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Using dietary analysis and habitat selection to inform conservation management of reintroduced Great Bustards *Otis tarda* in an agricultural landscape

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Capsule Reintroduced Great Bustards achieve dietary and habitat diversity despite living in an intensive agricultural setting.

Aims To investigate dietary composition and habitat use of reintroduced Great Bustards *Otis tarda* released in southwest England and the impact of supplemental feed on autumn dietary selection.

Methods Faecal samples were collected from a mixed group of free-ranging bustards without (July 2012, May, September, and November 2013) and with (October and December 2012) access to supplemental feeds. Concurrently, diurnal land use observations were recorded for all months but September and December. Composite monthly faecal samples were micro-histologically analysed to assess dietary composition. Year-round landscape-level habitat use was determined using re-sightings and satellite telemetry data for birds surviving more than 182 days post-release. Generalized linear models were used to test for differences in habitat selection across the year, by sex and within and outside release areas for each habitat type, and habitat diversity was quantified using the Shannon–Weaver Index.

Results Dietary composition varied depending on plant availability and phenological stage, and invertebrates were rarely selected. Agricultural crops – primarily oil-seed rape, mustard, barley grass, lucerne, and barley seed – comprised the bulk of the diet, but grassland and weedy forbs were always important secondary foods (>25%), except when provided extruded pellets. Monthly changes in habitat use suggest sex-based habitat segregation, with females living in higher habitat diversity settings. Grasslands were used across the year. When supplemental food was provided, it came to dominate dietary intake.

Conclusion Great Bustards can adapt to an intensive agricultural setting, but require unrestricted access to adjacent grasslands. They would be best served with small-scale habitat mosaics. If supplemental foods are to be provided to juvenile birds, quantities must be limited and the birds weaned off before dispersal to maximize reintroduction success.

Reintroducing extirpated species to areas within their former range is an important conservation tool, but despite some notable successes, many such projects fail (Griffith *et al.* 1989, Fischer & Lindenmayer 2000, Oro *et al.* 2011). Even if the immediate causes of extirpation are remedied, a combination of factors including habitat change (Jachowski *et al.* 2001, Michel *et al.* 2010) and phenotypic and behavioural incongruencies of the reintroduced population (Håkansson 2007, Badyaev 2009, Robert 2009) can contribute to elevated mortality and the ultimate

failure to establish a self-sustaining breeding population (Sarrazin & Barbault 1996, Seddon *et al.* 2007).

Before initiating a re-introduction project an extensive evaluation of habitat quality is advised, yet it is often difficult to determine what metrics need to be assessed in order to deem a site suitable for release and how this can be carried out in a quantitative framework (Osborne & Seddon 2012). Habitats are spatially and temporally heterogeneous (Southwood 1977), meaning that a species' historical range is not necessarily indicative of present-day habitat suitability. Target habitat may need to be restored or created and then managed to aid colonization, and the complexity

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of this management task is often underappreciated (Osborne & Seddon 2012). Without a detailed knowledge of the nutritional profiles of potential foods, their distribution in time and space, and how these meet the animal's nutritional requirements, ecologists and conservation practitioners may make rather simplistic assumptions (Robbins 1983, Simpson & Raubenheimer 2011). For reintroduction projects where the species has been absent for a prolonged period, an understanding of this complex habitat–animal interplay is nevertheless necessary if the chances of establishing a self-sustaining population are to be optimized. Post-release habitat use and diet selection monitoring is therefore essential to inform post-release management.

Supplemental feeding has been recognized as a potentially useful wildlife management approach, enabling managers to compensate for gaps between nutritional demand and the biologically available supply offered by the landscape, improving reproductive rates and over-winter survival (Boutin 1990, Robb *et al.* 2008). It can further benefit translocation and reintroduction projects, where the released individuals may be initially ineffective foragers in their new environment (Palacín *et al.* 2011, Haddaway *et al.* 2012, Riebel *et al.* 2012) and may form an important bridge for captive-reared individuals until they have the necessary skills to survive on their own (Morgan & Tromborg 2007). As a conservation tool, however, it is not without risk. Animals, and especially young or naive ones, may become dependent on the artificial food (Castro *et al.* 2003, Rickett *et al.* 2013), learn inappropriate foraging lessons, and become vulnerable to predators attracted to feeding stations (Dunn & Tessaglia 1994). Shifts in nutrition resulting from supplemental feed may also alter the sex ratio within a population (Clout *et al.* 2002) and mask a broader issue of inadequate foraging habitat from wildlife managers. When provided, post-release monitoring is necessary to assess its possible immediate and longer term effects.

