J. Zool., Lond. (1999) **247**, 201–214

Seasonal changes in diet and diet selection of great bustards (*Otis t. tarda*) in north-west Spain

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(Accepted 9 June 1998)

Abstract

Faecal analysis was used to study the diet of great bustards in north-west Spain on a monthly basis for 1 year. After correction for differential digestibility, the diet composition by dry weight varied from 48.4% green plant material, 40.9% invertebrates and 10.6% seeds in August, to consisting almost completely of green plant material between December and March. At least 65 plant species were represented in the green plant material, but most occurred rarely and the bulk of this portion of the diet consisted of alfalfa. Eight invertebrate orders were detected in the faeces, of which Coleoptera, Hymenoptera and Orthoptera were most important by numbers. From August to November when seeds were important by dry weight, wheat and barley seeds were found in more faecal pellets than other species. Estimates of use and abundance were obtained to evaluate diet selection in the green plant material and invertebrate components. Alfalfa was strongly selected throughout the year, but grasses were used less often than expected. Coleoptera were always eaten in greater numbers than expected, Orthoptera were used either in proportion to abundance or less often than expected, and Hymenoptera less often in May, more often in September and November, and as expected at other times. The results support the suggestion that increasing alfalfa cultivation would be a useful management tool for maintaining endangered great bustard populations, but further work on the cost-effectiveness of this option is needed.

Key words: alfalfa, diet, great bustard, management implications, Spain

INTRODUCTION

The great bustard *Otis tarda* is a large bustard (adult males to 18 kg, females to 5.25 kg) which occurs in agro-steppe habitats from the Iberian peninsula to eastern Asia (Cramp, 1980). Although widely distributed, great bustards generally occur in separated populations of a few tens to several hundred individuals. In many regions their numbers are declining. In Hungary, the second most important country for great bustards in Europe, numbers decreased from 8557 individuals in 1941 to 1100 in 1993, probably due to the introduction of unfavourable agricultural practices (Faragó, 1993, 1996). In several other European countries (e.g. Bulgaria, Czech Republic, Moldova, Poland, Romania, Slovakia and former Yugoslavia) the species is now extinct or nearly so (del Hoyo, Elliot & Sargatal, 1996; Kollar 1996). Fortunately, great bustards do have a stronghold in Spain, where numbers are thought to be stable and have been estimated recently at 19 000 individuals (Alonso & Alonso, 1996). However, the dramatic losses in the face of habitat alterations elsewhere suggest strongly that active habitat management will be required in the Iberian peninsula to secure this species. Clearly, any conservation action must be based on an accurate understanding of their requirements, but despite the declining and 'vulnerable' status of great bustards (Blanco & González, 1992; Heredia, Rose & Painter, 1996) comparatively little is known about their biology.

Great bustards are omnivorous, with the main dietary components consisting of green plant material, arthropods and seeds. Two previous studies have been conducted on diet composition in Spain (Palacios, Garzón & Castroviejo, 1975; Lucio, 1985) and these indicated that great bustards have a remarkably catholic diet. Palacios *et al.* (1975) showed 12 plant families and at least 55 species were represented in the vegetable

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component of the diet and Lucio (1985) recorded 12 families and 38 species. Each study also indicated the importance of the Coleoptera and Orthoptera in the animal fraction. Palacios *et al.* (1975) suggested that seeds of cultivated species such as chickpeas *Cicer arietinum*, wheat *Triticum aestivum* and grape *Vitis vinifera*, increased in importance in the autumn.

Whilst these earlier works provided valuable information on diet content, they were most complete only during spring, and currently seasonal changes in diet composition are less well known. Moreover, they did not attempt to relate food abundance with usage. Food selection throughout the year may be an important parameter for predicting the effect on endangered great bustard populations of common farm management practices such as herbicide or pesticide applications. In principle, such information could also be used to develop integrated land management programmes that aim to enhance great bustard food supplies in areas already used by the species and to attempt to improve vacant agro-steppe areas into which the species might expand.

In this study we estimate the relative importance and seasonal changes of invertebrates, plant foliage and grains in the diet of a great bustard population in north-west Spain. We go on to assess diet selectivity in the plant foliage and invertebrate components of the diet for one year by quantifying use and abundance on a monthly basis.

Study area

The study was conducted from August 1987 to July 1988 at the Reserve of Las Lagunas de Villafáfila, which occupies 32 682 ha in north-west Spain (41° 50′ N, 5° 36′ W). The terrain is gently undulating, largely treeless, and mainly used for cereal cultivation. More than 80% of the surface was used for wheat or barley (*Hordeum vulgare*) production, *c.* 8% was in alfalfa (*Medicago sativa*) cultivation, *c.* 9% was natural grassland for sheep grazing, and less than 1% was occupied by small vineyards. Many cereal fields are cultivated every other year, and are left fallow (usually after ploughing, but occasionally as stubble) during intervening years. For a more detailed description of this area see J. A. Alonso *et al.* (1995) or Alonso & Alonso (1990).

The great bustard population in the Reserve is probably one of the most dense anywhere in the world: in April 1988, 612 males and 1045 females were counted (Alonso & Alonso, 1990). Following the spring display period (mid-March to the end of April), many of the males (*c.* 55%) leave the Reserve to spend the summer at locations 15–25 km from their display sites and begin to return in the autumn (J. C. Alonso *et al.*, 1995). Females remain in the Reserve throughout the summer and some attempt to rear broods of 1 or 2 chicks which hatch in early June. This study deals with the diet of those birds present in the Reserve.

METHODS

Hunting of the great bustard is no longer permitted or desirable and capturing live individuals is difficult, which precludes diet analysis through examination of regurgitated material or stomach contents. Consequently diets were determined through faecal analysis. Samples of fresh droppings were obtained by following bustard flocks or individuals. Originally the aim was to gather 20 droppings per month, but in the event between 15 and 21 were collected.

Each dropping was dried (60 °C for 48 h) and partitioned into three components (green plant material, animal remains and seeds) which were weighed separately. These components were expressed as proportions and single factor ANOVAs were used after arcsine$\sqrt{}$ transformations to detect any seasonal changes with months acting as factors.

The proportions by dry weight of these three components in the faeces are unlikely to reflect their proportions by dry weight in the diet as a result of differential digestibilities. To correct accurately for this it would be necessary to obtain an estimate of the apparent assimilated mass coefficient, AMC^*, for each component, i, of the diet and to divide the dry weight of i in the faeces by $(1 - AMC_i^*)$. Such AMC_i^* estimates could only reasonably be obtained through trials with captive birds which were not available. To crudely estimate the proportion by dry weight of foliage, seed and invertebrates in the diet we therefore made this correction taking AMC^* estimates from elsewhere. For green plant material we used Withers' (1983) estimate of 0.34 for ostrich *Struthio camelus* eating alfalfa, for seeds Halse's (1984) estimate of 0.75 for spur-winged goose *Plectropterus gambensis* consuming corn, and for arthropods 0.781 derived by Bell (1990).

