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RESEARCH ARTICLE

Dietary divergence in the most sexually size-dimorphic bird

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ABSTRACT

In sexually size-dimorphic species, physiological constraints derived from differences in body size may determine different food requirements and thus a trophic niche divergence between males and females. These relationships between sexual size dimorphism (SSD) and dietary overlap are not well understood in birds. We analyzed differences between the sexes in diet composition, dietary diversity, diet selection, and volume and density of droppings, as well as the dietary overlap between sexes, in the Great Bustard (*Otis tarda*), the species showing the highest SSD among birds. We discuss the differences that we found in relation to various predictions derived from ecological and physiological differences between the sexes, under the hypothesis that these differences are ultimately determined by the strong SSD of this species. As expected, our best linear mixed-effects food selection models included sex as a main factor explaining differences in diet composition and dietary diversity of Great Bustards throughout the annual cycle. Both sexes were mostly herbivorous, consuming legumes when they were available. Males consumed fewer arthropods, but of significantly larger size, than females. The droppings of males were larger, heavier, and slightly denser than those of females. Males showed higher dietary diversity than females, except during the postmating season. The mean dietary overlap between the sexes was 0.7, one of the smallest values among birds. Overall, our results suggest that the species' extreme SSD along with the distinct reproductive role of each sex might explain the trophic niche divergence in the Great Bustard.

Keywords: sexual segregation, foraging ecology, body size, resource partitioning, agro-steppe, dietary overlap, herbivory, trophic behavior

Divergencia en la dieta del ave con más dimorfismo sexual de tamaño

RESUMEN

En las especies con dimorfismo sexual de tamaño, las limitaciones fisiológicas derivadas de las diferencias en el tamaño corporal pueden determinar diferentes requerimientos alimentarios y por ende una divergencia del nicho trófico entre los machos y las hembras. Estas relaciones entre el dimorfismo sexual de tamaño corporal (DST) y el solapamiento de la dieta no están bien entendidas en las aves. Analizamos las diferencias sexuales en la composición de la dieta, la diversidad de la dieta, la selección de la dieta, y el volumen y la densidad de las heces, así como el solapamiento de la dieta entre sexos en *Otis tarda*, la especie con mayor DST entre las aves. Las diferencias encontradas fueron analizadas con relación a varias predicciones derivadas de las diferencias ecológicas y fisiológicas entre los sexos, bajo la hipótesis de que estas diferencias están determinadas en última instancia por el fuerte DST en esta especie. Como esperábamos, nuestros mejores modelos lineales de efectos mixtos de selección de alimentos incluyeron al sexo como el factor principal que explica las diferencias en la composición y en la diversidad de la dieta en *O. tarda* a lo largo del ciclo anual. Ambos sexos fueron principalmente herbívoros, consumiendo legumbres cuando estaban disponibles. Los machos consumieron menos artrópodos pero de tamaño significativamente más grande que las hembras. Las heces de los machos fueron de mayor tamaño y más pesadas, y levemente más densas que las de las hembras. Los machos mostraron una mayor diversidad en la dieta que las hembras, excepto durante la estación post reproductiva. El solapamiento promedio de la dieta entre los sexos fue 0.7, uno de los valores más pequeños entre las aves. En conjunto, nuestros resultados sugieren que el enorme DST en esta especie, junto con el rol reproductivo distintivo de cada sexo, podrían explicar la divergencia del nicho trófico en *O. tarda*.

Palabras clave: agro-estepa, comportamiento trófico, ecología de forrajeo, herbivoría, partición del recurso, segregación sexual, solapamiento de la dieta, tamaño corporal

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INTRODUCTION

Sexual size dimorphism (SSD) is widespread among animals. Male-larger dimorphism is extreme in some polygynous species, where sexual selection, operating through male competition and female choice, favors larger males (Shine 1989, Andersson 1994, Fairbairn 2013). Distinct reproductive roles, sex-specific metabolism, and sexual segregation behavior also contribute to dietary divergence between males and females. In birds, sexual differences in energetic and nutritional requirements are fulfilled through sex-specific habitat selection (Pasinelli 2000, Elson et al. 2007), foraging behavior (González-Solís et al. 2000, Markman et al. 2006), food intake patterns (Pepper et al. 2000, Odden et al. 2003), diet (Le V. Dit Durell et al. 1993, Forero et al. 2002), and even digestion (Markman et al. 2006).

In this study, we analyzed differences in the diets of male and female Great Bustards (*Otis tarda*) (Figure 1) through a detailed analysis of their food selection patterns during a complete annual cycle. We discuss the differences that we found in relation to various ecological and physiological differences between the sexes, which are ultimately determined by the strong SSD of this species. Indeed, Great Bustards show the most extreme SSD among birds, with adult males being 2.44 times heavier than adult females (Alonso et al. 2009a). This species is therefore an excellent candidate to investigate SSD-related differences in the diets of males and females.

Previous studies have described the species' diet, but have not analyzed sexual differences in the diet or diet selection patterns of males and females (Palacios et al. 1975, Lucio 1985, Lane et al. 1999). In a previous study, we found some sexual differences in the diet composition of juvenile Great Bustards (Bravo et al. 2012), and hypothesized that some of these differences could increase as SSD increases toward adulthood. In contrast, the less-dimorphic North African Houbara Bustard (*Chlamydotis undulata undulata*) does not show any apparent dietary divergence between the sexes (Bourass et al. 2012).

In our study area, Great Bustards of both sexes are partial migrants, with sedentary and migratory individuals living together in the same population. The migratory fraction of the population shows differential migration patterns by sex (Alonso et al. 2009b, Palacín et al. 2009), which obviously could lead to sexual differences in their diets. However, here we were interested in unravelling any subtle sexual differences in the diets of Great Bustards living in sympatry throughout the whole year. Like migratory individuals, sedentary individuals sharing the same area also live year-round in sexually segregated flocks, and meet only for mating. Previous studies have concluded that both the sexually differentiated migration patterns of migratory Great Bustards and the marked sexual segregation of sedentary individuals are consequences of the marked SSD (Alonso et al. 2009a, in press, Palacín et al. 2009), which is ultimately determined by the strong sexual selection operating in this species (Alonso et al. 2010). In this study, we suggest that the strong SSD might also be the primary ultimate cause of the dietary divergence between the sexes, probably mediated through subtle spatial segregation and sexual differences in microhabitat selection when males and females share the same area and main habitat (Alonso et al. in press).



FIGURE 1. Adult male Great Bustard foraging on legumes, a preferred food source, in central Spain. Photo credit: ©Carlos Palacín

It is known that males and females of species with marked SSD exploit different food resources, either because they have different nutritional and energetic requirements or because in this way they reduce resource competition between the sexes (Shine 1989, Ruckstuhl and Neuhaus 2006). Also, as a consequence of extreme SSD, many physiological and biochemical processes, such as heartbeat, respiration, and metabolic rate, are expected to show allometric scaling, primarily associated with the ratio between body surface and mass or volume (Karasov 1990, Witmer and Van Soest 1998, Brown and Downs 2003, van Gils et al. 2005a, Santiago-Quesada et al. 2009). Overall energetic requirements should be size-specific, and thus SSD-induced dietary differences between the sexes should be expected in sexually size-dimorphic species, in addition to differences imposed by their typically polygynous breeding system and associated differential reproductive roles of males and females.

Therefore, based on the marked sexual segregation in the Great Bustard, in this study we made the following predictions. First, we expected a noticeable divergence between the diets of the sexes due to their extraordinary

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SSD, and, consequently, a relatively low dietary overlap value compared with other birds with lower SSD. Second, we expected sexual differences in food selection values throughout the year, due to the marked differences in the reproductive roles of this strongly polygynous species (Fairbairn 1997). Third, as prey size is usually related to the size of the predator (Andersson 1994), we expected differences in the size of prey consumed by males and females. Such differences have been found in the Australian Bustard (*Ardeotis australis*; Ziembicki 2010) and in juvenile Great Bustards (Bravo et al. 2012), with males consuming bigger prey than females in both cases. Fourth, we expected sexual differences in the physical characteristics of droppings (weight, volume, and density) and in the seasonal patterns of variation in these characteristics. Our rationale was that sexual differences in diet composition could vary among seasons because food availability changes seasonally and nutritional requirements change throughout the annual cycle in a different way for each sex. In addition, dietary changes impose nutritional and physical limits on the digestive system and vice versa. Birds may survive on a low-quality diet by reducing their metabolism and altering their gut morphology (Geluso and Hayes 1999) to compensate for decreased digestive efficiency associated with a low-quality diet. Alternatively, the length of the intestinal tract may increase during periods of hyperphagia (Karasov et al. 1996), and gut morphology may change in relation to food quality and quantity (Castro et al. 1989, DeGolier et al. 1999). Because the surface and volume of the gut affect assimilation efficiency (Santiago-Quesada et al. 2009), these factors may also have an effect on the size and density of droppings.

Finally, extending the Jarman-Bell principle (a lower ratio of metabolic requirement to gut capacity allows larger herbivores to subsist on lower-quality diets compared with smaller herbivores) to the intraspecific level, we expected larger males to have a lower-quality diet (Bell 1970, Jarman 1974, Demment and Van Soest 1985). Although this prediction has been verified in herbivorous mammals, where males seem to have a simpler, lower-quality diet than females (Staines et al. 1982, Bowyer 1984, 2004, Beier 1987, Ruckstuhl and Neuhaus 2006, Pérez-Barbería et al. 2008), only a few studies with raptors and fish-eating species have explored sexual divergence in the diets of birds (Boal and Mannan 1996, Webster 1997, González-Solís et al. 2000, Ishikawa and Watanuki 2002, Lee and Severinghaus 2004, Xavier et al. 2006). In herbivorous birds, body size has been suggested as an important factor driving foraging behavior and diet (Durant et al. 2003, Mini 2012). Some trophic niche partitioning between the sexes has been recently suggested in the Greater Prairie-Chicken (*Tympanuchus cupido*; Blanco-Fontao et al. 2013). However, the relationships between SSD and dietary overlap between males and females are still poorly known in birds (Székely et al. 2007), and our study aimed to gain some insight into this topic.

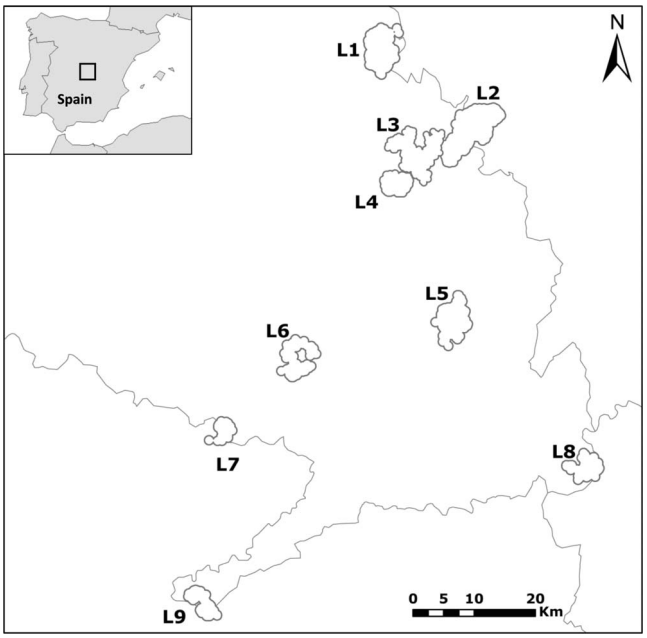


FIGURE 2. Locations of the study areas in central Spain. Nine Great Bustard areas (L1–L9) were sampled. The perimeters of these areas were drawn as a 500 m buffer around all bustard locations from censuses done in 2004–2010.