The Great Bustard is a globally threatened, sexually dimorphic bird which formerly occupied lowland grassland and steppe regions extending across the middle latitudes from Morocco to China (Morales & Martin 2002). Expanding and thriving in low- to medium-intensity agricultural landscapes (Martínez 1991, Moreira *et al.* 2004, Shlyakhtin *et al.* 2004), its range has diminished with the proliferation of intensive agricultural practices and excessive hunting (Palacín & Alonso 2008); it is currently classified

as Vulnerable to extinction (IUCN). One of the world's heaviest flying birds (males: 7–13 kg; females: 3.5–7.2 kg; Raihani *et al.* 2006), adults are primarily herbivorous, eating a wide range of leafy plant matter supplemented seasonally by seeds, invertebrates, and some small mammals (Morales & Martin 2002). In comparison, juveniles show a preference for invertebrates in the summer and autumn (c. 30% of juvenile diet, compared to 6% in adults), and legumes and weedy plants in the winter (Bravo *et al.* 2012). The birds typically move on foot rather than wing when foraging between patches; a small-scale agricultural system that incorporates rotational cereal and fallow fields without movement barriers in a mosaic has been recommended for species-specific habitat management (Moreira *et al.* 2004).

The UK breeding population became extirpated in the 1830s (Osborne 2005), however, in 2004, Great Bustard juveniles from Russia were released along the edge of the Salisbury Plain, the largest remnant chalk grassland in western Europe, as part of a ten-year trial reintroduction (Burnside *et al.* 2012). Release sites have been managed to provide habitats and food resources similar to those favoured by wild populations in Continental Europe. Although Salisbury Plain is considered to have been a stronghold for the historical Great Bustard population, the surrounding small, compositionally complex farm plots have long since given way to large-scale intensive agricultural practices. Fences now restrict movement between land covers in all but the military training area, hindering foraging by females with young chicks. Here, we aimed to collect high-quality information on the diet and habitat use of individuals released in southwest England across the year to inform effective habitat management for this species in the UK. In addition, we test for differences in the dietary components of individuals without and with access to supplemental food.

METHODS

Study site

From 2004 to 2010, 123 Great Bustard juveniles, reared from eggs threatened by farming practices in Saratov, Russia, have been transported and released at a single site on Salisbury Plain, Wiltshire, UK (A second release site was established in 2011, with 40 juveniles released from 2011 to 2012 at both sites, Ashbrook *et al.* in press). Dietary sampling and fine-scale behavioural observations were recorded from groups of

birds at these release sites; many of the known surviving released birds remained to live at or near to these sites for much of the year. Year-round landscape-level observational data were recorded from individuals both within and away from release areas. Individuals were considered to have left the release area when they were located more than 2 km from one of the release pens.

Land use observations and faecal sampling

Faecal samples were collected Mondays and Fridays for two consecutive weeks from a small group of free-flying bustards of mixed sex and age structure in each of spring (06–17 May 2013), summer (16–27 July 2012), and autumn (22 October–02 November 2012, 28 October–08 November 2013). In total, 87 samples were collected (autumn 2012 = 22; spring = 21; summer = 26; autumn 2013 = 18). Additional faecal samples were collected at dispersal ($n = 13$, 6 December 2012) and during moult ($n = 10$, 20–27 September 2013). Each sample was divided into two parts and then dried at 60°C for 48 hours. One part of each sample was examined for evidence of invertebrate structures using a dissecting stereomicroscope (Leica MZ75), while the other part was combined according to collection month to form monthly composite samples for micro-histological analysis. Samples were analysed at the Washington State University Wildlife Nutrition Laboratory using frequency–density conversion sampling procedures (Sparks & Malechek 1968, Holechek *et al.* 1982). A total of 200 microscope views over 25 slides were examined per faecal sample. In each view the number of cells from each plant species was counted and then the proportion of each species in each composite sample calculated. The principle challenge with this process is that fragile structures completely digested by the animal cannot be identified, and that more robust elements will be over-reported.

To assess the scale of possible error between measured and actual dietary composition resulting from different food digestibilities, correction factors were calculated for the July, October, and December 2012 diets. This was done by reconstructing the measured diets using study site-sourced plant material at the appropriate phenological stage, exposing them to pepsin-cellulase *in vitro* digestion (Carabaño *et al.* 2008, Villamide *et al.* 2009), and then repeating micro-histological analysis on the digested samples. Using multiple regression

(Leslie *et al.* 1983), the differences between corrected and uncorrected values were found to be relatively small ($3.0 \pm 1.0\%$), allowing us to assume that measured values closely reflected actual intake. Because seeds were not present in the samples analysed, their effect was not assessed.

Supplemental feed, consisting mainly of regular and layer pellets (Lundi Regular, Hof Bremehr GmbH & Co, Germany) augmented by pumpkin and mealworms, was provided twice daily to support the newly released juveniles for much of autumn 2012. Greater post-ingestion stomata integrity of pelleted food material and the visible presence of a boundary layer surrounding the processed cuticle cells, a product of reduced gizzard retention times and lignification during manufacture (Robbins 1983, McCusker *et al.* 2011, Bruce Davitt, pers. comm.), allowed ingredients found both in the pellets and forage plants to be differentiated. We paired faecal analysis with behavioural observations (defined below) in autumn with supplemental feed available (2012) and without (2013) to examine how supplemental feeding affects bustard diet, recognizing that juvenile birds were not present in 2013 as they had been in 2012. We carried out plant and invertebrate sampling to provide a reference library for the faecal analysis. Sampling was performed to coincide with the behavioural observations, but on days when birds were not being observed to reduce possible disturbance. In addition, invertebrate sampling was carried out on grass and crop lands similar to those available to the birds but adjacent to the sites being monitoring, which involved series of eight pitfall traps spaced at 2 m intervals (Ausden 1996).