Selectivity of plant species and invertebrate orders

We tested the null hypotheses that each month great bustards consumed the plant species (green plant material) and invertebrate orders present in the Reserve in proportion to their abundance. For each plant species and invertebrate order this required monthly estimates of abundance and occurrence in the diet.

Occurrences in the diet

The green plant component of each droppings was ground up, immersed in warm water and the resulting suspension passed through two screens of 1 mm and 0.1 mm respectively. Particles of 0.1–1.0 mm were retained on the 0.1 mm screen. A small quantity of these were spread evenly onto a microscope slide with 2 or 3 drops of Hertwig's Solution. Twenty fields were examined under a microscope (× 100) and in each field the presence or absence of different plant species were recorded. Species were identified from their epidermal cells with the aid of our own reference photographs. From these data an index of occurrence, A, of species i in the diet was calculated from:

$$A_i = t_i / 20n \qquad (1)$$

where t_i is the number of microscope fields in which species i occurred and n is the total number of droppings examined.

The invertebrate remains found in each faecal pellet were identified with the aid of our reference collection and published identification aids (Calver & Wooller, 1982; Moreby, 1988). The number of invertebrates eaten was estimated by counting insect parts and following recommendations in Calver & Wooller (1982).

Occurrences in the Reserve

At the start of the study (August 1987) the whole Reserve was surveyed by car and the habitat types noted in 5059 fields to determine absolute areas of each habitat. Habitats were grouped into 7 categories: alfalfa, germinated cereal, cereal stubble, ploughed land, vineyards, fallow land, and pastures. The area of an eighth category, borders between cultivated fields and tracks, was determined independently through the use of maps and by measuring the width of the borders at random locations and then considered constant throughout the study. To assess changes in availability of the other 7 habitats over the following year, 5 car transects (total length 40 km) were driven each month to sample the Reserve. Habitat type was recorded for every field encountered on the left and right of the vehicle.

During each transect, 8 stops were made at predetermined sampling points to estimate the abundance of all plant species. Forty stops (5 transects × 8 stops) were made per month and at least 2 stops where made in each of the 8 habitats. Where possible the sampling points remained constant throughout the study, but when the ground type changed, for example when a cereal was harvested and became stubble, then it was relocated to another nearby site of the original habitat type if it was available. At each sampling point a metal frame (25 × 25 cm) was placed in 20 random locations and in each frame the presence or absence of all plant species was scored. When plants could not be identified in the field they were given a code number and removed to the laboratory for identification. An index of the occurrence P of species i in the whole Reserve was then calculated each month from:

$$P_i = \sum_{j=1}^{8} H_j S_{ji} \qquad (2)$$

where, for the 8 habitats j, H_j is the proportion of land surface in the Reserve covered by habitat j, and S_{ji} is the proportion of frames thrown in habitat j in which species i occurred. Thus P_i is essentially the probability that species i will occur in a 25 × 25 cm quadrat thrown at random anywhere in the Reserve in that month and for the purpose of this study is synonymous with abundance. In terms of biomass this method will underestimate the importance of larger plants (e.g. mature alfalfa) and overestimate the importance of small dicotyledonous weeds. However, this approach was adopted in view of the many habitats and plant species occurring. Attempting to estimate the biomass of each species in every habitat each month would have been impracticable.

At each stop an estimate was also made of invertebrate abundance. A tape measure 30 m long was laid out from a random point and the investigator walked slowly along the tape counting and, as far as possible, identifying the invertebrates seen 1 m to one side of the tape. In late spring, when invertebrates were more numerous, only those within 0.5 m of the tape were counted. Identification was sometimes to genus, but often only to family or order. Consequently invertebrates were grouped into the following categories: Orthoptera (grasshoppers, crickets), Coleoptera (beetles), Dictyoptera (Mantidae), Hymenoptera (ants, wasps and bees), Hemiptera (bugs), Dermaptera (earwigs), Odonata (dragonflies and damselflies), Lepidoptera (butterflies), Diptera (flies), and Araneae (spiders). These transects were not conducted in the hottest period of the day and we assume that the timing of observations did not affect the relative detectability of the invertebrate groups. Mean density m^{-2} of invertebrates in each habitat was obtained and then proportions calculated for each category. These values were substituted for S in equation 2 to obtain an estimate of the proportion of each category in the Reserve.

Statistical analyses

Bonferroni simultaneous (95%) confidence levels were used to test the null hypotheses that each species of plant or category of invertebrate was used in proportion to abundance (Neu, Byers & Peek, 1974; Byers, Steinhorst & Krausman, 1984). If the index of occurrence P_i of an item (expected use) fell above or below the confidence levels estimated for its occurrence in the faeces A_i (observed use), then the null hypothesis was rejected and we concluded that the item was either selected or avoided respectively.

Occurrence of seeds in the diet

It was not feasible to attempt to estimate the proportion of different types of seed occurring in the reserve on a monthly basis, and so a use–abundance analysis was not possible for this component. However, after we compiled a reference collection, it was possible to identify seed types found within the faecal samples to indicate which species were consumed and when.

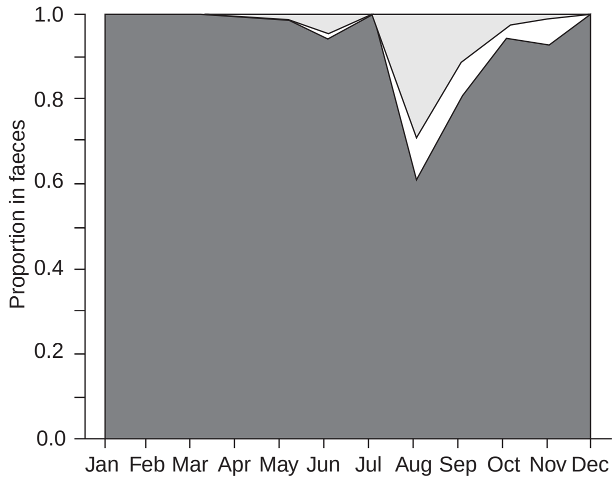


Fig. 1. Seasonal changes in proportion by dry weight of green plant material (shaded), arthropods (stippled), and seeds (unshaded) in great bustard droppings.

RESULTS

Diet composition

Overall, the composition of the droppings (n = 212) by dry weight was 92.3% green plant material, 4.7% invertebrate material, and 3.0% seeds (Fig. 1). However, significant seasonal variation was apparent for each of these components (green plant material $F_{11,211} = 20.0$, $P < 0.0001$; invertebrates $F_{11,211} = 12.8$, $P < 0.0001$; seeds $F_{11,211} = 5.0$, $P < 0.001$; Fig. 1). In the mid-winter period (December to March) droppings consisted almost entirely of green plant material and only traces of invertebrates or seeds were found. Invertebrates formed part of the faeces from April to November, although curiously few were detected in June and July. Seeds made up an important component only between August and November.