METHODS

Study Area

We conducted our fieldwork in central Spain, where a population of ca. 1,500 Great Bustards has been intensively studied through 2 decades (Martín et al. 2012). Here, Great Bustards behave as partial migrants, but the numbers of males and females found in the study area year-round are still high (during the study period, numbers varied from a maximum of 507 males and 1,231 females in the spring of 2007 to a minimum of 235 males and 841 females in the summer of 2007; J. C. Alonso personal observation). Droppings and food availability were sampled in all 9 Great Bustard areas of Madrid province (Figure 2). The areal extents of these 9 Great Bustard areas were calculated by merging 500 m buffers around each bustard location recorded in our censuses of the species in Madrid province in 2004–2010. The habitat in these areas is mostly dedicated to cereal crop production (>80% of the land surface is occupied by common wheat [*Triticum aestivum*] and common barley [*Hordeum vulgare*] fields). Some olive (*Olea europaea*) groves and wine grape (*Vitis vinifera*) vines have been planted in the remaining area. Occasional sheep grazing occurs in stubble and fallow fields. Cereal is

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usually grown in a traditional 2-yr rotation; it is sown between October and December, harvested in late June–early July, and the field is later left fallow for a whole year.

Diet Analysis

The diets of Great Bustards were studied using 619 droppings (299 from females and 320 from males) collected in the 9 Great Bustard areas across 3 seasons: winter (November, 2006–January, 2007), mating (April, 2007), and postmating (July, 2007). We analyzed the composition of the diet, dietary overlap between the sexes, dietary diversity, diet selection by compositional analysis, and size of arthropod prey species.

Fresh droppings were collected at roosting sites at dawn (>75% of droppings), at midday resting sites after Great Bustards resumed foraging (>20%), and throughout the day at foraging sites (<5%). We assumed that droppings collected at roosting and resting sites accounted for the food intake of the previous evening and morning, respectively (see Bautista et al. [2013] for collection method details). We also recorded the UTM coordinates of the collection site, the substrate type (stubble, ploughed, legume, sown, fallow, and field border), the date of collection, and sex of the flock. Male and female Great Bustards live in separate single-sex flocks, so droppings from each sex were easily distinguished (Bautista et al. 2013, Bravo et al. 2014). Droppings were mostly collected from stubble, ploughed, and cereal fields (>70% of droppings), with some collected from fallow and legume fields (<20% and >10%, respectively). All droppings were dried for 48 hr at 60°C and then weighed (accuracy: 0.001 g). The volume of each dropping was measured using a graduated cylinder and glass spheres (1.5 mm diameter). Dry droppings were introduced into a graduated cylinder and covered with glass spheres. The cylinder was shaken until there was no further decrease in total volume. The dropping volume was then calculated as the difference between the total volume and the volume of glass spheres. Dropping density (g per cm^3) was calculated as dry weight divided by volume.

Each dropping was partitioned into green plant material, arthropods, seeds, and fruits, the latter of which were identified through their undigested seeds. These components were weighed separately and the dry weight proportion of each was calculated per dropping. Plant species were identified and quantified by microhistological techniques (Catán et al. 2003) using our reference collection of tissues from the study area. From each sample, 80 fields were examined with a microscope (40×), recording the presence or absence of each plant species. We calculated the percentage of each species in the diet as $OD = n_i \times 100 / 80$, where n_i is the number of microscope fields in which species i occurred. We also estimated the percentage of each plant species in the diet as the percentage of dry mass in the droppings. All identified plants and their percentages in the diet are shown in Appendix Table 6. For statistical tests of dry weight percentages and compositional analysis, we grouped plant species into 3 functional groups: cultivated cereals, leguminous species, and weeds.

Arthropods were identified to order or family level using our reference collection and published identification keys (Calver and Wooller 1982, Moreby 1988). We estimated a minimum number of ingested individuals for each arthropod order or family using key body parts (Moreby 1988). In each dropping, recognizable prey remains were measured (e.g., head width, pronotum length, elytra length, and mandible length) with a pair of digital calipers (0.01 mm precision). Length (mm) and dry weight (mg) were estimated for each individual prey item by means of published linear regressions for each taxon (Hódar 1997). Average prey body size (mm) was calculated for each dropping. We calculated the percentage of arthropods in the diet as the percentage dry mass of each family or order in the droppings (Appendix Table 7).

Seeds and fruits were classified to family or species. We calculated the percentage of seeds and fruits in the diet as the percentage dry mass of each taxon in the droppings (Appendix Table 8). The fruit component of the diet was calculated as the dry weight of whole olives, grapes, and black nightshades (*Solanum nigrum*), estimated according to the number of their seeds found in the droppings and using dry masses and mean numbers of seeds obtained from samples of these fruits. For dietary diversity and overlap analyses, we used the percentages of all identified plants, arthropods, seeds, and fruits (Appendix Tables 6, 7, and 8).

Food Availability

For diet selection analyses, the availability of plants, arthropods, seeds, and fruits was estimated in the 9 Great Bustard areas (Figure 2). Within each Great Bustard area, a 400 m buffer around buildings and roads was excluded to obtain the total farmland surface available as foraging substrate (Torres et al. 2011). Buffers were calculated with ArcGIS 9.3 (ESRI, Redlands, California, USA). In the resulting total buffer area comprising all 9 Great Bustard areas, 3,108 fields were randomly chosen to determine the relative surface of each substrate per Great Bustard area and season. The main substrate types were legumes, sprouted cereals, cereal stubble, ploughed fields, fallow fields, and borders between cultivated fields. In each season, several fields were sampled from each substrate type (range: 14–33 fields per Great Bustard area and season), totaling 479 fields with availability data for plants, seeds, and arthropods. In winter, 2 samples were taken, one each in November, 2006, and January, 2007, and the results were averaged to get single values for the wintering

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season. A mating season sample was collected in April, 2007, and a postmating season sample was collected in July, 2007.

Plant and seed availabilities (kg ha^{-1}) were estimated by randomly throwing a 25 × 25 cm metal square 20 times per sampling field, which is adequate to get reliable information about plant composition (Ponce et al. 2011). In each square, plants were identified and sorted into 3 functional groups (cultivated cereals, legumes, and weeds), and their biomasses (kg) were calculated from estimated cover values through allometric equations (Smith and Brand 1983). The mean plant biomass per substrate type was then estimated for each Great Bustard area and season. The total surfaces of the different substrate types varied among Great Bustard areas, and therefore the mean plant biomass (kg) was multiplied by the relative surface area of each substrate type.

Seeds were counted and sorted by size into 4 groups (<1 mm; 1–5 mm; 5–10 mm; >10 mm) within each sample square. The mean weight of each group was obtained in the laboratory and the total seed biomass availability (kg ha^{-1}) was then calculated for each Great Bustard area and season by multiplying the relative surface area of each substrate type by the mean seed biomass in each substrate type and Great Bustard area.

Fruit availability (kg ha^{-1}) was estimated for olives, grapes, and black nightshades. The mean dry weight of each fruit was calculated in the laboratory ($n = 20$ fruits of each species). The total fruit biomass availability (kg ha^{-1}) was then calculated for each Great Bustard area and season. In the case of olives and grapes, the number of fruits was counted on a sample of olive trees and grapevines ($n = 20$) and multiplied by the total number of olive trees and grapevines in the Great Bustard area, which was estimated from aerial photographs using SIGPAC software (http://sigpac.mapa.es/fega/visor/). For black nightshade, the number of *Solanum* plants was estimated by randomly throwing a 25 × 25 cm metal square 20 times per field in each substrate and counting nightshade fruits within each sampling square. Mean fruit biomass was estimated for each substrate type per Great Bustard area and multiplied by the relative surface area of each substrate type in the Great Bustard area.

Arthropod availability (kg ha^{-1}) was estimated in transects (30 m long × 1 m wide) by walking slowly and counting and identifying all invertebrates observed to the family level (Lane et al. 1999, Ponce et al. 2014). We collected a random sample of 7,515 arthropods (12% of the total detected). To estimate arthropod biomass we followed the protocol described in Hódar (1996), in which length–weight equations are provided for adult arthropods of the Mediterranean region. Maximum body length excluding all appendages (legs, wings, antennae, and ovipositors) was measured for all collected adult arthropods with a pair of digital calipers (0.01 mm precision). Estimates of weights were calculated by means of linear regressions of body weight on body length for each family (order in some cases) for each transect and, subsequently, for each sampled field (Clere and Bretagnolle 2001, Jiguet 2002). For each season, mean arthropod biomass was estimated for each substrate type per Great Bustard area and multiplied by the relative surface area of each substrate type in the Great Bustard area (Ponce et al. 2014).

Statistical Analyses

We used the relative availabilities of the main food types, season, and sex as potential predictors of the composition and diversity of Great Bustard diets. Variables that significantly explained diet composition and diversity were selected with linear mixed-effects models (McCullagh and Nelder 1989). We assumed a binomial error distribution and a logit-link function in predictive models of the percentages of legumes, weeds, cultivated cereals, arthropods, seeds, and fruits in droppings (dependent variables). The normal distribution was selected to calculate the Shannon index (H') as a measure of dietary diversity. Sex and season (wintering, mating, and postmating) were defined as independent variables. We included the availability of legumes, weeds, cultivated cereals, arthropods, seeds, and fruits as covariates. As diet composition and food availability may vary among areas, Great Bustard area was included as a random effect in the models. Following Zuur et al. (2007), we built 'beyond optimal' models (the most complex models, with all factors and their plausible interactions) with different random error structures using the restricted maximum likelihood estimation procedure. Once the random structure had been defined, we defined the fixed effects structure using the maximum likelihood ratio test. Models were evaluated with Akaike's Information Criterion to determine the best predictive model. A model was defined as the best model when it had the lowest AIC_c value with a difference (ΔAIC_c) >2 compared with the second-best model. Model-averaging was performed when more than 1 model had $\Delta AIC_c < 2$. To evaluate the amount of variance explained, we calculated the R^2 values of the models using the methods of Nakagawa and Schielzeth (2013). We calculated the marginal R^2 (R^2_m), which describes the variance explained by the fixed effects, and the conditional R^2 (R^2_c), which is concerned with the variance explained by both the fixed and random effects (Nakagawa and Schielzeth 2013). We verified the normal distribution of model residuals by visually checking the normal probability plots and also with a Shapiro-Wilk's test. The homogeneity of variance and goodness-of-fit was checked with plots of residuals vs. fitted values.

The diversity of dietary items in the droppings was calculated using the Shannon diversity index: $H' =$

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$-\sum(p_i \cdot \ln(p_i))$, where p_i is the proportion of taxon i per dropping. We evaluated overlap in the diet between the sexes with the simplified Morisita index (Horn 1966), which ranges from 0 (no overlap) to 1 (complete overlap). This index has relatively low bias and is appropriate for studies in which the selection of resources is reported as a proportion of the total resources used by the animal (Krebs 1989). Firstly, we calculated an overlap index for plants, arthropods, seeds (including fruits), and total diet for each season and Great Bustard area using the proportions of identified taxa (family or species level). Secondly, we analyzed seasonal changes in the overlap index using Kruskal-Wallis tests, where the overlap index was the dependent variable and season was a fixed factor. We used the FSA package (Ogle 2013) in R 2.15.1 (R Development Core Team 2012) to calculate the overlap index.