Land use

Land use data were collected at two scales: fine-scale, using observers during discrete observation sessions around release sites, and landscape-scale, using re-sighting and telemetry data throughout the year. Fine-scale data were collected from sunrise to sunset Tuesdays to Thursdays, concurrent with the faecal collection weeks (Total observation hours: October 2012 = 60.6; May = 87.3; July = 94.8; October 2013 = 56.6). At five-minute intervals the principle activity and land cover for each marked bird in view was recorded from 300 to 450 m away in either a vehicle or a hide using a Swarovski Optik ATS 65 HD telescope. These observations were then categorized

into the following habitat types: (1) barley; (2) oil-seed rape; (3) semi-natural and reversion (restored) grassland; (4) improved grassland (grazed paddocks), wet grassland (low ground, riverine fields), and temporary grassland (arable pasture in rotation); (5) wheat; (6) lucerne; (7) mustard; (8) fallow, to include 2 ha unsown, tilled fallow Stone-curlew *Burhinus oedicnemus* management plots (Macdonald *et al.* 2012). In autumn 2012, time spent at the feeding station was also recorded. Sward depth was measured in 10 cm increments on days that the birds were not present. Observers followed the main group whenever the birds relocated. On average, at least three adult males and two adult females were observed at any given time. Autumn 2012 samples also included six juveniles (three males and three females) but just one adult female, but because these similarly sized birds could not always be differentiated, data for all seven were pooled. When the birds were observed in the main release pen, observations of captive birds were also included as they tended to join the group.

Landscape-scale habitat use

At the landscape-scale, we used the location of bustards surviving more than 182 days post-release from re-sightings and satellite telemetry data to assess habitat use after they had settled into their released environment (2420 records from 10 females and 3957 from 6 males). Of these data, 99.8% were within Wiltshire, with the remaining 0.2% of data from locations in Hampshire and Dorset. At and within a 500-m radius of these focal points the vegetative cover type was recorded by visual inspection. To give a measure of habitat diversity at these locations, we used Shannon–Weaver Index, calculated as $H = -\sum(P_i \ln P_i)$, where P_i is the proportion of area covered by each habitat type. We classed months into seasons: winter = December–February; spring = March–May; summer = June–August; and autumn = September–November.

Landscape-level habitat observations were categorized using the same eight habitat types used for the fine-scale observations. However, Great Bustards generally only had access to lucerne and mustard within the specially managed release pen. Further, many fields were not exclusively one crop species: crop rotations often result in the current crop supporting plants self-seeded by the previous crop. These secondary plants, referred to here as volunteer crops, may be found growing in field margins or along tramlines. In these cases, we did not assume that bustards only foraged in the dominant

crop type in mixed vegetation fields, and classed observations under more than one habitat type. Therefore, each habitat type was modelled separately and the proportion of observations across all habitat types does not sum to 100%. The proportion of observations for each sex, month, and location (whether within 2 km or outside 2 km from release sites) for each habitat category was calculated. Generalized linear models (GLMs) with quasi-binomial error structures were used to test for differences in habitat selection across the year, by sex, and location for each habitat type. We created global models for each habitat type with a three-way interaction between location, month, and sex, incorporating month as a quadratic term. For all models, empirical scale parameters (residual scaled deviance divided by the degrees of freedom) were calculated to check models were not over-dispersed, and plots of residuals were checked to ensure homoscedasticity, normality of errors, and negligible influence of outliers in the data. In all cases models were over-dispersed and quasi-binomial error structure was used. We then simplified the global models by sequential removal of the least significant terms (Crawley 2007) and calculated significance using the ‘dropterm’ function in R package MASS to perform *F*-tests. The minimum adequate model (MAM) was defined as a model containing only significant terms. Given the differences in landscape-level and fine-scale habitat selection data sets, we used the MAMs determined using landscape-level data to determine whether habitat selection in the fine-scale differed. For each habitat type, we included habitat selection data from both data sets as the response variable, with fixed factors determined by the relevant MAM and included data set as an additive fixed term within the model.

We tested for differences between the sexes and seasons in both the number of habitat types and the Shannon–Weaver Index within a 500-m radius of Great Bustard locations using generalized linear mixed-effects models, with Poisson error structures and bird identity as a random factor to control for variation between individuals. All analysis was performed using R v. 3.1.2 (R Core Team 2013).

RESULTS

Diet composition

Grassland plants and cultivated crops were both important dietary constituents throughout the year,

except when supplemental foods were made available (Table 1, Fig. 1). In May, 59.3% of the dietary intake was grassland and weedy herbaceous plants (forbs), with fat hen *Chenopodium album* being especially important. Young oil-seed rape and pre-jointing cereal represented 17.0% and 24.1% of the May diet, respectively. By July, grassland and weedy cover intake had declined to 31%, with lucerne becoming the principle food item (46.7%), and then declined further to 25.0% in September.