After correction for differential digestibility the estimated proportion of these components in the diet could be determined. Over the whole year the diet was estimated to consist of 90.4% green plant material, 2.7% seeds and 6.9% invertebrates. Thus the plant and seed components of the diet were slightly overestimated in the faeces at the expense of the animal component. The composition of the diet ranged from 99.9% green plant material between December and March, to 48.4% green plant material, 10.6% seeds and 40.9% invertebrates in August.

Seasonal changes in occurrence and selection of plant species (green plant material)

Over the year, the botanical surveys of ground vegetation recorded at least 122 species from 26 families on the Reserve. Faecal analyses showed that 65 species from 20 families occurred in the diet of the great bustards (Table 1), but the majority of these were recorded infrequently, always in less than 5% of the microscope fields examined each month. There were 10 exceptions which made up the bulk of the vegetative component of the diet (in this instance Gramineae are included in a single 'taxonomically similar' category) and for which the use–abundance analyses are presented (Fig. 2).

Cultivated alfalfa occurred most frequently in the microscope fields and was strongly selected throughout the year (Fig. 2a). This species was especially prevalent in the diet from November to May, but its use declined in the period June to October. Gramineae always occurred in the diet less often than expected, although in August grasses were recorded in 31% of microscope fields and so it would be better to conclude that they were less preferred rather than avoided (Fig. 2b). When considered separately, neither wheat nor barley occurred in more than 1.25% of the microscope fields during the period October to June when cultivated cereals were available in quantity (25.1% of frames thrown contained wheat and 24.8% contained barley during this period), suggesting that the grasses which are eaten are those growing wild and not the cultivated species.

Common poppy *Papaver rhoeas* was present in the diet throughout the year except during October and November and was positively selected in February, April, May and July (Fig. 2c), while the leaves of grape vine were strongly selected in July and August but were absent from the diet for much of the rest of the year (Fig. 2d). When eaten, the remaining six species (Fig. 2e–j) which occurred in more than 5% of the microscope fields in at least one month of the year were generally used in proportion to their abundance. Principal exceptions were the selection of the composite *Anacyclus clavatus* and white wall rocket *Diplotaxis erucoides* in July, and of purple viper's bugloss *Echium plantagineum* in April.

Seasonal changes in the occurrence and selection of invertebrate orders

Of the 10 arthropod orders identified and counted in the field, eight were also detected in great bustard droppings (Table 2) and only two, the Dictyoptera and the Odonata, were not recovered from the faecal samples. Four orders, Araneae, Dermaptera, Diptera and Lepidoptera, occurred infrequently in the droppings. Within the Coleoptera 11 families were detected of which the Curculionidae (49% of all Coleoptera identified) and Scarabaeidae (20%) occurred most frequently. In the remaining orders, the Acrididae accounted for 96% of all Orthoptera, the Formicidae 99% of the Hymenoptera, and the Pentatomidae 78% of the Hemiptera.

During the months December to March the few arthropods that were detected in the droppings were mostly Coleoptera (Table 2). From April to June the invertebrate proportion in the diet increased steadily (Fig. 1) with the Coleoptera accounting for 56%, 88% and 58% of arthropods eaten, respectively. In July few invertebrates were detected in the diet (Fig. 1; Table 2)

Table 1. Seasonal changes in plant species present (+) or absent (–) in the faeces of great bustards. Species occurring in the Reserve, but not detected in the faeces, are given in the footnote

Family/species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Boraginaceae												
Echium plantagineum	+	+	+	+	+	+	+	–	+	+	+	+
Heliotropium europaeum	–	–	–	–	–	+	+	+	+	+	–	–
Myosotis sp.	–	–	–	–	–	+	–	–	–	–	–	–
Caryophyllaceae												
Cerastium holosteoides	–	–	–	+	+	–	–	–	–	+	–	–
Holosteum umbellatum	+	+	+	+	+	+	–	–	–	+	+	+
Silene sp.	–	–	–	–	–	–	–	–	–	–	+	–
Spergularia sp.	–	–	–	–	–	+	–	–	–	–	–	–
Chenopodiaceae												
Chenopodium album	–	–	–	–	–	–	+	+	+	+	–	–
Compositae												
Anacyclus clavatus	+	+	+	+	+	+	+	+	+	+	+	+
Andryala integrifolia	–	–	–	–	+	–	+	+	+	–	–	–
Anthemis arvensis	–	+	–	+	+	+	+	–	–	–	+	–
Bellis perennis	–	–	–	–	–	–	–	–	–	+	–	+
Carthamus lanatus	–	–	–	–	+	+	+	+	–	–	–	–
Filago pyramidata	–	–	–	–	–	+	+	+	+	+	–	–
Lactuca viminea	–	–	–	–	–	–	–	+	–	–	–	–
Senecio vulgaris	–	–	+	–	+	+	+	+	+	–	–	–
Taraxacum sp.	+	+	+	+	+	+	+	+	+	+	–	+
Tolpis barbata	–	–	–	–	+	+	–	+	–	–	–	–
unidentified	+	+	+	+	+	+	+	+	+	+	+	+
Convolvulaceae												
Convolvulus arvensis	–	–	–	–	–	+	–	–	–	–	–	–
Cruciferae												
Alyssum minus	–	–	–	–	–	–	–	+	–	–	–	–
Camelina microcarpa	–	–	–	–	–	–	+	–	–	–	–	–
Camelina sativa	–	–	–	–	+	+	–	+	–	–	–	–
Camelina sp.	–	–	–	+	+	+	+	+	–	–	–	–
Capsella bursa-pastoris	+	+	+	+	+	–	+	+	+	+	+	+
Diplotaxis erucoides	+	+	+	+	+	+	+	–	+	+	+	+
Erophila verna	–	–	–	–	+	–	–	–	–	–	–	–
unidentified	–	+	–	–	+	+	+	–	–	+	+	–
Dipsacaceae												
Cephalaria syriaca	–	–	–	–	–	–	+	+	+	–	–	–
Scabiosa sp.	+	–	–	–	+	–	+	+	+	–	–	–
Geraniaceae												
Erodium cicutarium	+	+	+	–	–	–	+	+	+	+	+	+
Geranium molle	–	+	–	–	+	+	+	–	–	+	–	–
Gramineae												
Antinoria agrostidea	–	+	–	–	–	–	–	–	–	–	–	–
Bromus diandrus	–	+	–	–	–	–	–	–	–	–	–	–
Bromus rubens	–	–	–	–	–	+	–	+	–	–	–	–
Bromus sp.	+	–	+	–	+	+	+	+	+	+	–	+
Hordeum asperum	–	+	–	–	+	+	+	–	+	+	–	–
Hordeum murinum	–	+	–	–	+	–	+	–	–	–	–	–
Hordeum vulgare	–	+	+	+	+	–	+	+	+	+	+	–
Mibora minima	+	–	–	–	–	–	–	–	–	–	–	–
Phleum pratense	–	–	–	–	–	–	–	+	–	–	–	–
Poa annua	–	+	–	+	+	–	–	–	–	+	+	+
Poa bulbosa	–	–	–	–	–	–	–	–	–	+	–	+
Triticum aestivum	–	–	–	+	+	–	+	+	+	+	+	+
Vulpia sp.	–	–	–	–	+	+	+	+	+	+	+	+
unidentified	+	+	+	+	+	+	+	+	+	+	+	+
Liliaceae												
Muscari comosum	–	–	+	–	+	–	–	–	–	–	–	–
Muscari racemosum	–	+	+	+	+	–	–	–	–	–	–	+

Table 1. (*cont*.)