Diet selection was examined using a compositional analysis (Aebischer et al. 1993) in the Excel Macro version Compositional Analysis 6.1 plus (Smith 2010), which examines food use in relation to availability, taking the log-ratio differences of used and available foods. The proportional availabilities of all plants (weeds, cultivated cereals, and legumes), arthropods, seeds, and fruits were compared with their respective proportions in the droppings. Null proportions were replaced with 0.01 (Aebischer et al. 1993). The value of t, which measures the significance of the deviation in the use of each food category relative to random, was also obtained for each food category (Aebischer et al. 1993). This was determined by randomization 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 food type. From the log-ratios matrix, the sexual effect on rank preference was analyzed with a generalized linear model (GLM), in which the dependent variable was the log-ratios matrix and sex was defined as a fixed factor. This analysis was performed in SPSS 19.0 (IBM Corporation, Armonk, New York, USA).

A total of 1,528 prey items from 179 mating and postmating droppings was measured to explore differences in prey size of male vs. female Great Bustards. Average prey body size was sorted into 5 size categories ($\leq$10.0, 10.1–20.0, 20.1–30.0, 30.1–40.0, $>$40.1 mm), and the relative frequency of each size class was calculated for each dropping. Sexual differences were analyzed with a chi-square test. These analyses were carried out in R 2.15.1 (R Development Core Team 2012).

Differences in the weight, volume, and density of droppings between the sexes and among seasons were assessed with generalized linear mixed models (GLMMs). The weight, volume, and density of droppings could depend on diet composition. Therefore, dry weight percentages of plants, arthropods, seeds, and fruits were included as covariates. Sex and season were defined as fixed effects, and Great Bustard area was defined as a random effect. We utilized a Poisson distribution and a log-link function for the models. GLMMs were run as explained above. Firstly, we compared 'beyond optimal' models with different random error structures. Once the random structure had been defined, we defined the fixed effects structure using maximum likelihood. Models were ranked with Akaike's Information Criterion to determine the best predictive model. Marginal R^2 and conditional R^2 were also calculated as explained above. Normal distribution was checked as explained above. All GLMMs were run in R 2.15.1 (R Development Core Team 2012).

RESULTS

Diet Composition

The dry weight fractions of the whole sample of droppings ($n = 619$) were 79.6 $\pm$ 29.5% green plant material, 9.8 $\pm$ 23.0% arthropods, 6.5 $\pm$ 18.2% fruits, and 4.1 $\pm$ 11.0% seeds (mean $\pm$ SD). Up to 67 green plant species were identified, although most of these plants were recorded only occasionally (Appendix Table 6). The most frequently recorded functional groups were weeds (45.9 $\pm$ 31.1% SD dry weight) and legumes (25.1 $\pm$ 28.1% SD dry weight; Figure 3). The best models included season and sex as significant factors influencing the percentages of the 6 food types considered (legumes, weeds, cultivated cereal plants, arthropods, seeds, and fruits; Table 1, Appendix Table 9). The best model for legume consumption also included legume availability (Table 1). Legume consumption increased with legume availability (0.03 $\pm$ 0.01, estimate $\pm$ SE; Table 1), reaching its highest value during the mating season for both sexes (Figure 3A). Legume consumption was higher for females during the wintering season, and weed consumption was higher for males in all seasons (Table 1, Figures 3A, 3B). Males consumed more cultivated cereal plants than females in winter, with both sexes showing much lower consumption during the mating season (Figure 3C).

A total of 4,612 individuals of 7 arthropod orders was identified in the droppings (Appendix Table 2). The most frequently observed orders were Coleoptera (found in 36.5% of droppings), Hymenoptera (15.7%), Hemiptera (12.1%), and Orthoptera (5.5%). The best model explaining arthropod consumption included season, sex, and arthropod availability as significant factors (Table 1, Appendix Table 9). Arthropod consumption was higher during the postmating period (3.21 $\pm$ 0.07, estimate $\pm$ SE; Table 1) than in the other 2 seasons (Figure 3D), and was positively influenced by arthropod availability (0.20 $\pm$ 0.06, estimate $\pm$ SE; Table 1, Figure 3D). Females consumed more arthropods than males during the postmating season (Figure 3D).

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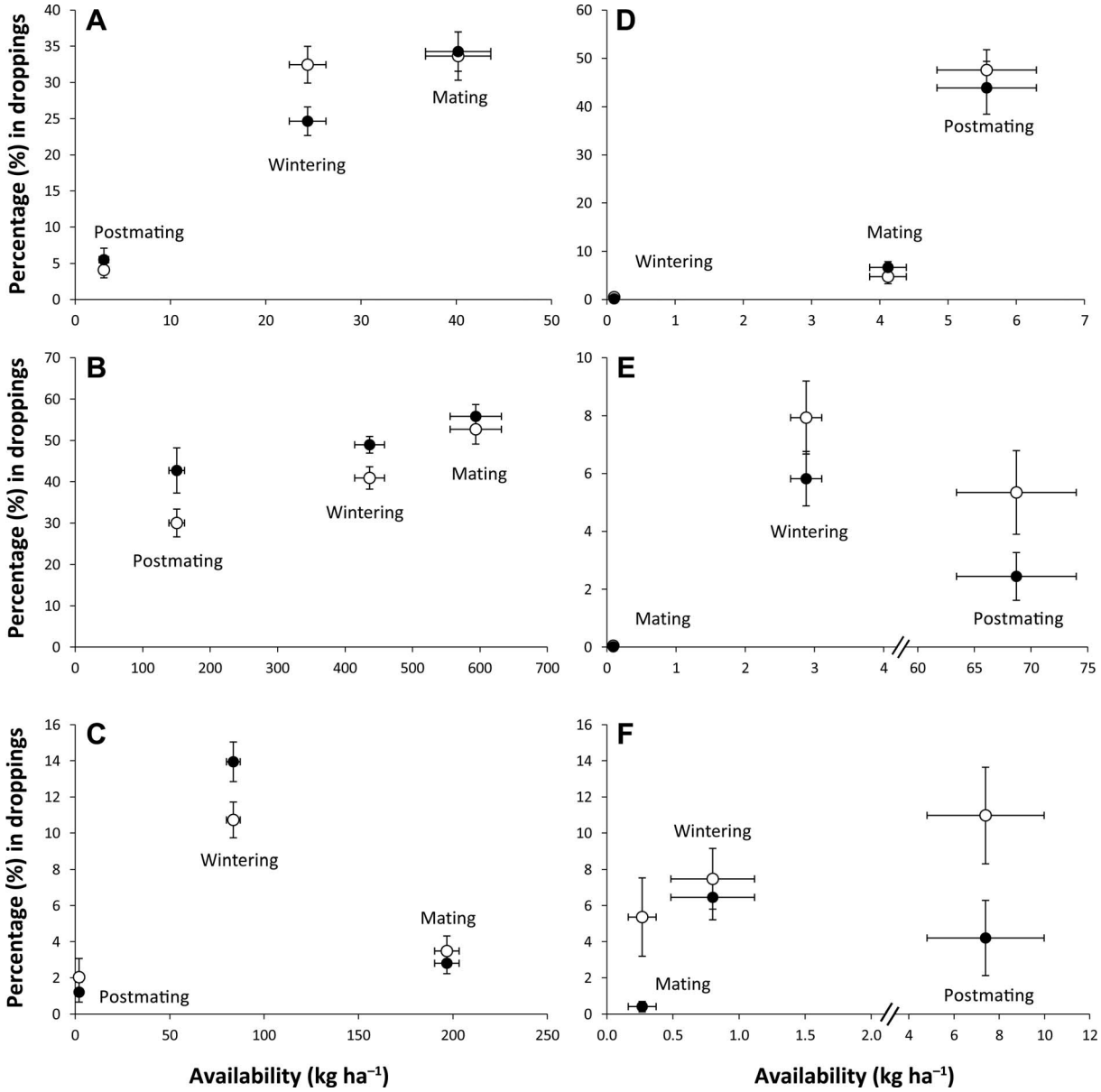


FIGURE 3. Consumption (% in Great Bustard droppings; mean ± SE) vs. availability (kg ha^{-1}; mean ± SE) of (**A**) legumes, (**B**) weeds, (**C**) cereal plants, (**D**) arthropods, (**E**) seeds, and (**F**) fruits by season (wintering, mating, and postmating) in central Spain. Open circles = females; filled circles = males.

The seeds of 11 plant families were identified in Great Bustard droppings (Appendix Table 3), with the highest frequencies coming from cereal species, such as common wheat (*Triticum aestivum*) and common barley (*Hordeum vulgare*), which were in 39.9% of all droppings. Model selection for seed consumption resulted in 2 models with $\Delta AIC_c < 2$. Model-averaging resulted in a GLMM that included season and seed availability as significant factors (Table 1, Appendix Table 9). Seed consumption was higher during the wintering and postmating seasons than in the mating season (Table 1, Figure 3E). Females tended to consume more seeds than males in all seasons, although this difference was not significant (–12.17 ± 28.67, estimate ± SE; $P = 0.67$; Table 1).

The best model describing fruit consumption included season, sex, and fruit availability as significant factors (Table 1, Appendix Table 9). Olive consumption was highest in winter (8.7% of droppings; Appendix Table 3), while grape and black nightshade consumption was highest during the postmating season (1.2% and 6.8% of droppings, respectively; Appendix Table 8). Females consumed more fruits than males in all seasons (Figure 3F). Fruit consumption

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TABLE 1. Final generalized linear mixed models (GLMMs) for the most frequently found food types in droppings of Great Bustards in central Spain: green vegetables (legumes, weeds, and cereal plants), arthropods, seeds, and fruits.