By early November 2013, the birds continued to rely heavily on barley grass (36.1%), oil-seed rape (25.6%), and grassland forbs (34.6%), despite spending over 90% of daylight hours within an oil-seed rape and volunteer barley field. The most commonly selected grassland plants were clovers (12.8%) and autumn hawkweed *Hieracium aurantiacum* (12.4%). In contrast, the previous autumn when supplemental pellets were available, the grassland forb dietary fraction was all but absent, with pellets taking their place (barley grass: 26.1%; oil-seed rape: 39.7%; pellets: 31.0%). In December of that year, supplemental feed was still being supplied and its intake had increased to 73.4% of the diet (66.2% pellets, 7.2% pumpkin *Cucurbita pepo*, plus a quantity of mealworms *Tenebrio molitor* provided daily by the project staff but that did not appear in the faecal analysis). Barley consumption persisted (19.5%), while oil-seed rape all but disappeared (3.8%).

Remnants of just six larvae mandibles were present in the May samples, one beetle structure in each of half the July faecal samples, and none in the remaining diets. When faecal sub-samples were ground and placed on a slide during micro-histological analysis no invertebrate fragments were recorded, suggesting that they represented <0.1% of the overall sampled material. Not appearing in the faeces, but observed to be opportunistically consumed, were earthworms, the occasional flying insect, and mealworms (supplemental feed) in December 2012. However, despite not featuring highly in the diet, pitfall traps in agricultural areas caught common beetles (*Pterostichus melanarius*, *Anchomenus dorsalis*, and *Amara similata*), flies, woodlice, and spiders (*Diptera*, *Isopoda*, and *Araneae* spp.) in grassland areas, suggesting that invertebrates were indeed available.

Trace amounts of seeds (<0.1%) were present in the faeces for all months but September 2013, after plant senescence and crop harvest but just as the winter forb crop sprouted. Then, large amounts of barley grain were found in the faeces (61.2%), along with trace amounts of *Asteraceae* seed.

Habitat use

With landscape-scale data and for all habitat types modelled, month modelled as a quadratic term explained significantly more variation in the data than as a linear term. The proportion of observations on habitat types across the year tended to vary by month and, in some cases, between sexes, but for all habitat types, selection did not differ between locations either within a 2-km radius of release sites or outside (Table 2). For barley habitats, selection increased slightly in the spring months compared to other times of the year, with no difference between the sexes (GLM with quadratic Month term; Table 2; Fig. 2). Oil-seed rape was selected more in the autumn and winter than in the spring and summer, and more by females than males in the winter (GLM with quadratic two-way Month \times Sex interaction; Table 2; Fig. 2). Selection of semi-natural grassland was greater during the spring and summer than for the rest of the year (GLM with quadratic Month: Table 2; Fig. 2), with both sexes showing similar preferences (Table 2). Males were observed on improved, wet, and temporary grassland more often than females in the spring and summer months (GLM with quadratic two-way Month \times Sex interaction; Table 2). In contrast, females chose wheat habitats more often than males in the spring; both sexes showed lower preference for these habitats at other times of the year (GLM with quadratic two-way Month \times Sex interaction; Table 2; Fig. 2). However, selection of fallow and Stone-curlew plot habitats was not found to differ between months, sexes, or locations (Table 2).

In some cases, the proportion of observations on habitat types was different between the landscape-scale and fine-scale habitat use. Both males and females were recorded in barley habitats and oil-seed rape habitats more often in the autumn during the dietary observations than landscape-scale observations (barley GLM with quasi-binomial error structure: Data set: $F_{1,55} = 54.1$, $P < 0.001$; Oil-seed rape GLM: Data set: $F_{2,55} = 12.5$, $P = 0.001$; Fig. 2). Also, both sexes were recorded more often in semi-natural grassland habitats in the spring and summer dietary observations than during the larger landscape-scale data set (GLM: data set: $F_{1,55} = 117.0$, $P < 0.0001$; Fig. 2). In contrast, both sexes were recorded less often in wheat habitats during fine-scale observations than during landscape-scale observations (GLM: data set: $F_{1,55} = 68.0$, $P < 0.0001$; Fig. 2). However, selection of fallow and Stone-curlew habitats was similar across the year between data sets (GLM: data set: $F_{1,55} = 0.7$, $P = 0.4$).

Table 1. Dietary composition (% total diet). Where plants in the faeces were only identified to family or genus, possible local candidates are identified in parentheses. As the growing season progressed plant degradation reduced, allowing more asters to be identified to species level in the autumn rather than genus or family. Shepherd's purse may have been included in Brassica crops. *n* refers to the number of faecal samples.