Family/species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Leguminosae												
Coronilla scorpioides	–	–	–	–	–	–	+	–	–	–	–	–
Lupinus angustifolius	–	+	–	–	+	–	–	–	–	–	–	+
Medicago sativa	+	+	+	+	+	+	+	+	+	+	+	+
Ornithopus compressus	–	–	–	+	+	+	–	–	–	–	–	–
Trifolium angustifolium	–	–	+	–	+	+	+	+	–	–	–	–
Trifolium sp.	–	+	+	+	+	+	+	–	+	+	+	+
Vicia sativa	–	+	+	–	–	+	+	–	+	+	+	+
unidentified	–	+	–	+	+	+	+	–	–	+	–	+
Papaveraceae												
Papaver rhoeas	+	+	+	+	+	+	+	+	+	–	–	+
Plantaginaceae												
Plantago coronopus	–	+	–	+	+	+	+	+	–	+	+	+
Plantago lanceolata	–	+	–	–	+	+	+	+	+	+	+	+
Plantago sp.	–	–	–	–	+	–	–	–	–	–	–	–
Polygonaceae												
Polygonum aviculare	–	–	–	–	–	–	+	–	+	–	–	–
Ranunculaceae												
Ranunculus arvensis	–	–	–	–	–	–	+	–	–	–	–	–
Rosaceae												
Sanguisorba minor	–	–	–	–	–	–	+	–	+	–	–	–
Scrophulariaceae												
Parentucellia latifolia	+	–	–	–	–	+	+	–	–	–	–	+
Veronica hederifolia	–	+	+	–	–	–	–	–	–	+	–	+
Veronica triphyllos	–	–	+	–	–	–	–	–	–	–	–	–
Solanaceae												
Solanum nigrum	–	–	–	–	–	–	+	+	+	+	–	–
Umbelliferae												
Daucus carota	–	–	–	–	–	+	+	+	+	–	–	–
Vitaceae												
Vitis vinifera	–	–	–	–	–	–	+	+	+	–	–	–
Unidentified	+	+	+	+	+	+	–	+	+	+	+	+

Species present in the Reserve, but not detected in the faeces: Boraginaceae: *Anchusa undulata*, *Buglossoides arvensis*. Caryophyllaceae: *Cerastium fontanum*, *Corrigiola litoralis*. Compositae: *Anthemis altissima*, *Carduncellus* sp., *Carduus* sp., *Centaurea calcitrapa*, *Centaurea cyanus*, *Chondrilla juncea*, *Cirsium* sp., *Evax carpetana*, *Filago vulgaris*, *Leontodon taraxacoides*, *Onopordum* sp., *Scolymus hispanicus*, *Scorzonera hirsuta*, *Senecio gallicus*, *Sonchus arvensis*, *Taraxacum obovatum*, *Taraxacum officinale*. Crassulaceae: *Crassula tillaea*. Cruciferae: *Biscutella auriculata*, *Lepidium perfoliatum*. Cyperaceae: *Carex* sp. Euphorbiaceae: *Euphorbia serrulata*. Geraniaceae: *Erodium botris*. Gramineae: *Agrostis castellana*, *Avena fatua*, *Bromus maximus*, *Bromus mollis*, *Bromus tectorum*, *Cynodon dactylon*, *Dactylis glomerata*, *Elymus repens*, *Festuca* sp. Labiatae: *Lamium amplexicaule*, *Salvia verbenaca*. Liliaceae: *Gagea arvensis*. Leguminosae: *Lathyrus angulatus*, *Melilotus* sp., *Ononis spinosa*, *Trifolium repens*, *Vicia lutea*. Papaveraceae: *Hypecoum procumbens*, *Roemeria hybrida*. Plantaginaceae: *Plantago maritima*. Polygonaceae: *Rumex acetosella*, *Rumex* sp. Ranunculaceae: *Ranunculus bulbosus*, *Ranunculus* sp. Resedaceae: *Reseda lutea*. Rubiaceae: *Crucianella angustifolia*, *Galium* sp. Scrophulariaceae: *Linaria* sp. Umbelliferae: *Eryngium campestre*, *Scandix pectenveneris*, unidentified sp.

even though density in the Reserve was high at this time (Fig. 3). In August, when arthropods were most important in the diet by both dry weight (Fig. 1) and numbers (Table 2), 69% of animals in the faeces were Orthoptera, 18% were Hymenoptera and most of the remainder were Coleoptera. From September to November the numbers (Table 2) and dry weight (Fig. 1) of animals recorded declined as did the importance of Orthoptera. At this time the invertebrate diet generally consisted of Coleoptera (76% in October) and Hymenoptera (53% and 69% in September and October, respectively). Unidentified larvae were detected in the faeces from January to July and were most numerous in February and April.

Use vs. abundance analyses were conducted for arthropod orders from April to November (Fig. 4). Coleoptera were always eaten in greater numbers than expected, whilst the converse was true for the Diptera. For most of the year Hymenoptera were consumed in proportion to their abundance except in May when they were taken less often than expected and in September and November when they were selected. Orthoptera

Table 2. Seasonal changes in numbers of animals from different arthropod orders detected in the droppings of great bustards