Fixed effects [a]		Estimate	SE	*Z*	*P*
Legume consumption					
Intercept		−1.37	0.33	−4.10	0.000
Sex (male)		−0.19	0.05	−3.54	0.000
Season	Wintering	0.29	0.04	7.54	0.000
	Postmating	−2.25	0.08	−28.38	0.000
LegAVAIL [b]		0.03	0.01	4.92	0.000
Sex*Season	Male*Wintering	−0.28	0.05	−5.49	0.000
	Male*Postmating	0.00	0.11	−0.04	0.969
Sex*LegAVAIL [b]		0.01	0.01	2.14	0.032
Weed consumption					
Intercept		0.71	0.27	2.66	0.008
Sex (male)		−0.11	0.04	−2.41	0.016
Season	Wintering	−0.85	0.03	−26.19	0.000
	Postmating	−1.61	0.04	−37.25	0.000
WeedAVAIL [b]		0.00	0.00	−13.43	0.000
Sex*Season	Male*Wintering	0.19	0.04	4.33	0.000
	Male*Postmating	1.36	0.06	22.28	0.000
Sex*WeedAVAIL [b]		0.00	0.00	14.14	0.000
Cereal consumption					
Intercept		−2.75	0.24	−11.33	0.000
Sex (male)		0.09	0.13	0.72	0.473
Season	Wintering	0.73	0.08	8.97	0.000
	Postmating	−1.35	0.13	−10.40	0.000
CerealAVAIL [b]		0.00	0.00	−8.65	0.000
Sex*Season	Male*Wintering	0.35	0.11	3.15	0.002
	Male*Postmating	−0.73	0.22	−3.37	0.008
Sex*CerealAVAIL [b]		0.00	0.00	−2.43	0.015
Arthropod consumption					
Intercept		−3.20	0.30	−10.75	0.000
Sex (male)		0.49	0.07	7.18	0.000
Season	Wintering	−2.36	0.13	−17.95	0.000
	Postmating	3.21	0.07	48.65	0.000
ArthroAVAIL [b]		0.20	0.06	−3.56	0.004
Sex*Season	Male*Wintering	−0.61	0.08	−7.24	0.000
	Male*Postmating	−1.91	0.25	−7.75	0.000
Seed consumption					
Intercept		−8.05	0.63	12.71	0.000
Sex (male)		−12.17	28.67	0.42	0.672
Season	Wintering	5.32	0.58	9.18	0.000
	Postmating	5.50	0.58	9.39	0.000
SeedAVAIL [b]		−0.01	0.00	6.30	0.000
Sex*Season	Male*Wintering	11.93	28.67	0.42	0.678
	Male*Postmating	10.99	28.68	0.38	0.702
Sex*SeedAVAIL [b]		0.00	0.01	0.63	0.528
Fruit consumption					
Intercept		−3.16	0.35	−9.06	0.000
Sex (male)		−2.71	0.17	−16.26	0.000
Season	Wintering	0.14	0.06	2.38	0.017
	Postmating	−0.04	0.10	−0.42	0.675
FruitAVAIL [b]		0.12	0.01	13.92	0.000
Sex*Season	Male*Wintering	2.49	0.17	14.40	0.000
	Male*Postmating	1.25	0.24	5.23	0.000
Sex*FruitAVAIL [b]		0.03	0.01	2.23	0.026

[a] The estimated variances for the random effects are as follows: Legume consumption = 0.99; weed consumption = 0.63; cereal consumption = 0.45; arthropod consumption = 0.77; seed consumption = 0.59; and fruit consumption = 1.07.

[b] Availability of legumes (LegAVAIL), arthropods (ArthroAVAIL), cereals (CerealAVAIL), weeds (WeedAVAIL), seeds (SeedAVAIL) and fruits (FruitAVAIL).

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TABLE 2. Final linear mixed model (LMM) for the dietary diversity of Great Bustards in central Spain.

Fixed effect [a]		Estimate	SE	*t*	*P*
Intercept		1.46	0.08	18.19	0.000
Sex (male)		0.15	0.07	2.06	0.040
Season	Wintering	−0.12	0.06	−2.02	0.043
	Postmating	−0.05	0.08	−0.68	0.496
LegAVAIL [b]		−0.04	0.01	−4.71	0.000
Sex*Season	Male*Wintering	−0.05	0.08	−0.67	0.501
	Male*Postmating	−0.34	0.11	−3.08	0.002
Sex*LegAVAIL	Male*LegAVAIL	0.03	0.01	2.88	0.004

[a] The estimated variance for the random effect = 0.40.
[b] Availability of legumes (LegAVAIL).

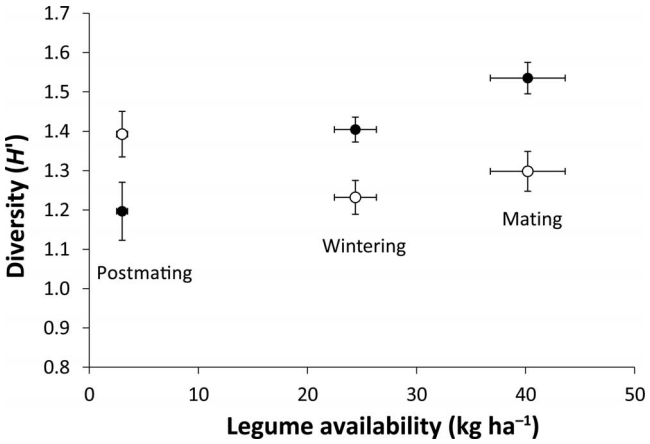


FIGURE 4. Dietary diversity (*H'*; mean ± SE) vs. legume availability (kg ha^{-1}; mean ± SE) by season (wintering, mating, and postmating) of Great Bustards in central Spain. Open circles = females; filled circles = males.

was positively influenced by fruit availability (0.12 ± 0.01, estimate ± SE; Table 1, Figure 3F).

Dietary Diversity

The best model for predicting dietary diversity included sex, season, and legume availability as significant factors (Table 2, Appendix Table 10). Dietary diversity was higher for males than for females (0.15 ± 0.07, estimate ± SE; Table 2). There was a significant interaction between sex and legume availability; female dietary diversity was highest when legume availability was lowest (during the postmating season), while the opposite was true for males (Table 2, Figure 4). The dietary diversity of males increased with legume availability (0.03 ± 0.01, estimate ± SE; Table 2).

Dietary Overlap between the Sexes

Dietary overlap between males and females was 0.73 ± 0.22 across the whole year (mean ± SD). The lowest overlap value was found during the postmating season (0.65 ± 0.06; Table 3). Splitting the sample by food classes, the overlap index between males and females did not show significant seasonal changes (Table 3). The highest overlap index for a single food class was that of plants in the mating season (0.84 ± 0.22).

Diet Selection

There was a significant effect of season on diet selection, and this effect differed between the sexes. Great Bustards preferentially selected legumes in the wintering and mating seasons, but not in the postmating season, when arthropods were the most preferred food (Table 4). There were significant sexual differences in food selection values in the wintering and postmating seasons, but not in the mating season (Table 4). In winter, males selected weeds and legumes equally, preferring these foods to cereals and seeds, whereas females significantly preferred legumes to seeds. During the mating season, both sexes preferentially selected legumes, but females selected weeds and seeds equally, while males significantly selected weeds over seeds. Finally, both sexes selected arthropods during the postmating season, but females preferred fruit as a second food type, whereas males preferred weeds (Table 4). In summary, females showed a more marked preference than males for legumes in winter.

Prey Size

Average prey length was 13.1 ± 10.1 mm (range: 2–83 mm). Splitting prey length by taxon, Acrididae and Meloidae were the largest prey, at 32.9 ± 7.0 mm (n = 39) and 31.3 ± 7.2 mm (n = 85), respectively, and Chrysomelidae and Cerambycidae were the smallest, at 6.9

TABLE 3. Overlap in the 3 main dietary components and the whole diet between male and female Great Bustards in central Spain. The Morisita index of overlap (mean ± SD) is shown for the 3 seasons (wintering, mating, and postmating). The number of Great Bustard areas available to calculate the index varied among seasons and food types (n = 5–9 Great Bustard areas).

	Wintering	Mating	Postmating	df	χ^{2} [a]	*P*
Plants	0.82 ± 0.10 (9)	0.84 ± 0.22 (9)	0.65 ± 0.19 (9)	28	3.45	0.178
Arthropods	0.55 ± 0.36 (8)	0.69 ± 0.23 (5)	0.65 ± 0.23 (9)	24	0.52	0.770
Seeds and fruits	0.71 ± 0.74 (9)	0.81 ± 0.15 (9)	0.67 ± 0.10 (7)	26	4.07	0.131
All	0.78 ± 0.13 (9)	0.76 ± 0.14 (9)	0.65 ± 0.06 (9)	28	2.44	0.295

[a] Kruskal-Wallis test to analyze seasonal changes in the overlap index.

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TABLE 4. Compositional analysis matrix based on the comparison between available food types and those used by Great Bustards in central Spain.

Season	Sex	Ranked food type sequence (most to least used) [a]	λ [b]	df	*F* [c]	*P*
Wintering	Male	Legume > Weed >> Cereal > Seed >> Arthropod > Fruit				
	Female	Legume >> Seed >> Weed > Cereal >> Arthropod >> Fruit	0.16	333	2.79	0.026
Mating	Male	Legume >> Weed >> Seed > Arthropod >> Fruit >> Cereal				
	Female	Legume >> Weed > Seed >> Fruit > Arthropod >> Cereal	0.19	173	0.99	0.456
Postmating	Male	Arthropod >> Weed > Legume >> Fruit > Seed > Cereal				
	Female	Arthropod >> Fruit > Weed > Legume > Seed >> Cereal	0.15	103	2.69	0.026

[a] >> denotes a significant difference between 2 consecutively ranked food types.
[b] Wilk's lambda statistic of diet selection was not at random. Randomized $P < 0.010$ in all λ.
[c] GLM test to analyze the sexual differences in log-ratios of compositional analysis.

± 1.2 mm ($n = 86$) and 7.4 ± 3.0 mm ($n = 11$), respectively. There were significant differences in the length of prey eaten by male and female Great Bustards ($\chi^2 = 9.82$, $P = 0.04$), with males consuming larger individuals than females (Figure 5). Within taxa, there were differences in the sizes of Meloidae and Tenebrionidae eaten by males vs. females ($\chi^2 = 6.2$, $P = 0.04$ and $\chi^2 = 8.0$, $P = 0.005$, respectively), but not other taxa (Acrididae, Scarabaeidae, Carabidae, Curculionidae, Cerambicidae, Formicidae, and Hemiptera; all $P > 0.05$).

Weight, Volume, and Density of Droppings

The weight, volume, and density of droppings varied between the sexes, among seasons, and by dropping composition (Table 5). The droppings of males were significantly heavier and more voluminous (3.6 ± 3.1 g and 7.5 ± 5.4 cm^3) than the droppings of females (1.5 ± 1.2 g and 3.5 ± 2.9 cm^3; Table 5). The weight of droppings also depended upon diet composition, increasing with the percentage of fruit ingested (Table 5). The 3 best models for dropping volume showed similar AIC_c values (Appendix Table 11). Model-averaging resulted in a GLMM that included sex and season as significant factors (Table 5). The volume of droppings did not depend significantly on dropping composition (percentage of plants, arthropod, seeds, and fruits; Table 5).

The average density of droppings was 0.54 ± 0.49 g per cm^3 (females: 0.49 ± 0.26 g per cm^3; males: 0.58 ± 0.63 g per cm^3). Model selection for the density of droppings resulted in 4 models with $\Delta AIC_c < 2$ (Appendix Table 11). Model-averaging of the top models resulted in a GLMM that included sex and season as significant factors (Table 5). Dropping density was significantly higher for males than for females in the postmating season (0.17 ± 0.05, estimate ± SE; Table 5).

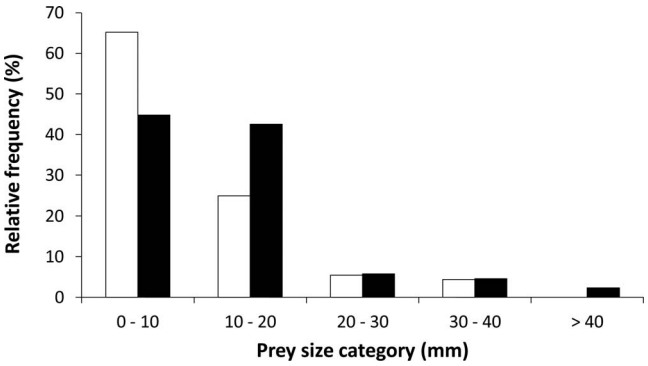


FIGURE 5. Relative frequency of Great Bustard droppings containing arthropods of different sizes. White bars = females; black bars = males.