Dietary component		Without supplements				With supplements	
		May (<i>n</i> = 21)	July (<i>n</i> = 26)	Sep (<i>n</i> = 10)	Nov (<i>n</i> = 18)	Oct (<i>n</i> = 22)	Dec (<i>n</i> = 13)
Common name	Scientific name						
Grasses							
Non-crop grasses	Graminoid spp.	–	2.9	–	2	–	–
Barley	<i>Hordeum</i> spp.	8.2	–	–	36.1	26.1	19.5
Wheat	<i>Triticum</i> spp.	15.9	–	–	–	1	0.8
Totals		24.1	2.9	–	38.1	27.1	20.3
Forbs							
Crops							
Mustard	<i>Brassica juncea</i>	–	22.3	–	–	–	–
Oil-seed rape	<i>Brassica napus</i>	17	–	13.8	25.6	39.7	3.8
Lucerne	<i>Medicago sativa</i>	–	46.7	–	1.7	–	–
Totals		17	69	13.8	27.3	39.7	3.8
Grasslands/Weeds							
Amaranth:							
Amaranthaceae:							
Fat hen	<i>Chenopodium alba</i>	14.3	–	–	–	–	–
Aster:							
Asteraceae:							
Hawksbeard spp.	<i>Crepis</i> spp.	–	–	0.2	0.8	–	–
Hawkweeds spp.	<i>Hieracium</i> spp.	0.4	23.3 ^a	–	–	–	–
Autumn hawkweed, (Mouse-eared hawkweed)	<i>H. aurantiacum</i> , (<i>H. officinarum</i>)	–	–	–	12.4	–	–
Nipplewort	<i>Lapsana communis</i>	2.9	–	–	–	0.3	–
Rough hawkbit	<i>Leontodon hispidus</i>	–	2.9	–	–	–	–
Oxeye daisy	<i>Leucanthemum vulgare</i>	7.5	–	–	–	–	–
Senecio spp.	<i>Senecio</i> spp.	–	–	5.4	3	–	–
(Groundsel, Ragwort)	(<i>S. vulgare</i> , <i>S. jacobaea</i>)						
Dandelion	<i>Taraxacum officinale</i>	–	–	5	–	–	–
Scentless mayweed	<i>Tripleurospermum perforatum</i>	0.9	–	–	–	–	–
Other Asteraceae	Other aster	17.4	–	–	–	–	–
Borage:							
Boraginaceae:							
(Forget-me-not, Giant viper bugloss)	(<i>Myosotis</i> spp., <i>Echium pininana</i>)	–	–	–	1.6	–	–
Legume:							
Leguminosae:							
Clover	<i>Trifolium</i> spp.	7.9	–	–	12.8	0.7	1
Kidney vetch	<i>Anthyllis vulneria</i>	4	1.1	–	1.4	–	–
Mustard:							
Brassicaceae:							
Shepherd's purse	<i>Capsella bursa-pastoris</i>	–	–	1	1	0.4	–
Plantain:							
Plantaginaceae:							
Ribwort plantain	<i>Plantago lanceolata</i>	–	–	12.8	0.4	–	–
Speedwell spp.	<i>Veronica</i> spp.	–	–	0.4	–	–	–
Primula:							
Primulaceae:							
Oxlip	<i>Primula elatior</i>	–	–	0.2	–	–	–
Reseda							
Resedaceae:							
Wild mignonette	<i>Reseda lutea</i>	0.9	0.8	–	–	–	–
Other Forbs		2.7	–	–	1.2	0.8	1.5

(Continued)

Table 1. Continued

Dietary component	Common name	Scientific name	Without supplements				With supplements	
			May (n = 21)	July (n = 26)	Sep (n = 10)	Nov (n = 18)	Oct (n = 22)	Dec (n = 13)
Totals			58.9	28.1	25	34.6	2.2	2.5
Invertebrates			Trace	Trace	–	–	–	–
Seeds								
Barley		<i>Hordeum</i> spp.	–	–	61.2 ^b	–	–	–
Supplemental feed								
Pellets			–	–	–	–	31	66.2
Pumpkin		<i>Cucurbita pepo</i>	–	–	–	–	–	7.2
Mealworm		<i>Tenebrio molitor</i>	–	–	–	–	–	Limited
Totals			–	–	–	–	31	73.4

^aIncludes other asters.

^bIncludes trace amounts of aster seed.

Using landscape-scale data, the number of different habitat types within a 500-m radius of Great Bustard locations was found to be significantly greater for females than males across all seasons, but particularly