Order/family	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Araneae												
Araneidae	0	0	1	0	0	4	1	0	2	0	1	0
Coleoptera												
Carabidae	1	0	3	3	11	12	4	6	1	0	1	1
Carabidae	0	0	0	0	1	0	2	0	0	0	0	0
Chrysomelidae	0	0	0	2	2	2	8	24	3	0	0	0
Coccinellidae	0	0	0	0	0	0	4	14	0	0	0	0
Curculionidae	5	2	1	8	85	68	3	13	5	58	5	3
Histeridae	0	0	0	1	0	0	0	0	0	0	0	0
Meloidae	0	0	0	1	0	0	0	0	0	0	0	0
Melyridae	0	0	0	1	0	0	0	0	0	0	0	0
Scarabaeidae	0	2	1	1	23	20	3	21	27	8	4	0
Staphylinidae	1	5	2	4	0	0	1	0	1	3	0	0
Tenebrionidae	0	0	0	2	2	6	1	5	7	4	2	0
unidentified beetles	1	5	5	3	25	30	10	17	10	8	8	7
Dermaptera												
Forficulidae	0	0	0	0	0	6	0	1	0	0	0	0
Diptera												
unidentified flies	0	1	0	0	1	1	0	1	0	0	1	0
Hemiptera												
Pentatomidae	0	0	0	0	1	33	9	9	5	0	0	0
unidentified bugs	0	0	0	0	1	13	0	1	1	0	0	0
Hymenoptera												
Formicidae	3	3	1	1	4	7	5	156	116	22	51	3
unidentified ants	0	1	0	0	0	3	0	0	0	1	0	0
Lepidoptera												
unidentified butterflies	0	0	0	0	0	1	1	1	0	0	0	0
Orthoptera												
Acrididae	0	2	0	1	2	27	9	594	32	0	1	0
Gryllotalpidae	0	0	0	0	0	0	0	0	1	0	0	0
Tettigoniidae	0	1	0	0	0	0	0	17	5	2	0	0
unidentified insects	1	1	0	0	2	3	0	2	3	0	0	2
unidentified insect larvae	1	16	9	18	9	4	7	0	0	0	0	0
Total	13	39	23	46	169	240	68	882	219	106	74	16
No. droppings examined	15	18	18	19	20	17	16	20	18	16	18	19
Mean no. invertebrates per dropping	0.87	2.17	1.28	2.42	8.45	14.12	4.25	44.1	12.17	6.63	4.11	0.84
SD	1.07	2.78	1.37	2.43	16.62	26.90	4.21	47.6	13.38	9.93	7.77	0.83

were used in proportion to abundance from April to June and also in August, were apparently less preferred in July and September and seemed to be avoided in October and November.

Johnson (1980) pointed out that the inclusion of a common but rarely used resource in use–abundance analyses can greatly effect the overall results. In this case the Diptera accounted for much of the invertebrates present especially from April to June (Fig. 3), but were rarely found in great bustard faeces. We therefore repeated the use–abundance analysis excluding the order Diptera. From April to June the Coleoptera were always selected, as shown in the previous analysis, but the Hymenoptera were always less preferred, as were the Orthoptera in June. From July to November the conclusions were the same except that in August the Orthoptera were used marginally, but statistically significantly, below the amount expected, and in November the Coleoptera were used in proportion to abundance.

Occurrence of seeds in the diet

Seeds occurred in more than 50% of the droppings examined from April to November, but were infrequent in droppings collected during the winter months. At least 48 species from 19 families were identified (Table 3); however, 26 species were found only in one or two droppings over one or occasionally 2 months suggesting these were of minor importance. Considering the remaining species for the period August to November when seeds reached greatest importance by weight in the diet (Fig. 1), only cultivated barley and

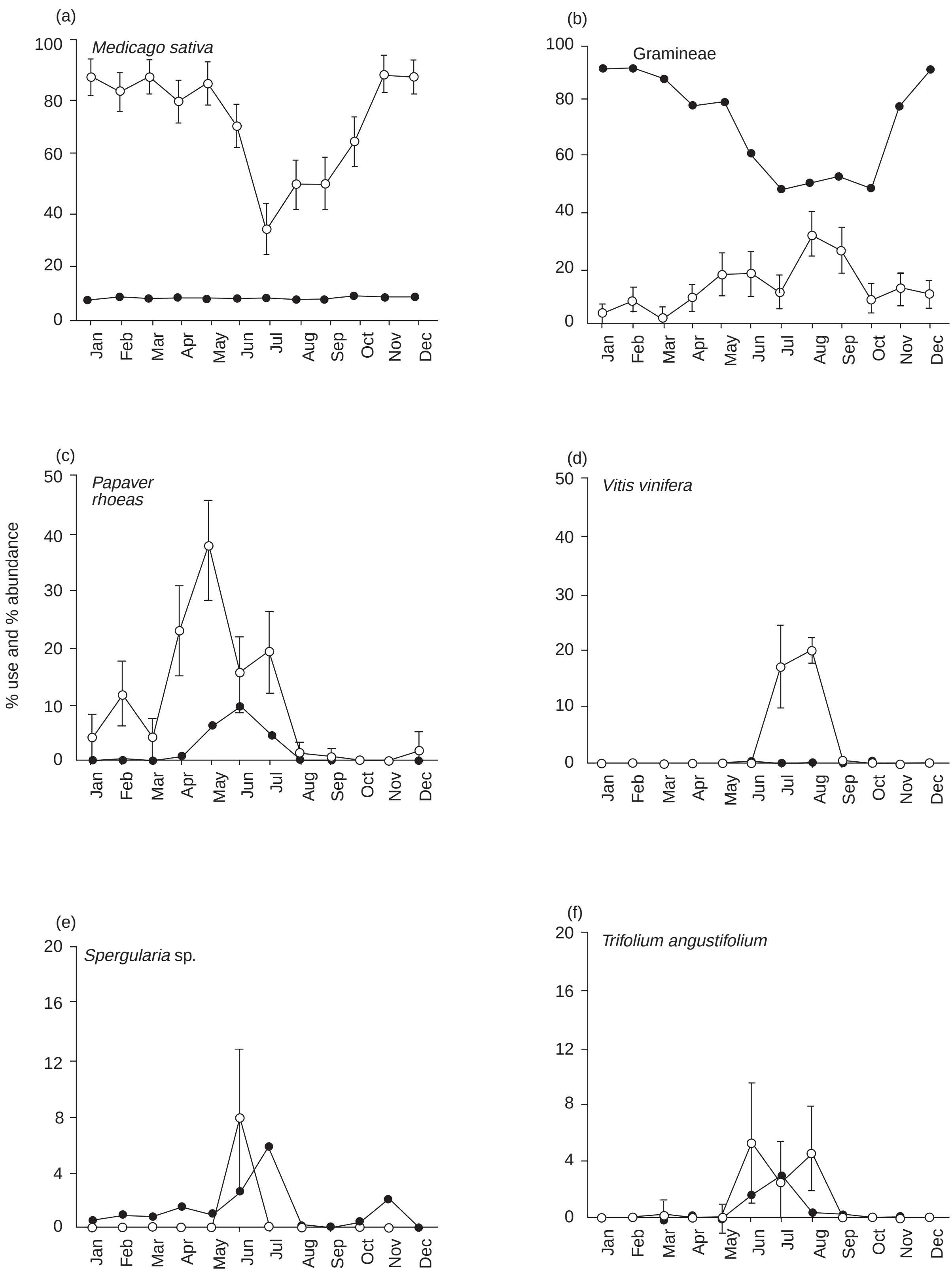
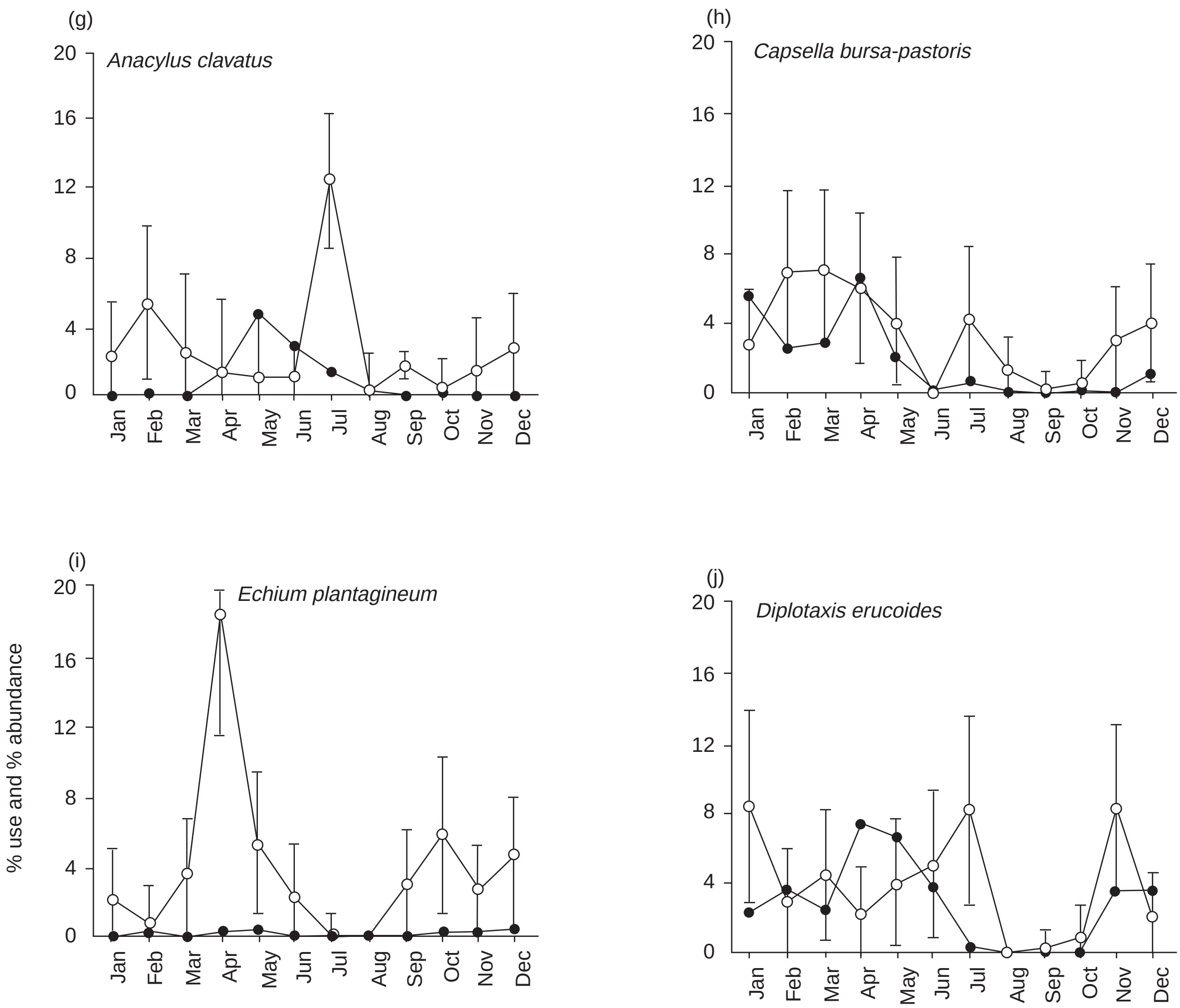