DISCUSSION

As expected, our best models included sex as a main factor explaining differences in the diet composition and diversity of Great Bustards throughout the annual cycle. Males and females shared a similar dietary spectrum, but consumed some of the available food resources in different proportions, and males showed higher dietary diversity than females, except during the postmating season.

The proportions of green plants, arthropods, seeds, and fruits in the diets of both sexes varied seasonally in relation to the availability of these elements. Being omnivorous, Great Bustards behaved as opportunistic foragers and showed ecological plasticity in their feeding behaviors. Similar seasonal changes in the Great Bustard diet have been reported in other areas of Spain (Lucio 1985, Lane et al. 1999) and in Portugal (Rocha et al. 2005). In spite of their relatively opportunistic and generalist foraging habits (note that their diet includes 103 species), Great Bustards have a clear preference for a few digestible and nutritious plants, with 5 species contributing ~40% to their year-round diet. These most-consumed species were *Convolvulus arvensis*, *Anacyclus clavatus*, *Papaver rhoeas*, *Raphanus raphanistrum*, and *Vicia sativa* (Appendix Table 1), showing the importance of weeds and legumes in the bustards' diet. The prevalent consumption of weeds and the strong selection of legumes are surely important for supporting

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TABLE 5. Final generalized linear mixed model (GLMM) for the weight, volume, and density of Great Bustard droppings in central Spain.

Fixed effect [a]		Estimate	SE	*Z*	*P*
Weight of droppings (g)					
Intercept		−0.10	0.04	−2.65	0.008
Sex (male)		0.56	0.04	12.97	0.000
Season	Wintering	0.22	0.04	5.68	0.000
	Postmating	0.20	0.06	3.16	0.002
% fruit in dropping		0.37	0.13	−2.91	0.004
Sex*Season	Male*Wintering	−0.16	0.05	−3.03	0.003
	Male*Postmating	−0.45	0.09	−5.20	0.000
Volume of droppings (cm^3)					
Intercept		164.56	363.25	0.45	0.651
Sex (male)		0.54	0.05	11.69	0.000
Season	Wintering	0.24	0.04	5.41	0.000
	Postmating	0.36	0.06	6.30	0.000
% plants in droppings		−3.61	4.68	0.77	0.440
% arthropods in droppings		−6.82	4.41	1.54	0.123
% fruit in droppings		−6.82	4.41	1.54	0.123
% seed in droppings		−2.09	3.98	0.52	0.600
Sex*Season	Male*Wintering	−0.18	0.06	3.22	0.001
	Male*Postmating	−0.45	0.08	5.89	0.000
Density of droppings (g per cm^3)					
Intercept		−53.71	174.66	0.31	0.759
Sex (male)		0.01	0.03	0.39	0.694
Season	Wintering	−0.24	0.04	5.71	0.000
	Postmating	−0.09	0.03	2.86	0.004
% plants in droppings		0.71	1.98	0.36	0.721
% arthropods in droppings		1.32	2.55	0.52	0.603
% fruit in droppings		0.82	2.11	0.39	0.697
% seeds in droppings		0.53	1.75	0.30	0.761
Sex*Season	Male*Wintering	−0.01	0.04	0.23	0.821
	Male*Postmating	0.17	0.05	3.16	0.002

[a] Estimated variances for the random effects are as follows: Weight of droppings = 0.063; volume of droppings = 0.050; and density of droppings = 0.001.

the high food requirements of large-bodied birds such as Great Bustards. Weeds are generally abundant in their habitat and legumes are one of the best protein sources among green plants. Despite the observed seasonal variation in diet, green plants were so prevalent that Great Bustards could be described as mainly herbivorous. Females were more selective than males, with higher legume consumption and, consequently, lower dietary diversity values. They followed a primary prediction of optimal foraging theory, which proposes that when the preferred resource is abundant, foragers concentrate on this resource and have narrow food niches. As the preferred resource becomes scarce, lower-quality resources are added to the diet and individuals become more opportunistic (MacArthur and Pianka 1966, Araújo et al. 2008). In contrast to females, the dietary diversity of males did not decrease with increasing legume availability, in accordance with their lower preference for legumes and their less selective diet. Our compositional analysis corroborated the higher selection of legumes by females, particularly during winter (Table 4).

A less specialized diet when alternative highly nutritious resources are available seems paradoxical, but it could be a consequence of sexual dimorphism. For example, in Red Knots (*Calidris canutus*), individuals with smaller gizzards selected higher-quality prey rather than larger prey, due to digestive constraints (van Gils et al. 2005a, 2005b). The larger sex could meet its nutritional needs by feeding on a wide range of prey items due to its bigger body and gut size, but the smaller sex had to exploit the opportunity provided by the abundance of the most nutritious resource. Our results agree with those of studies of sexually dimorphic herbivorous mammals (Demment and Van Soest 1985, Bowyer 2004), where larger-bodied individuals were found to be less selective than smaller-bodied individuals.

Because females showed a greater proportion of legumes in their diet and lower dietary diversity than males, the

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dietary overlap between the sexes was relatively low in all seasons. Although males and females fed on the same spectrum of available food items, their dietary overlap was ca. 0.73, one of the smallest overlap values among birds (C. Bravo personal observation). The highest dietary overlap was in the plants component of the diet and was observed in the mating season (0.84), when both sexes met at leks and considerably reduced their spatial segregation. In contrast, their dietary overlap was lowest during the postmating season, when females carry out chick rearing alone and males usually abandon the leks to recover from their high investment in mating (Alonso et al. 2009b, Palacín et al. 2009). This suggests that sexual differences in the diet are not only direct consequences of the bustards' SSD, but also mediated by the distinct reproductive roles of males and females, which may be another cause of dietary divergence (Fairbairn 1997). A similar pattern of seasonal diet partitioning between the sexes as a consequence of their different reproductive roles has been reported for Greater Prairie-Chickens (Blanco-Fontao et al. 2013). In addition, females consumed more arthropods and seeds than males, particularly during the postmating season. Arthropods and seeds are rich in crude protein, calcium, and phosphorus, and probably help females to restore their calcium levels after the egg-laying period. This result also suggests the importance of the reproductive role as a cause of the dietary divergence between the sexes.

Males consumed fewer arthropods, but of significantly larger size, than females. These sexual differences in the average size of prey eaten were also found in young Great Bustards (Bravo et al. 2012) and in Australian Bustards (*Ardeotis australis*; Ziembicki 2010). In addition, flying or highly mobile arthropods such as grasshoppers were more frequent in the female than in the male diet (Appendix Table 7), suggesting that females, being smaller and thus more agile than males, have a higher ability to capture mobile prey. Additionally, the female role as food provider to offspring could determine the selection of specific arthropods, as well as the most effective prey size (Andersson 1994). These differences likely contribute to reducing intersexual competition for food resources in size-dimorphic species (Selander 1966, Shine 1989, Fairbairn 1997).

The feces of males were 2.4 times heavier than the feces of females, as expected from sexual differences in body weight (males are ~2.4 times heavier than females; Alonso et al. 2009a). The sexual difference in average dropping weight could represent a proxy for the sexual difference in food intake, assuming a similar defecation rate for both sexes. Defecation rate currently cannot be sampled for Great Bustards, as they defecate mainly in roosts at night and at resting sites at midday (Bautista et al. 2013). A similar defecation rate could be assumed following published studies of avian herbivory in which a sex effect in defecation rate has not been reported (van Gils and Tijsen 2007, van Gils et al. 2007). It is noteworthy that the size and density of Great Bustard droppings changed among seasons. This seasonal change in dropping size could be related to a seasonal change in gut morphology determined by food quality and quantity, as shown for other bird species (Leopold 1953, Pendergast and Boag 1973, Geluso and Hayes 1999, Williamson et al. 2014). A sexual difference in dropping density is compatible with a sexual difference in digestive ability, and it would be worth investigating whether such a sexual difference does exist. Our results should be confirmed with further research on sexual differences in gut performance, gut allometry, and digestive efficiency in Great Bustards.

In summary, the results of this study confirm that the diets of adult male and adult female Great Bustards are different. The divergent nutritional and energetic requirements of males and females and their sexual differences in diet and foraging behavior could be explained in part by sexual segregation as a primary proximate factor. Sexual segregation may in turn be a consequence of the distinct reproductive roles and the extreme SSD of both sexes, both of which are ultimately determined by the strong sexual selection operating in this species. Sexual differences in microhabitat selection should be further investigated in this species to confirm these hypotheses and to establish the most plausible causal relationships.

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Ethics statement: Our research was carried out on private lands with landowner permission and on SPA 139 (corresponding to L1–L4) with permission from the Consejería de Medio Ambiente y Ordenación del Territorio de la Comunidad de Madrid. Sampling protocols were approved by National R and D Agencies (Ministry of Economy and

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Competitiveness), and the experiments and fieldwork complied with the current laws of Spain.

Author contributions: C.B., C.P., L.M.B., and J.C.A. conceived the idea, design, and experiment; C.B., C.P., and L.M.B. performed the experiments; C.B. and L.M.B analyzed the data; and C.B., C.P., L.M.B., and J.C.A. wrote the paper. All authors discussed the experiments and results and their interpretation.

LITERATURE CITED

Aebischer, N. J., P. A. Robertson, and R. E. Kenward (1993). Compositional analysis of habitat use from animal radio-tracking data. Ecology 74:1313–1325.

Alonso, J. C., M. Magaña, J. A. Alonso, C. Palacín, C. A. Martín, and B. Martín (2009a). The most extreme sexual size dimorphism among birds: Allometry, selection, and early juvenile development in the Great Bustard (*Otis tarda*). The Auk 126:657–665.

Alonso, J. C., M. Magaña, C. Palacín, and C. A. Martín (2010). Correlates of male mating success in Great Bustard leks: The effects of age, weight, and display effort. Behavioral Ecology and Sociobiology 64:1589–1600.

Alonso, J. C., C. Palacín, J. A. Alonso, and C. A. Martín (2009b). Post-breeding migration in male Great Bustards: Low tolerance of the heaviest Palaearctic bird to summer heat. Behavioral Ecology and Sociobiology 63:1705–1715.

Alonso, J. C., I. Salgado, and C. Palacín (2015). Thermal tolerance may cause sexual segregation in sexually dimorphic species living in hot environments. Behavioral Ecology (in press).

Andersson, M. (1994). Sexual size dimorphism. In Sexual Selection (J. R. Krebs and T. Clutton-Brock, Editors). Princeton University Press, Princeton, NJ, USA. pp. 247–292.

Araújo, M. S., P. R. Guimaraes, Jr., R. Svanbaeck, A. Pinheiro, P. Guimaraes, S. F. Dos Reis, and D. I. Bolnick (2008). Network analysis reveals contrasting effects of intraspecific competition on individual vs. population diets. Ecology 89:1981–1993.

Bautista, L. M., G. Silván, S. Cáceres, L. Martínez-Fernández, C. Bravo, J. C. Illera, J. C. Alonso, and G. Blanco (2013). Faecal sexual steroids in sex typing and endocrine status of Great Bustards. European Journal of Wildlife Research 59:815–822.