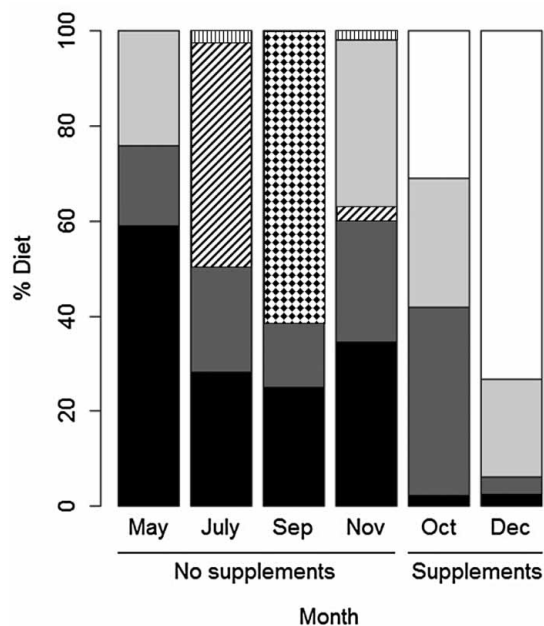


Figure 1. Dietary selection, by month, and autumn without (early November 2013) and with pelleted supplemental food (end October 2012, December). Grassland and weedy agricultural forbs (black), *Brassica* (mustard *B. juncea* in July, otherwise oil-seed rape *B. napus*) (dark grey), cereal grasses (light grey), lucerne (diagonal lines), barley seeds (stippled), other grasses (vertical lines), and supplemental feed (pellets, pumpkin, and mealworm) (clear).

in the autumn and winter (two-way interaction between sex and season: $\Lambda_{3,1025} = 13.5$, $P = 0.004$; $\Delta\text{AIC} = 7.5$). Moreover, females had a consistently higher Shannon–Weaver Index than males across the seasons, with greater differences in autumn, summer, and winter (interaction between sex and season: $\Lambda_{3,1025} = 9.1$, $P = 0.027$; $\Delta\text{AIC} = 3.1$; Fig. 3).

During fine-scale observations, bustards were not observed to forage in swards taller than 30 cm, and foraged primarily on vegetation less than 20 cm tall (males: $78.6 \pm 1.5\%$; females and juveniles: $82.1 \pm 3.0\%$). When eating plants higher than 20 cm, they stood in the adjacent shorter vegetation. Taller plants were sometimes used for resting and as shelter from the elements.

DISCUSSION

In wild Great Bustard populations, diet and habitat use is seasonally dynamic (Martínez 1991, Lane *et al.* 1999). Great Bustards are known to thrive within diverse habitat mosaics that support an abundant array of forbs, cereal crops, and invertebrates, and with limited anthropogenic disturbance (Alonso *et al.* 1994, Lane *et al.* 2001, Rocha *et al.* 2005, López-Jamar *et al.* 2010). Here, we show that Great Bustards reintroduced to the UK demonstrate similar dietary and habitat use to wild populations despite being captive-reared and released within a predominantly industrial agricultural landscape. This is achieved by seasonal and, when necessary, daily relocations among a variety of agricultural crops, grasslands, and fallow plots.

Table 2. Results of quasi-binomial GLMs investigating landscape-scale habitat usage by Great Bustards in the UK. Habitat types were modelled separately. Values below show results from step-wise model deletion with *F*-tests to determine significance of terms. Location refers to whether the re-sighting and telemetry data were within or outside a 2 km radius of release sites. Month (Month²) was modelled as a quadratic term. Significance of individual terms was assessed using *F*-tests; change in degrees of freedom (df), *F*-value and *P*-values are shown (with asterisks denoting significance level).

Habitat type	Variable	Estimate ± se	Change in df	<i>F</i>	<i>P</i> -value
Barley	Month	-1.72 ± 1.12	1	3.1	0.08
	Month ²	-2.26 ± 1.26	2	3.6	0.04*
	Sex	-0.32 ± 0.28	1	2.1	0.2
	Location	-0.05 ± 0.27	1	0.04	0.8
	Month × Sex	0.05 ± 0.09	1	0.4	0.5
	Month ² × Sex	5.30 ± 2.59	2	2.7	0.09
Oil-seed rape	Month	-1.86 ± 0.90	1	0.8	0.4
	Month ²	7.31 ± 1.08	2	40.1	<0.001***
	Sex	-0.26 ± 0.19	1	1.9	0.2
	Location	-0.06 ± 0.17	1	0.1	0.7
	Month × Sex	0.12 ± 0.08	1	2.2	0.1
	Month ² × Sex	-2.77 ± 1.38	2	3.9	0.027*
Semi-natural and reversion grassland	Month	-5.01 ± 1.01	1	20.5	<0.001***
	Month ²	-4.21 ± 1.11	2	21.7	<0.001***
	Sex	0.30 ± 0.25	1	1.5	0.2
	Location	0.25 ± 0.24	1	1.3	0.2
	Month × Sex	-0.02 ± 0.08	1	0.1	0.8
	Month ² × Sex	1.83 ± 2.52	2	0.3	0.7
Improved, wet and temporary grassland	Month	-0.59 ± 0.47	1	3.0	0.09
	Month ²	-1.19 ± 0.51	2	4.1	0.024*
	Sex	0.15 ± 0.12	1	1.5	0.2
	Location	0.006 ± 0.12	1	0.002	0.9
	Month × Sex	-1.01 ± 0.04	1	6.8	0.01*
	Month ² × Sex	-1.78 ± 0.96	2	5.6	0.007**
Wheat	Month	-0.67 ± 1.10	1	1.6	0.2
	Month ²	-4.48 ± 1.28	2	4.8	0.01*
	Sex	-0.49 ± 0.21	1	0.1	0.04*
	Location	-0.07 ± 0.19	1	0.1	0.7
	Month × Sex	0.14 ± 0.07	1	4.8	0.03*
	Month ² × Sex	3.12 ± 1.76	2	5.4	0.009**
Fallow and Stone-curlew plot	Month	-0.84 ± 1.00	1	1.5	0.2
	Month ²	-1.499 ± 1.098	2	1.87	0.2
	Sex	-0.047 ± 0.259	1	0.04	0.8
	Location	0.001 ± 0.254	1	0.00	0.9
	Month × Sex	-0.003 ± 0.08	1	0.002	0.9
	Month ² × Sex	3.367 ± 2.365	2	1.17	0.3