Fig. 2. Seasonal changes in use (open circles ± 95% CL) and abundance (filled circles) of ten plants in the Reserve. (All grass species were lumped into a single 'morphologically similar' category, Gramineae.) For each species, values for 'use' are the percentages of microscope fields viewed in which it occurred and values of 'abundance' are the likelihood of the species occurring in a 25 × 25 cm quadrat tossed anywhere in the Reserve. Note different scales on the *y*-axes.



wheat were recorded in each month, but always in fewer than 43% (wheat in August) of the droppings examined. Three other species were occasionally found in the droppings in 3 months of this period: clover *Trifolium angustifolium*, knotgrass *Polygonum aviculare*, and black nightshade *Solanum nigrum*.

DISCUSSION

We examined the diet and evaluated diet selection of great bustards in north-west Spain on a monthly basis for 1 year. Great bustards were predominantly herbivorous during the winter and spring, but more omnivorous at other times; arthropods made up a substantial proportion of the diet in August, and seeds were eaten during autumn.

Methodological considerations

The methods used to assess selectivity of plant species are subject to a number of biases, notably the possibility of differential digestibility between species, for which we have not controlled. Of necessity we had to examine the diet through faecal analysis and we had no captive birds to which we could feed test diets to control for such problems. However, unless large differences in digestibility exist between plant species our results may not differ markedly from true selection. Also, since differential digestibility is not accounted for, our presence/absence method of faecal examination is probably more robust to any differences than methods which attempt to estimate absolute biomass consumed.

For invertebrates we were able to consider true densities in both diet and field, but by considering numbers and not biomass we have overestimated the importance of small invertebrates such as Hymenoptera and underestimated the importance of comparatively larger animals such as Orthoptera. We are also likely to have overlooked any soft-bodied, highly digestible animals such as caterpillars, molluscs, or annelid worms.

Green plant material

Alfalfa was the most important species in the green plant material component of the diet, especially in

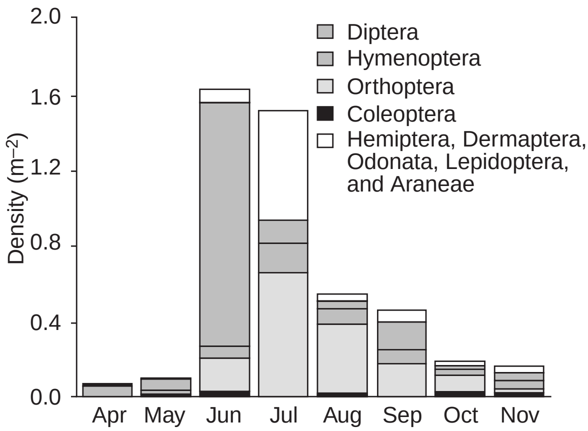


Fig. 3. Density (numbers m^{-2}) of arthropod orders in the Reserve.

winter, and was selected throughout the year. Grasses were also present, but were used less often than expected. Foliage of 65 or more plant species was detected in the faeces but few species contributed more than a small proportion to the diet. Since discrimination between plant species of different quality has been shown for many herbivorous birds (Sedinger, 1997), it seems reasonable to assume that alfalfa is being selected over other potential foods on the basis of one or more nutritional parameters. The consistent presence of many other species in the diet may occur because the birds require additional nutrients not obtained from alfalfa or because they continuously sample other potential foods in their environment (Robbins, 1993). A strikingly similar pattern of food selection was observed for greater rheas *Rhea americana* in an agricultural area of Argentina (Martella *et al*., 1996).