Beier, P. (1987). Sex-differences in quality of white-tailed deer diets. Journal of Mammalogy 68:323–329.

Bell, R. H. V. (1970). The use of the herb layer by grazing ungulates in the Serengeti. In Animal Populations in Relation to their Food Resources (A. Watson, Editor). Blackwell, Oxford, UK. pp. 111–123.

Blanco-Fontao, B., B. K. Sandercock, J. R. Obeso, L. B. McNew, and M. Quevedo (2013). Effects of sexual dimorphism and landscape composition on the trophic behavior of Greater Prairie-Chicken. PLOS One 8:e79986. doi:10.1371/journal.pone.0079986

Boal, C. W., and R. W. Mannan (1996). Prey sizes of male and female Northern Goshawks. Southwestern Naturalist 41:355–358.

Bourass, K., J. F. Leger, A. Zaime, A. Qninba, H. Rguibi, M. A. El Agbani, A. Benhoussa, and Y. Hingrat (2012). Observations on the diet of the North African Houbara Bustard during the non-breeding season. Journal of Arid Environments 82:53–59.

Bowyer, R. T. (1984). Sexual segregation in southern mule deer. Journal of Mammalogy 65:410–417.

Bowyer, R. T. (2004). Sexual segregation in ruminants: Definitions, hypotheses, and implications for conservation and management. Journal of Mammalogy 85:1039–1052.

Bravo, C., L. M. Bautista, M. Garcia-Paris, G. Blanco, and J. C. Alonso (2014). Males of a strongly polygynous species consume more poisonous food than females. PLOS One 9: e111057. doi:10.1371/journal.pone.0111057

Bravo, C., C. Ponce, C. Palacín, and J. C. Alonso (2012). Diet of young Great Bustards *Otis tarda* in Spain: Sexual and seasonal differences. Bird Study 59:243–251.

Brown, K. J., and C. T. Downs (2003). Digestive efficiency of a generalist avian feeder, the Cape White-eye (*Zosterops pallidus*). Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology 134:739–748.

Calver, M. C., and R. D. Wooller (1982). A technique for assessing the taxa, length, dry-weight and energy content of the arthropod prey of birds. Australian Wildlife Research 9:293–301.

Castro, G., N. Stoyan, and J. P. Myers (1989). Assimilation efficiency in birds: A function of taxon or food type? Comparative Biochemistry and Physiology Part A: Physiology 92:271–278.

Catán, A., C. A. M. Degano, and L. Larcher (2003). Modificaciones a la técnica microhistologica de Peña Neira para especies forrajeras del Chaco Semiárido Argentino. Quebracho 10:71–75.

Clere, E., and V. Bretagnolle (2001). Food availability for birds in farmland habitats: Biomass and diversity of arthropods by pitfall trapping technique. Revue D'Écologie—La Terre et la Vie 56:275–297.

DeGolier, T. F., S. A. Mahoney, and G. E. Duke (1999). Relationships of avian cecal lengths to food habits, taxonomic position, and intestinal lengths. The Condor 101:622–634.

Demment, M. W., and P. J. Van Soest (1985). A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. American Naturalist 125:641–672.

Durant, D., H. Fritz, S. Blais, and P. Duncan (2003). The functional response in three species of herbivorous Anatidae: Effects of sward height, body mass and bill size. Journal of Animal Ecology 72:220–231.

Elson, L. T., F. E. Schwab, and N. P. P. Simon (2007). Winter food habits of *Lagopus lagopus* (Willow Ptarmigan) as a mechanism to explain winter sexual segregation. Northeastern Naturalist 14:89–98.

Fairbairn, D. J. (1997). Allometry for sexual size dimorphism: Pattern and process in the coevolution of body size in males and females. Annual Review of Ecology and Systematics 28: 659–687.

Fairbairn, D. J. (2013). Odd Couples: Extraordinary Differences between the Sexes in the Animal Kingdom. Princeton University Press, Princeton, NJ, USA.

Forero, M. G., K. A. Hobson, G. R. Bortolotti, J. A. Donazar, M. Bertellotti, and G. Blanco (2002). Food resource utilisation by the Magellanic Penguin evaluated through stable-isotope analysis: Segregation by sex and age and influence on offspring quality. Marine Ecology Progress Series 234:289–299.

Geluso, K., and J. P. Hayes (1999). Effects of dietary quality on basal metabolic rate and internal morphology of European

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Starlings (*Sturnus vulgaris*). Physiological and Biochemical Zoology 72:189–197.

González-Solís, J., J. P. Croxall, and A. G. Wood (2000). Sexual dimorphism and sexual segregation in foraging strategies of Northern Giant Petrels, *Macronectes halli*, during incubation. Oikos 90:390–398.

Hódar, J. A. (1996). The use of regression equations for estimation of arthropod biomass in ecological studies. Acta Oecologica 17:421–433.

Hódar, J. A. (1997). The use of regression equations for the estimation of prey length and biomass in diet studies of insectivore vertebrates. Miscelània Zoològica 20:1–10.

Horn, H. S. (1966). Measurement of "overlap" in comparative ecological studies. American Naturalist 100:419–424.

Ishikawa, K., and Y. Watanuki (2002). Sex and individual differences in foraging behavior of Japanese Cormorants in years of different prey availability. Journal of Ethology 20:49–54.

Jarman, P. J. (1974). The social organization of antelope in relation to their ecology. Behaviour 48:215–267.

Jiguet, F. (2002). Arthropods in diet of Little Bustards *Tetrax tetrax* during the breeding season in western France: Seasonal, age- and sex-related variations in the diet were studied during March to October. Bird Study 49:105–109.

Karasov, W. H. (1990). Digestion in birds: Chemical and physiological determinants and ecological implications. In Avian Foraging: Theory, Methodology, and Applications (M. L. Morrison, C. J. Ralpa, J. Verner, and J. R. Jehl, Jr., Editors). Studies in Avian Biology 13:391–415.

Karasov, W. H., D. Afik, and B. W. Darken (1996). Do northern Bobwhite Quail modulate intestinal nutrient absorption in response to dietary change? A test of an adaptational hypothesis. Comparative Biochemistry and Physiology Part A: Physiology 113:233–238.

Krebs, C. J. (1989). Ecological Methodology. HarperCollins Publishers, New York, NY, USA.

Lane, S. J., J. C. Alonso, J. A. Alonso, and M. A. Naveso (1999). Seasonal changes in diet and diet selection of Great Bustards (*Otis tarda*) in north-west Spain. Journal of Zoology 247:201–214.

Lee, Y.-F., and L. L. Severinghaus (2004). Sexual and seasonal differences in the diet of Lanyu Scops Owls based on fecal analysis. Journal of Wildlife Management 68:299–306.

Leopold, A. S. (1953). Intestinal morphology of gallinaceous birds in relation to food habits. Journal of Wildlife Management 17:197–203.

Le V. Dit Durell, S. E. A., J. D. Goss-Custard, and R. W. G. Caldow (1993). Sex-related differences in diet and feeding method in the Oystercatcher *Haematopus ostralegus*. Journal of Animal Ecology 62:205–215.

Lucio, A. J. (1985). Datos sobre la alimentación de la avutarda (*Otis tarda* L. 1758) en la Cuenca del Duero. Alytes 3:69–86.

MacArthur, R. H., and E. R. Pianka (1966). On optimal use of a patchy environment. American Naturalist 100:603–609.

Markman, S., H. Tadmor-Melamed, A. Arieli, and I. Izhaki (2006). Sex differences in food intake and digestive constraints in a nectarivorous bird. Journal of Experimental Biology 209:1058–1063.

Martín, B., J. C. Alonso, C. A. Martín, C. Palacín, M. Magaña, and J. Alonso (2012). Influence of spatial heterogeneity and temporal variability in habitat selection: A case study on a Great Bustard metapopulation. Ecological Modelling 228:39–48.

McCullagh, P., and J. A. Nelder (1989). Generalized Linear Models, second edition. Chapman & Hall/CRC, London, UK.

Mini, A. E. (2012). The role of body size in the foraging strategies and management of avian herbivores: A comparison of Dusky Canada Geese (*Branta canadensis occidentalis*) and Cackling Geese (*B. hutchinsii minima*) wintering in the Willamette Valley of Oregon. Ph.D. dissertation, Oregon State University, Corvallis, OR, USA.

Moreby, S. J. (1988). An aid to the identification of arthropod fragments in the feces of gamebird chicks (Galliformes). Ibis 130:519–526.

Nakagawa, S., and H. Schielzeth (2013). A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4:133–142.

Odden, M., P. Wegge, S. Eliassen, and M. H. Finne (2003). The influence of sexual size dimorphism on the dietary shifts of Capercaillie *Tetrao urogallus* during spring. Ornis Fennica 80:130–136.

Ogle, D. H. (2013). FSA: Fisheries Stock Analysis. R package version 0.3.5. https://cran.r-project.org/web/packages/FSA/index.html

Palacín, C., J. C. Alonso, J. A. Alonso, C. A. Martín, M. Magaña, and B. Martín (2009). Differential migration by sex in the Great Bustard: Possible consequences of an extreme sexual size dimorphism. Ethology 115:617–626.

Palacios, F., J. Garzón, and J. Castroviejo (1975). La alimentación de la avutarda (*Otis tarda*) en España, especialmente en primavera. Ardeola 21:347–406.

Pasinelli, G. (2000). Sexual dimorphism and foraging niche partitioning in the Middle Spotted Woodpecker *Dendrocopos medius*. Ibis 142:635–644.

Pendergast, B. A., and D. A. Boag (1973). Seasonal changes in internal anatomy of Spruce Grouse in Alberta. The Auk 90:307–317.

Pepper, J. W., T. D. Male, and G. E. Roberts (2000). Foraging ecology of the South Australian Glossy Black-Cockatoo (*Calyptorhynchus lathami halmaturinus*). Austral Ecology 25:16–24.

Pérez-Barbería, F. J., E. Pérez-Fernéndez, E. Robertson, and B. Álvarez-Enríquez (2008). Does the Jarman-Bell principle at intra-specific level explain sexual segregation in polygynous ungulates? Sex differences in forage digestibility in Soay sheep. Oecologia 157:21–30.

Ponce, C., C. Bravo, and J. C. Alonso (2014). Effects of agri-environmental schemes on farmland birds: Do food availability measurements improve patterns obtained from simple habitat models? Ecology and Evolution 4:2834–2847.

Ponce, C., C. Bravo, D. García de León, M. Magaña, and J. C. Alonso (2011). Effects of organic farming on plant and arthropod communities: A case study in Mediterranean dryland cereal. Agriculture Ecosystems & Environment 141:193–201.

R Development Core Team (2012). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rocha, P., A. T. Marques, and F. Moreira (2005). Seasonal variation in Great Bustard *Otis tarda* diet in south Portugal with a focus on the animal component. Ardeola 52:371–376.

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Ruckstuhl, K., and P. Neuhaus (2006). Sexual Segregation in Vertebrates: Ecology of the Two Sexes. Cambridge University Press, New York, NY, USA.

Santiago-Quesada, F., J. A. Masero, N. Albano, A. Villegas, and J. M. Sanchez-Guzman (2009). Sex differences in digestive traits in sexually size-dimorphic birds: Insights from an assimilation efficiency experiment on Black-tailed Godwit. Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology 152:565–568.

Selander, R. K. (1966). Sexual dimorphism and differential niche utilization in birds. The Condor 68:113–151.