**P* < 0.05.

***P* < 0.001.

****P* < 0.001.

Agricultural forbs provide generalist herbivores with an abundance of high-density, high-energy, highly digestible foods, enabling some animals to thrive in anthropologically modified settings (McCabe & McCabe 1997). No single food, however, can provide a completely balanced diet and the over-consumption of any single plant will result in the accumulation of

toxic levels of secondary metabolites or the over-consumption of particular nutrients (Guerrero *et al.* 1999, Raubenheimer *et al.* 2009, Villalba & Provenza 2009). We found that, even in the presence of favoured agricultural forbs such as lucerne and oil-seed rape, at least a quarter of the total Great Bustard dietary intake remains grassland and agricultural weedy

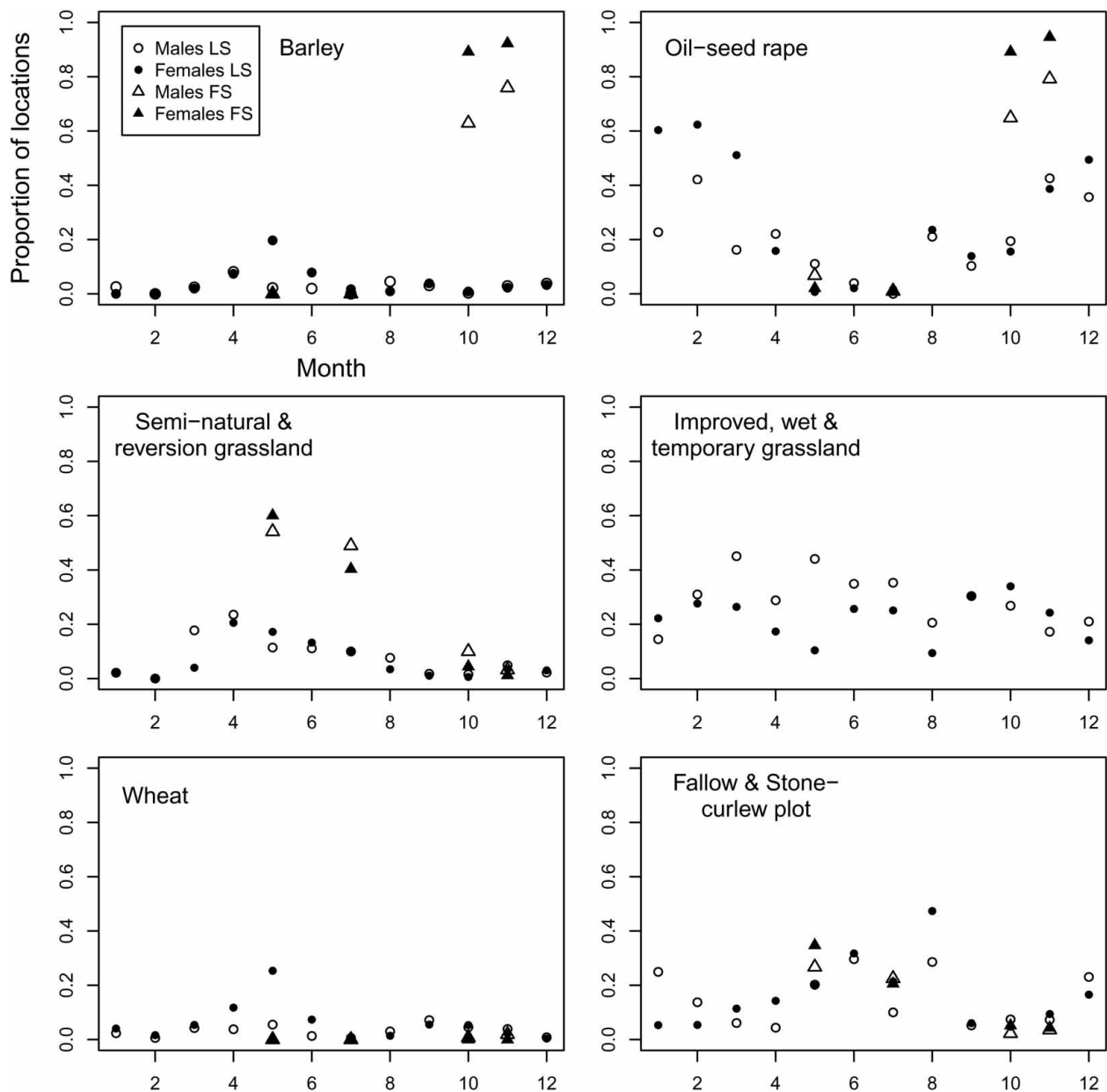


Figure 2. Habitat use across the year by male and female Great Bustards from landscape-scale (LS, represented by circles) and fine-scale (FS, represented by triangles) habitat use data sets. Males are shown by open symbols; females by filled symbols.

forbs during the months studied, highlighting the importance of these habitats for Great Bustard populations.