Despite the overwhelming importance of alfalfa in this study, it would be misleading to imply that the presence of alfalfa cultivation is a prerequisite for the occurrence and survival of great bustards. In Spain, great bustards are also found in several regions where alfalfa is not cultivated (Alonso & Alonso, 1990), including two important areas in Extremadura (Hellmich, 1990) and nine localities around Madrid. Studies elsewhere suggest that other Leguminosae, or species of Compositae and Cruciferae, would assume greater importance in the diet in these areas (Cramp, 1980; Johnsgard, 1991).

Invertebrates

Invertebrates are known to occur in great bustard diets during the summer months and can make up 40–87% of the diet by weight (Johnsgard, 1991). However the results of this study for June and especially July deviate from this pattern. Only a small proportion of the diet consisted of invertebrates during these months even though invertebrates reached highest abundance. The importance of invertebrates may be underestimated in these months if chick droppings were missed during field work and chick-rearing females allocate most invertebrates caught to their chicks, but consume mostly vegetation themselves. Alternatively, the invertebrates present in June and July, predominantly Diptera and young Orthoptera, might have been too small and fast to be captured efficiently by great bustards. This might explain why most of the arthropods that were detected in the faeces during these months were slower, ground-dwelling Coleoptera. The substantial increase in the proportion of invertebrate material in the diet in August occurred when Orthoptera were consumed in large numbers. By this time Orthoptera are larger and presumably become more energetically advantageous to pursue.

Seeds

Of the three components, seeds appeared to be least important by dry weight, reaching an estimated maximum of only 10.6% and 9.6% of the diet in August and September respectively. Only wheat and barley occurred consistently in these months and were almost certainly consumed as spilled grains in stubble fields after the harvest. Grape seeds were found in one dropping which suggests great bustards might depredate grape crops in the region (J. A. Alonso *et al*., 1995).

Other food types

Previous studies, summarized in Cramp (1980), have suggested that vertebrates are sometimes eaten, including amphibia, lizards, chicks of ground-nesting birds and voles *Microtus* sp. In this study there was no faecal evidence that vertebrates were taken, but a female was observed feeding her chick with a vole during a vole population explosion in the Reserve (E. Martín & M. Morales, pers. obs., 1995). It seems that great bustards do prey on small vertebrates but infrequently and opportunistically.

Management and conservation implications

Farmers in the Reserve sometimes complain that great bustards damage cereal crops, but the results of this study imply that the impact, if any, is small. Yield reductions can occur through winter defoliation of germinated cereal by herbivorous birds but in general grazing needs to be sustained over several weeks by a large number of birds for an appreciable loss to occur. Leaves of wheat or barley rarely occurred in the great bustard diet and the use–abundance analyses indicated avoidance of cereal leaves. Moreover, cereal grains occurred in the diet only after the harvest (July onwards), suggesting that great bustards occasionally gleaned spilled grains from stubble fields but never depredated ripe ears.

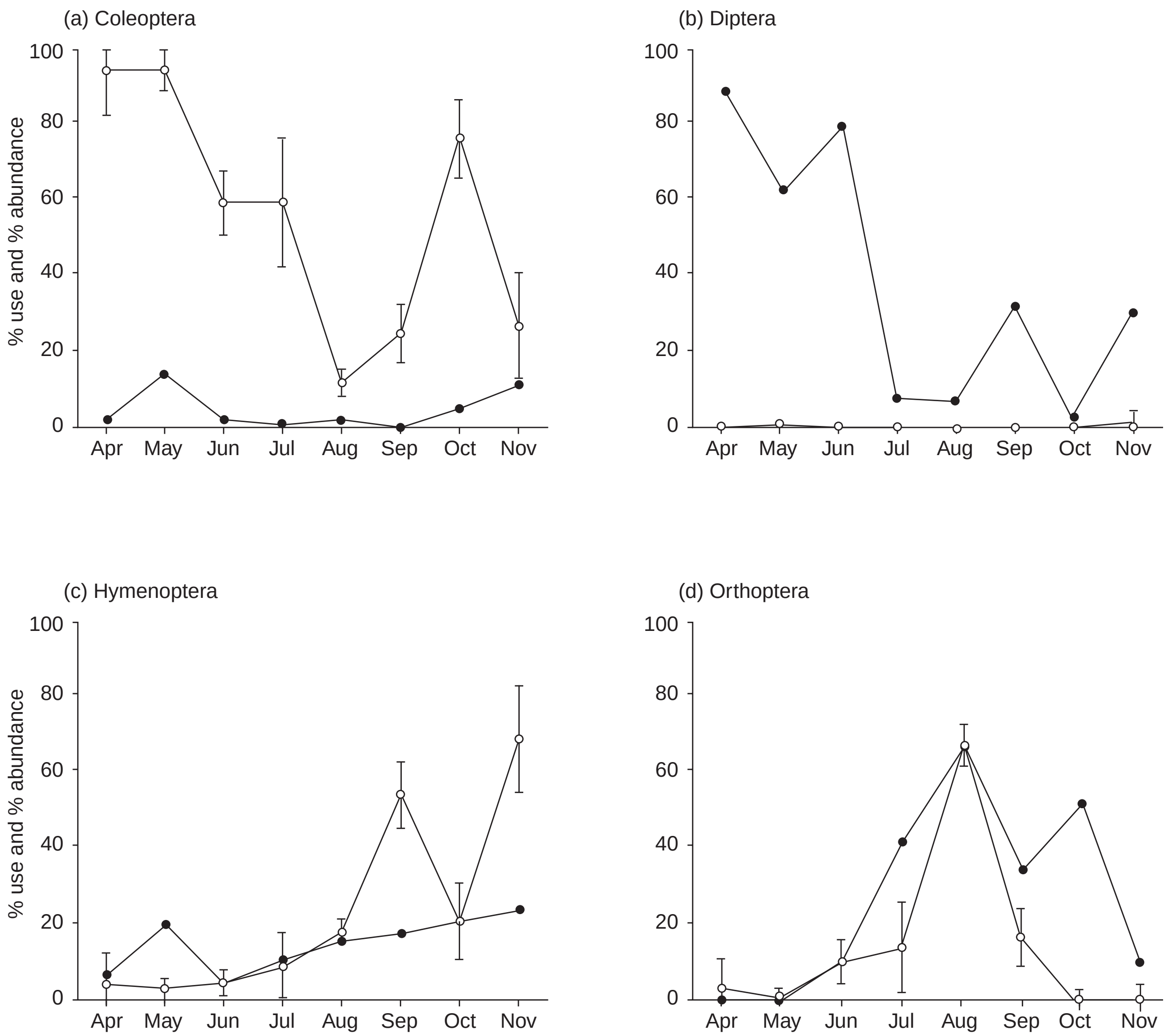


Fig. 4. Seasonal changes in percentage use (open circles ± 95% CL) and abundance (filled circles) of four arthropod orders.