Shine, R. (1989). Ecological causes for the evolution of sexual dimorphism: A review of the evidence. Quarterly Review of Biology 64:419–461.

Smith, P. G. (2010). Compos Analysis v6.3. http://www.smithecology.com/

Smith, W. B., and G. J. Brand (1983). Allometric biomass equations for 98 species of herbs, shrubs, and small trees. Research Note NC-299. USDA Forest Service, North Central Forest Experiment Station, St. Paul, MN, USA.

Staines, B. W., J. M. Crisp, and T. Parish (1982). Differences in the quality of food eaten by red deer (*Cervus elaphus*) stags and hinds in winter. Journal of Applied Ecology 19:65–77.

Székely, T., T. Lislevand, and J. Figuerola (2007). Sexual size dimorphism in birds. In Sex, Size, and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism (D. J. Fairbairn, W. U. Blanckenhorn, and T. Székely, Editors). Oxford University Press, Oxford, UK. pp. 27–37.

Torres, A., C. Palacín, J. Seoane, and J. C. Alonso (2011). Assessing the effects of a highway on a threatened species using Before-During-After and Before-During-After-Control-Impact designs. Biological Conservation 144:2223–2232.

van Gils, J. A., and W. Tijsen (2007). Short-term foraging costs and long-term fueling rates in central-place foraging swans revealed by giving-up exploitation times. American Naturalist 169:609–620.

van Gils, J. A., A. Dekinga, B. Spaans, W. K. Vahl, and T. Piersma (2005b). Digestive bottleneck affects foraging decisions in Red Knots *Calidris canutus*. II. Patch choice and length of working day. Journal of Animal Ecology 74:120–130.

van Gils, J. A., S. R. De Rooij, J. van Belle, J. van der Meer, A. Dekinga, T. Piersma, and R. Drent (2005a). Digestive bottleneck affects foraging decisions in Red Knots *Calidris canutus*. I. Prey choice. Journal of Animal Ecology 74:105–119.

van Gils, J. A., A. Gyimesi, and B. Van Lith (2007). Avian herbivory: An experiment, a field test, and an allometric comparison with mammals. Ecology 88:2926–2935.

Webster, M. S. (1997). Extreme sexual size dimorphism, sexual selection, and the foraging ecology of Montezuma Oropendolas. The Auk 114:570–580.

Williamson, S. A., S. K. C. Jones, and A. J. Munn (2014). Is gastrointestinal plasticity in King Quail (*Coturnix chinensis*) elicited by diet-fibre or diet-energy dilution? Journal of Experimental Biology 217:1839–1842.

Witmer, M. C., and P. J. Van Soest (1998). Contrasting digestive strategies of fruit-eating birds. Functional Ecology 12:728–741.

Xavier, J. C., G. A. Tarling, and J. P. Croxall (2006). Determining prey distribution patterns from stomach-contents of satellite-tracked high-predators of the Southern Ocean. Ecography 29: 260–272.

Ziembicki, M. (2010). Australian Bustard. CSIRO Publishing, Collingwood, Victoria, Australia.

Zuur, A. F., E. N. Ieno, and G. M. Smith (2007). Analysing Ecological Data. Springer, New York, NY, USA.

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APPENDIX TABLE 6. Green plant species identified in Great Bustard droppings by season and sex. The occurrence of each plant species is shown as the percentage of droppings containing the species, and dry weight is shown as the percentage of the total dry weight of the droppings.

		Frequency (%)						Dry weight (%)					
		Wintering		Mating		Postmating		Wintering		Mating		Postmating	
Family	Species	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
Boraginaceae	*Anchusa azurea*	3.9	5.4		6.2			0.05	0.15		0.15		
	Echium plantagineum	15.6	28.3	6.2	9.3	8.8	7.7	0.77	1.75	0.11	0.22	0.22	0.08
	Echium sp.			2.5						0.03			
	Heliotropium europaeum	0.6				2.9	2.6	0.01				0.01	0.02
	Lithospermum sp.	3.9	5.4	2.5	3.1	5.9		0.03	0.17	0.09	0.09	0.18	
Cariophyllaceae	*Cerastium holosteoides*	0.6	1.1					0.01	0.02				
	Holosteum umbelatum			1.2						0.01			
Chenopodiaceae	*Chenopodium album*	0.6	0.5			2.9	2.6	0.02	0.01			0.00	0.02
Compositae	*Anacyclus clavatus*	50.0	71.2	53.1	62.9	5.9	7.7	7.05	7.13	7.31	8.82	0.05	0.28
	Andryala integrifolia	9.1	10.9	18.5	4.1	5.9	10.3	0.78	0.59	1.21	0.14	1.21	2.65
	Carthamus lanatus			1.2	1.0	1.5				0.02	0.01	0.02	
	Cirsium sp.	3.2	1.1	2.5	1.0			0.06	0.01	0.03	0.01		
	Cnicus benedictus	1.3			2.1			0.08			0.05		
	Filago sp.	7.1	14.7	3.7	1.0	1.5		0.08	0.29	0.58	0.01	0.01	
	Taraxacum officinale	7.1	6.5	12.3	15.5			0.07	0.14	0.44	1.87		
	Tolpis barbata		3.3						0.60				
	Scorzonera sp.					8.8	2.6					0.98	0.02
Convolvulaceae	*Convolvulus* sp.	13.6	20.1	12.3	1.0	66.2	89.7	1.73	4.70	2.30	0.02	14.98	28.85
Cruciferae	*Alyssum minus*	5.8	13.0	3.7	3.1			0.18	1.06	1.01	0.05		
	Biscutella auriculata	28.6	35.3	21.0	23.7			2.13	2.03	2.16	3.59		
	Brassica nigra	2.6	2.7	1.2	4.1			0.04	0.18	0.15	0.20		
	Camelina micrarpa	1.3	5.4	8.6	10.3			0.01	0.36	0.31	0.99		
	Capsella bursa-pastoris	29.2	33.7	40.7	25.8			2.49	3.76	6.27	1.82		
	Descurainia sophia	14.3	9.8	1.2	8.2	11.8	5.1	1.51	1.41	0.04	1.04	0.91	0.91
	Diplotaxis erucoides	1.9	0.5					0.23	0.02				
	Eruca vesicaria	1.3	5.4	33.3	29.9			0.11	0.53	3.10	1.99		
	Malcolmia africana	2.6			3.1			0.17			0.25		
	Neslia paniculata					1.5						0.01	
	Raphanus raphanistrum	40.9	53.3	40.7	44.3			4.75	6.48	3.86	3.92		
Dypsacaceae	*Scabiosa stellata*	5.2	1.6				2.6	0.05	0.02				0.15
Geraniaceae	*Erodium* sp.	2.6	10.3	1.2	1.0			0.03	0.98	0.04	0.02		
Gramineae	*Aegilops* sp.				1.0						0.01		
	Avena sterilis		0.5						0.03				
	Bromus sp.	14.9	18.5		2.1			0.88	2.05		0.06		
	Bromus squarrosus		1.1						0.05				
	Cynodon dactylon					27.9	38.5					1.12	1.05
	Hordeum murinum	34.4	30.4	18.5	16.5			1.79	3.17	1.01	0.78		
	Hordeum vulgare	57.8	56.0	28.4	35.1			7.10	5.46	2.05	1.64		
	Lolium rigidum	16.9	12.5	1.2				1.29	0.28	0.03			
	Taeniatherum caput-medusae	1.9	3.8		3.1			0.05	0.05		0.14		
	Triticum aestivum	9.1	19.6	8.6	4.1		5.1	0.27	1.18	0.19	0.10		0.23
Labiatae	*Lamium amplexicaule*	43.5	45.7	4.9	10.3			7.72	5.35	0.08	0.78		
	Salvia verbenaca	0.6	0.5	2.5				0.01	0.00	0.06			
Leguminosae	*Astragalus incanus*	2.6	0.5	16.0	12.4			0.03	0.00	0.63	0.91		
	Cicer arietinum	5.8	0.5					1.66	0.02				
	Coronilla scorpioides	0.6						0.03					
	Lathyrus sp.		1.1						0.02				
	Medicago sp.	16.9	17.4	63.0	66.0	36.8	15.4	1.41	2.02	10.53	13.84	3.10	0.41
	Ononis spinosa	2.6	0.5			19.1	33.3	0.06	0.00			0.96	4.65
	Ornithopus compressus		1.6						0.02				
	Pisum sativum		0.5										
	Trifolium angustifolium	7.1	7.6	11.1	22.7	2.9	5.1	0.14	0.45	0.22	1.03	0.03	0.44
	Trifolium sp.		1.6						0.11				
	Trigonella monspeliaca	2.6	3.8	1.2				0.04	0.09	0.01			
	Vicia sativa	24.7	19.0	23.5	19.6			16.89	10.43	12.12	10.81		

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APPENDIX TABLE 6. Continued.

		Frequency (%)						Dry weight (%)					
		Wintering		Mating		Postmating		Wintering		Mating		Postmating	
Family	Species	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
	Vicia sp.	40.3	46.7	35.8	41.2			8.98	13.36	9.25	8.63		
Malvaceae	*Malva sylvestris*	1.9	4.3			2.9	2.6	0.04	0.12			0.02	0.01
Papaveraceae	*Papaver rhoeas*	50.6	46.7	77.8	86.6			6.71	7.32	21.54	24.89		
	Roemeria hybrida	8.4	6.0					0.76	0.46				
Plantaginaceae	*Plantago* sp.	2.6	2.7	3.7	11.3	1.5		0.00	0.05	0.02	0.47	0.00	
Polygonaceae	*Polygonum aviculares*					8.8	17.9					0.15	0.22
Primulaceae	*Anagallis arvensis*	0.6	0.5					0.01	0.01				
Ranunculaceae	*Ranunculus arvensis*	1.9	2.2			20.6	2.6	0.04	0.03			1.38	0.27
Rubiaceae	*Galium tricornutum*	1.3	1.1			1.5		0.10	0.01			0.01	
	Sherardia arvensis		0.5						0.07				
Scrophulariaceae	*Veronica heredifolia*	13.6	12.0	4.9	7.2			0.58	0.31	0.16	0.11		
Umbelliferae	*Torilis nodosa*		0.5	3.7					0.01	0.07			
Unidentified		40.3	48.4	48.1	49.5	69.1	59.0	2.41	1.91	2.80	3.48	3.24	3.20

APPENDIX TABLE 7. Arthropod orders and families identified in Great Bustard droppings by season and sex. The occurrence of each arthropod taxon is shown as the percentage of droppings containing each taxon, and dry weight is shown as the percentage of the total dry weight of the droppings.

