identify a curvilinear feeding intensity pattern because in that study the morning foraging data were grouped in only two periods (05:00-08:00 hrs and 08:00-11:00 hrs). Therefore, both studies are not contradictory or at least are not comparable with respect to the form of the morning feeding intensity curve.

Males could feed less intensively if they accepted more food types than females. In fact, the female diet is more selective and less diverse (Bravo *et al.*, 2016), which could explain why the feeding intensity of males was lower than that of females. This sex difference decreased in sites with greater legume availability (significant interaction between sex and legume availability, Table 2), in agreement with optimal foraging theory (Stephens & Krebs, 1986). Above a saturation threshold of legume availability, Great Bustards would not need to optimise foraging behaviour and feeding intensity would not differ between flocks of males and flocks of females.

Males that foraged slightly less intensively than females could compensate with longer periods of foraging (Martínez, 2000) and bigger bite size (Alonso *et al.*, 2009) that would allow them to obtain enough food relative to their absolute daily energy requirements, as found in other species (Gross *et al.*, 1993; Pérez-Barbería & Gordon, 1999). In summary, we found that FI was not greater in males than in females nor was MFA size larger in males than in females. Therefore, we conclude that the larger body size of Great Bustard males was not associated with a more extensive morning foraging area in winter. This conclusion does not rule out the possibility of a significant effect of body size over longer periods (e.g., daytime from dawn to dusk). A test of that hypothesis deserves further research.

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## SUPPLEMENTARY ELECTRONIC MATERIAL

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**Table S1.** Universal Transverse Mercator (UTM) coordinates of sites where Great Bustard flocks were observed.

**Table S2.** Candidate GLMM models to explain the morning foraging area and feeding intensity of Great Bustard flocks in central Spain.

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**FOOD AVAILABILITY BUT NOT SEX DETERMINES MORNING  
FORAGING AREA SIZE IN THE GREAT BUSTARD *OTIS TARDA*,  
THE MOST SEXUALLY SIZE-DIMORPHIC BIRD SPECIES**

**LA DISPONIBILIDAD DE ALIMENTO Y NO EL SEXO DETERMINA EL  
TAMAÑO DEL ÁREA DE FORRAJE O MATINAL EN LA AVUTARDA COMÚN  
*OTIS TARDA*, EL AVE CON MAYOR DIMORFISMO SEXUAL**

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**TABLE S1**

Universal Transverse Mercator (UTM) coordinates of sites where Great Bustard flocks were observed.

*[Coordenadas UTM de los sitios en los que fueron observados los bandos de avutardas.]*

Site	Local name	Longitude	Latitude	Altitude (m)
A	Buitrera	459035.73	4504577.81	677
B	Campoalbillo	459233.95	4507799.72	697
C	Camporeal	470569.34	4464869.83	774
D	Caraquiz	459092.69	4512766.02	706
E	Colegio	468053.86	4491917.72	683
F	Daganzo	462925.91	4485075.62	632
G	Fresno	462925.84	4492120.59	696
H	Gallinero	458744.22	4499583.96	689
I	Grullero	454436.16	4501151.53	621
J	Talamanca	458142.80	4509011.95	679

**TABLE S2**

Candidate GLMM models to explain the morning foraging area and feeding intensity of Great Bustard flocks in central Spain. Model selection was based on Akaike's Information Criterion corrected for small sample sizes (AICc). Delta and weight values ( $\Delta\text{AICc}$ ,  $w\text{AICc}$ ) for each AICc are also shown. Marginal  $R^2$  ( $R_m^2$ ) and conditional  $R^2$  ( $R_c^2$ ) were computed for each model using methods described by Nakagawa and Schielzeth (2013).

*[Modelos GLMM candidatos para explicar el área matutina de alimentación y la intensidad de alimentación de los bandos de avutardas en el centro de España. La selección del modelo se basó en el criterio de información de Akaike corregido para pequeños tamaños de muestra (AICc). También se muestran los valores de Delta y el peso ( $\Delta\text{AICc}$ ,  $w\text{AICc}$ ) para cada AICc. El  $R^2$  marginal ( $R_m^2$ ) y el  $R^2$  condicional ( $R_c^2$ ) se calcularon para cada modelo usando los métodos descritos por Nakagawa y Schielzeth (2013).]*

<b>Models</b>	<b>df</b>	<b>AICc</b>	<b><math>\Delta\text{AICc}</math></b>	<b>wAICc</b>	<b><math>R_m^2</math></b>	<b><math>R_c^2</math></b>
<b>Morning foraging area MFA</b>						
1) Legume abundance	3	1513.9	0	0.43	0.088	0.683
2) Sex $\times$ Legume abundance	5	1516.9	3.0	0.42	0.062	0.701
3) Sex	3	1519.8	5.9	0.15	0.033	0.715
<b>Flock feeding intensity FI</b>						
1) Sex + Legume abundance + Sex $\times$ Legume abundance + Time + Time <sup>2</sup>	8	55050.5	0	0.98	0.050	0.430
2) Legume abundance + Time + Time <sup>2</sup>	6	55058.8	8.3	0.02	0.046	0.427
3) Sex + Time + Time <sup>2</sup>	6	55117.8	67.4	0.00	0.026	0.042