The farmers in the region may have a better case when they suggest that great bustards reduce alfalfa yields. Over 1 year, the great bustard population consumes an estimated 22.8 tonnes dry weight of alfalfa (Alonso, Alonso & Naveso, 1988). Nevertheless it is equivocal what impact such grazing has on the eventual alfalfa yield. Grazing could delay and impair crop development and thus reduce yield as farmers claim. Alternatively it has been suggested that 'moderate' grazing pressure, in combination with faecal deposition, could stimulate growth and improve yields in at least some stages of crop development (Martella *et al*., 1996). Simulated grazing (clipping) or exclosure experiments (e.g Abdul Jalil & Patterson, 1989; Lane & Nakamura, 1996) might resolve this issue.

The attraction of alfalfa to great bustards has led to the suggestion that alfalfa cultivation could be a useful management tool in agro-steppe habitats (Dornbusch, 1996; Kollar, 1996; Palacios & Rodríguez, 1996). Consequently the Reserve is intending to maintain the area planted with alfalfa by purchasing land under the auspices of a European Union LIFE project (LIFE 96 NAT/E/3080). Alfalfa will then be cultivated in areas in the Reserve thought to be favoured by great bustards (Palacios & Rodríguez, 1996). The results of our study strongly support this management option in the Reserve but, to optimize this action, further research would be useful. At least three issues require attention: Firstly, how much land needs to be given over to alfalfa in relation to the number of birds? Secondly, where in the Reserve would maximum use of new alfalfa plots occur? And finally, what is the best management strategy of alfalfa fields for great bustards: when, how frequently, and to what height, should alfalfa fields be cut?

Acknowledgements

We thank A. Correas and G. Esteban for help with field work and faecal analysis and John Coulson, Enrique Martín, Carlos Martín de la Calle and Manuel Morales for comments on an earlier version of the manuscript. Field work was co-financed by the Dirección General de Investigación Cientifica y Técnica and the Instituto

Table 3. Seasonal changes in percentage of great bustard droppings examined which contained the seed species indicated

Family/species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Boraginaceae												
Heliotropium europaeum	0	0	0	0	6	0	0	0	0	0	0	0
Caryophyllaceae												
Cerastium holosteoides	0	0	6	21	50	6	0	0	0	0	0	0
Holosteum umbellatum	0	0	0	0	11	0	0	0	0	0	0	0
Silene sp.	0	0	0	0	6	0	0	0	0	0	0	0
Spergula morisonii	0	0	0	0	0	6	0	0	0	0	0	0
Spergularia rubra	0	0	0	0	6	18	7	0	0	0	0	0
unidentified	0	0	0	0	0	0	0	0	0	0	6	0
Chenopodiaceae												
Chenopodium album	0	0	0	0	0	12	0	0	0	0	0	0
Compositae												
Chondrilla juncea	0	0	0	0	0	0	7	0	0	0	0	0
Filago sp.	0	0	0	0	0	6	0	5	0	0	0	0
Leontodon taraxacoides	0	0	0	0	0	0	27	0	0	0	0	0
Senecio vulgaris	0	0	0	0	22	0	0	5	0	0	0	0
Sonchus arvensis	0	0	0	0	0	0	47	0	0	0	0	0
Sonchus asper	0	0	0	0	0	0	0	5	0	0	0	0
Taraxacum sp.	0	0	0	21	11	18	7	0	11	0	0	0
unidentified	0	0	0	0	11	29	20	5	0	0	0	0
Crassulaceae												
Crassula tillaea	0	0	0	0	11	0	0	0	0	0	0	0
Cruciferae												
Capsella bursa-pastoris	0	0	0	0	67	6	20	0	0	0	6	0
Erophila verna	0	0	6	17	11	0	0	0	0	0	0	0
Lepidium perfoliatum	0	0	0	0	0	0	7	0	0	0	0	0
unidentified	0	0	0	0	6	12	7	5	0	0	0	0
Scrophulariaceae												
Parentucellia latifolia	7	0	0	0	0	0	0	0	0	0	0	0
Veronica sp.	0	0	0	0	11	35	0	5	0	0	0	0
Geraniaceae												
Geranium molle	0	0	0	0	0	6	13	5	0	0	0	0
Gramineae												
Agrostis castellana	0	0	0	0	0	0	7	0	0	0	0	0
Antinoria agrostidea	0	0	0	0	0	6	7	0	0	0	0	0
Bromus diandrus	0	0	0	0	0	0	0	5	0	0	0	0
Bromus mollis	0	0	0	0	0	29	27	5	6	0	0	0
Bromus sp.	0	0	0	0	0	12	7	10	11	0	0	0
Dactylis glomerata	0	0	0	0	0	6	7	0	0	0	0	0
Festuca sp.	0	0	0	0	6	0	0	0	0	0	0	0
Hordeum asperum	0	0	6	0	0	0	0	0	0	0	0	0
Hordeum murinum	0	0	0	0	0	18	7	0	0	0	0	0
Hordeum vulgare	0	0	0	0	0	0	0	19	22	38	28	0
Phleum pratense	7	0	0	0	0	0	0	0	0	0	0	0
Poa annua	0	0	22	42	44	18	13	5	6	0	0	0
Poa bulbosa	0	0	0	5	6	0	0	10	0	0	0	0
Triticum aestivum	0	0	0	0	0	0	7	43	17	38	22	0
Vulpia sp.	0	0	0	0	0	24	27	19	11	0	0	0
unidentified	0	0	0	0	11	6	0	33	0	0	0	0
Juncaceae												
Juncus maritimus	0	0	0	0	0	0	7	0	0	0	0	0
Leguminosae												
Trifolium angustifolium	0	0	0	0	0	12	0	19	6	0	6	0
Papaveraceae												
Papaver rhoeas	0	0	0	0	0	6	0	0	0	0	0	0
Polygonaceae												
Polygonum aviculare	7	0	0	0	0	0	40	0	11	6	6	11
Rumex acetosella	0	17	0	0	0	0	0	0	0	0	0	0

Table 3. (*continued*)

Family/species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Resedaceae												
Reseda lutea	0	0	0	0	0	12	0	0	0	0	0	0
Rubiaceae												
Crucianella angustifolia	0	0	0	0	6	0	0	0	0	0	0	0
Solanaceae												
Solanum nigrum	0	0	0	0	0	0	0	10	28	0	6	0
Umbelliferae												
Daucus carota	0	0	0	0	0	0	0	10	0	0	0	0
Scandix pecten-veneris	0	0	0	0	0	6	0	0	0	0	0	0
unidentified	0	0	0	0	0	0	7	0	0	6	6	0
Vitaceae												
Vitis vinifera	0	0	0	0	0	0	0	0	6	0	0	0
Unidentified	0	11	0	0	11	35	13	0	6	0	0	0
No. droppings examined for seeds	15	18	18	19	18	17	15	21	18	16	18	19
No. droppings in which seeds found	3	4	4	11	16	14	13	16	12	8	11	2

Nacional para la Conservación de la Naturaleza. SJL was supported by a Marie Curie Research Training Grant awarded under the Training and Mobility of Researchers Programme by the European Commission Directorate General XII for Science, Research and Development.

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