		Occurrence (%)						Dry weight (%)					
		Wintering		Mating		Postmating		Wintering		Mating		Postmating	
Order	Family	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
Araneae						4.41	12.82					0.61	3.83
Coleoptera	Alleculidae	1.95	0.54		3.09			0.01	0.00		0.00		
	Cantharidae			12.35	31.96					0.00	0.01		
	Carabidae	1.95		2.47	1.03			0.01		0.01	0.02		
	Cerambycidae	0.65			8.25			0.00			0.03		
	Chrysomelidae	1.30	1.09	1.23	6.19		5.13	0.01	0.03		0.00		0.41
	Curculionidae	3.90	2.17	2.47	4.12	5.88	2.56	0.05	0.00	0.03	0.03	0.35	0.08
	Meloidae			4.94	15.46					0.92	1.62		
	Scarabidae		1.09	19.75	53.61	17.65	7.69		0.01	1.38	2.00	1.47	1.99
	Tenebrionidae	0.65	0.54	22.22	22.68	30.88	33.33	0.00	0.05	1.57	1.34	10.72	11.22
	Unidentified	9.74	16.30	11.11	17.53	11.76		0.14	0.03	0.09	0.04	1.19	
Diptera			1.09						0.00				
Hemiptera	Pentatomidae		0.54	14.81	34.02	33.82	15.38		0.02	0.76	1.28	12.23	8.45
Hymenoptera	Formicidae	2.60	4.35	2.47	3.09	79.41	66.67	0.01	0.01		0.00	14.58	13.37
	Unidentified				1.03	5.88					0.00	0.23	
Lepidoptera					4.12	2.94					0.29	0.21	
Orthoptera			0.54			35.29	23.08					5.86	4.44
Unidentified			1.63	3.70	1.03	1.47							

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APPENDIX TABLE 8. Seed and fruit species identified in Great Bustard droppings by season and sex. The occurrence of each taxon is shown as the percentage of droppings containing each taxon, and dry weight is shown as the percentage of the total dry weight of the droppings.

		Occurrence (%)						Dry weight (%)					
		Wintering		Mating		Postmating		Wintering		Mating		Postmating	
Family	Species	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
Seeds													
Amaranthaceae	*Amaranthus* sp.	2.60	2.72	1.23				0.01	0.01	0.00			
Caryophillaceae	Unidentified					1.47						0.02	
Chenopodiacea	*Chenopodium album*					1.47						0.01	
Compositae	*Sonchus oleraceus*					14.71	23.08					0.22	0.62
Cruciferae	*Rapistrum* sp.		1.09						0.01				
Gramineae	Cereal	42.21	51.63	1.23	7.22	55.88	56.41	9.20	6.46	0.04	0.01	5.73	2.88
	Unidentified	0.65	1.09	1.23			5.13	0.05	0.01	0.02			0.09
Leguminosae	*Coronilla scorpioides*						2.56						0.01
	Lens squlenta						2.56						0.02
	Medicago sp.					1.47	2.56					0.00	0.00
	Ornithopus compressus		0.54	1.23	3.09				0.00	0.00	0.00		
	Unidentified		0.54				2.56		0.00				0.02
Liliaceae	*Muscari* sp.					1.47						0.00	
Polygonaceae	Unidentified	2.60	5.98			1.47	2.56	0.01	0.03			0.02	0.03
Scrofulariaceae	*Veronica* sp.		0.54			4.41	10.26		0.01			0.06	0.13
Umbelliferae	Unidentified				2.06						0.00		
Unidentified		0.65	2.72	1.23	3.09	2.94	7.69	0.00	0.05	0.01	0.00	0.05	0.39
Fruits													
Oleaceae	*Olea europaea*	12.99	20.11	7.41	2.06	10.29	5.13	8.20	9.10	5.05	0.46	3.66	0.86
Solanaceae	*Solanum nigrum*		2.72			35.29	20.51		0.08			9.48	2.15
Vitaceae	*Vitis vinifera*	0.65				7.35	7.69	0.01				0.58	2.16

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APPENDIX TABLE 9. Best generalized linear mixed models (GLMMs) for legume, weed, cereal, seed, and arthropod consumption by Great Bustards in central Spain. Model selection was based on Akaike's Information Criterion corrected for small sample sizes (AIC_c). Delta (ΔAIC_c) and weight values ($wAIC_c$) for each AIC_c are also shown. Marginal R^2 (R^2_m; proportion of variance explained by the fixed factors alone) and conditional R^2 (R^2_c; proportion of variance explained by both the fixed and random factors) were computed for each model using methods described by Nakagawa and Schielzeth (2013).

Candidate models	df	AIC_c	ΔAIC_c	$wAIC_c$	R^2_m	R^2_c
Legume						
(1) Sex + Season + LegAVAIL [a] + Season*Sex + Sex*LegAVAIL	9	16635.7	0.0	0.78	0.17	0.36
(2) Sex + Season + LegAVAIL + Season*Sex	8	16638.2	2.5	0.22	0.15	0.35
(3) Sex + Season + Sex*Season	7	16684.9	49.2	0.00	0.16	0.38
(4) Season + LegAVAIL	5	16892.0	256.2	0.00	0.16	0.35
Weed						
(1) Sex + Season + WeedAVAIL [a] + Season*Sex + Sex*WeedAVAIL	9	22055.8	0.0	1.00	0.06	0.21
(2) Sex + Season + WeedAVAIL + Season*Sex	8	22257.5	201.8	0.00	0.06	0.21
(3) Sex + Season + Sex*Season	7	22310.4	254.6	0.00	0.07	0.22
(4) Season + WeedAVAIL	5	23361.3	1305.6	0.00	0.04	0.17
Cereal plants						
(1) Sex + Season + CerealAVAIL [a] + Season*Sex + Sex*CerealAVAIL	9	7903.8	0.0	0.87	0.19	0.29
(2) Sex + Season + CerealAVAIL + Season*Sex	8	7907.6	3.9	0.13	0.19	0.29
(3) Season + CerealAVAIL	5	8019.1	115.3	0.00	0.18	0.28
(4) Sex + Season + Sex*Season	7	8122.8	219.1	0.00	0.02	0.11
Arthropod						
(1) Sex + Season + ArthroAVAIL [a] + Season*Sex + Sex*ArthroAVAIL	9	8781.1	0.0	0.97	0.60	0.68
(2) Sex + Season + ArthroAVAIL + Season*Sex	8	8787.8	6.7	0.03	0.60	0.67
(3) Sex + Season + Sex*Season	7	8798.1	17.1	0.00	0.57	0.65
(4) Season + ArthroAVAIL	5	8883.4	102.3	0.00	0.26	0.38
Seed						
(1) Sex + Season + SeedAVAIL [a] + Season*Sex	8	8188.5	0.0	0.70	0.91	0.92
(2) Sex + Season + SeedAVAIL + Season*Sex + Sex*SeedAVAIL	9	8190.2	1.7	0.30	0.91	0.92
(3) Sex + Season + Sex*Season	7	8249.2	60.6	0.00	0.92	0.93
(4) Season + SeedAVAIL	5	8308.8	120.3	0.00	0.65	0.70
Fruit						
(1) Sex + Season + FruitAVAIL [a] + Season*Sex + Sex*FruitAVAIL	9	15069.9	0.0	0.82	0.23	0.42
(2) Sex + Season + FruitAVAIL + Season*Sex	8	15072.8	3.0	0.18	0.23	0.42
(3) Sex + Season + Sex*Season	7	15397.9	328.0	0.00	0.33	0.47
(4) Season + FruitAVAIL	5	15755.0	685.1	0.00	0.09	0.32

[a] LegAVAIL: legumes available (kg ha^{-1}); WeedAVAIL: weeds available (kg ha^{-1}); CerealAVAIL: cereal plants available (kg ha^{-1}); SeedAVAIL: seeds available (kg ha^{-1}); FruitAVAIL: fruits available (kg ha^{-1}); ArthroAVAIL: arthropods available (kg ha^{-1}).

APPENDIX TABLE 10. Best linear mixed models (LMMs) for the dietary diversity of Great Bustards in central Spain. Model selection was based on Akaike's Information Criterion corrected for small sample sizes (AIC_c). Delta (ΔAIC_c) and weight values ($wAIC_c$) for each AIC_c are also shown. Marginal R^2 (R^2_m; proportion of variance explained by the fixed factors alone) and conditional R^2 (R^2_c; proportion of variance explained by both the fixed and random factors) were computed for each model using methods described by Nakagawa and Schielzeth (2013).

Dietary diversity model	df	AIC_c	ΔAIC_c	$wAIC_c$	R^2_m	R^2_c
(1) Sex + Season + LegAVAIL [a] + Sex*Season + Sex*LegAVAIL	10	664.90	0.00	0.59	0.11	0.24
(2) Sex + Season + LegAVAIL + GramAVAIL [a] + SeedAVAIL [a] + Sex*Season	10	668.22	3.32	0.11	0.12	0.23
(3) Sex + Season + LegAVAIL + GramAVAIL + FruitAVAIL [a] + Sex*Season	9	668.23	3.33	0.11	0.12	0.23
(4) Sex + Season + LegAVAIL + GramAVAIL + WeedAVAIL [a] + Sex*Season	10	668.61	3.71	0.09	0.12	0.24

[a] LegAVAIL: legumes available (kg ha^{-1}); WeedAVAIL: weeds available (kg ha^{-1}); GramAVAIL: cereals available (kg ha^{-1}); SeedAVAIL: seeds available (kg ha^{-1}) FruitAVAIL: fruits available (kg ha^{-1}).

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APPENDIX TABLE 11. The 4 best generalized linear mixed models (GLMMs) for weight, volume, and density of Great Bustard droppings in central Spain. Model selection was based on Akaike's Information Criterion corrected for small sample sizes (AIC_c). Delta (ΔAIC_c) and weight values ($wAIC_c$) for each AIC_c are also shown. Marginal R^2 (R^2_m; proportion of variance explained by the fixed factors alone) and conditional R^2 (R^2_c; proportion of variance explained by both the fixed and random factors) were computed for each model using methods described by Nakagawa and Schielzeth (2013).

Candidate models	df	AIC_c	ΔAIC_c	$wAIC_c$	R^2_m	R^2_c
Weight						
(1) Season + Sex + %Fruit [a] + Season*Sex	9	209.91	0.00	0.83	0.40	0.42
(2) Season + Sex + %Veg [a] + %Arthro [a] + %Fruit + %Seed [a] + Season*Sex	12	214.36	4.45	0.09	0.40	0.43
(3) Season + Sex + %Veg + Season*Sex	9	214.60	4.69	0.08	0.39	0.43
(4) Season + Sex + Season*Sex	8	230.00	20.08	0.00	0.37	0.40
Volume						
(1) Season + Sex + %Seed [a] + Season*Sex	9	246.99	0.00	0.48	0.40	0.42
(2) Season + Sex + %Veg [a] + %Arthro [a] + %Fruit [a] + %Seed + Season*Sex	12	248.62	1.63	0.21	0.32	0.34
(3) Season + Sex + %Veg + Season*Sex	9	248.86	1.87	0.19	0.32	0.33
(4) Season + Sex + Season*Sex	8	251.17	4.18	0.06	0.31	0.33
Density						
(1) Season + Sex + %Veg [a] + %Seed [a] + Season*Sex	10	−176.24	0.00	0.32	0.16	0.17
(2) Season + Sex + %Arthro [a] + %Fruit [a] + %Seed + Season*Sex	11	−175.56	0.68	0.23	0.17	0.17
(3) Season + Sex + %Veg + %Arthro + %Fruit + %Seed + Season*Sex	11	−175.55	0.68	0.23	0.17	0.17
(4) Season + Sex + %Veg + %Fruit + %Seed + Season*Sex	11	−175.55	0.69	0.23	0.17	0.17

[a] %Veg: plant percentage in droppings; %Arthro: arthropod percentage in droppings; %Fruit: fruit percentage in droppings; %Seed: seed percentage in droppings.

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