Although oil-seed rape is a known favoured Great Bustard winter food, volunteer barley grass was, at times, consumed in greater quantities. It is possible that barley counter-balances the nutritional attributes of oil-seed rape; autumn volunteer barley had a lower digestibility but was higher in crude protein and fat (Gooch unpubl. data) while possessing much lower

calcium and phosphorus levels (Mayland *et al.* 1976, Bloem *et al.* 2010). The greater wheat and barley intake in May likely reflected the higher digestibility levels of pre-joining grasses (Van Soest 1967, Moore & Jung 2001). We found that emergent mustard leaves were consumed in large quantities in July only; high in fat and protein, the glucosinolate levels in the very young leaves may have been initially low enough to be considered palatable (Bellostas *et al.* 2004). Alternatively, in some populations toxic compounds

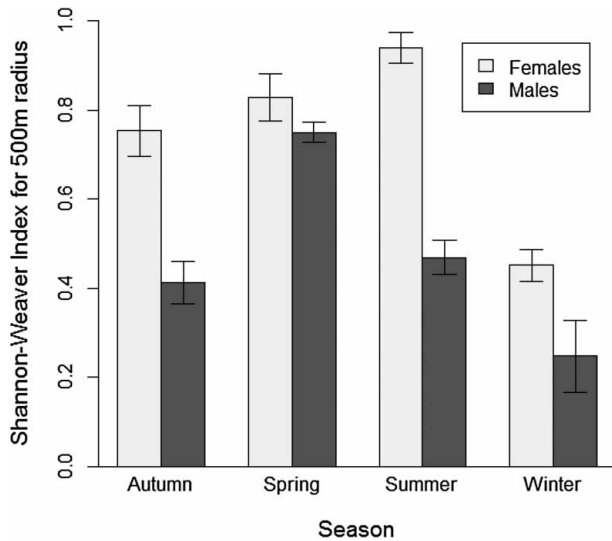


Figure 3. Mean Shannon–Weaver habitat diversity index within a 500-m radius around Great bustard locations by sex and season.

may be ingested in larger quantities by males to self-medicate and reduce their parasite load, increasing their breeding success (Bravo *et al.* 2014). However, we consider this to be an unlikely function of mustard consumption in the UK bustards, because it took place at the end of the breeding season.

Consumption of grassland and weedy forbs considered to be unpalatable, toxic, or undesirable to domestic livestock was common to both this study and in Spain and may pose a conservation challenge, because these are often targeted by eradication schemes. These include groundsel, hawkweeds, oxeye daisy, and wild mignonette (Vengris 1953, Moghaddam 1977, Dogan 2001, Poppenga & Puschner 2009). Plants containing high levels of toxic compounds such as glucosinolates, pyrrolizidine alkaloids, and saponins may have been merely sampled or consumed in limited amounts while capturing small herbivorous invertebrates. For example, a good host for an array of aphids (Wilkinson *et al.* 2001), poppy *Papaver* spp. is commonly consumed in Spain (Lane *et al.* 1999) but was not identified in the UK diet. On the other hand, bustards may have evolved mechanisms allowing them to consume small amounts of these toxins in the pursuit of particular nutrients (Davis 1997), so that these plants are in fact important food resources. It is important that these plants persist within agricultural grasslands to support Great Bustards.

In wild populations, invertebrates are an important component of adult diet in the summer; however, we found invertebrates to be nearly absent from the UK

bustard diet. Certainly many small and soft-bodied invertebrates went undetected in the faecal analysis, but this collective biomass was not significant. It is possible that invertebrate abundance in the UK is lower than in Russia and the Iberian Peninsula where agricultural practices are less intensive; however, we did not carry out sufficiently comprehensive invertebrate sampling to make comparisons. Agricultural seeds were also unexpectedly rare in diet, except in September. This may be an artefact of regional winter cropping practices; in England, unharvested seeds are often quickly ploughed under rather than being left to lie in fallow fields and available to herbivores.

We found that while fallow lands were seasonally favoured, grassland use was persistent. On fallow lands and Stone-curlew scrapes, plants are largely unmanaged and ungrazed by large herbivores, meaning that digestibility is highest during the growing season, declining somewhat as the season progresses (Abaye *et al.* 2009). Conversely, non-restored grasslands are often mowed or grazed, providing the shorter sward structure preferred by Great Bustards in the UK and elsewhere (Zhao *et al.* 2005) and fostering palatable new growth (Jeangros *et al.* 2002).

Females selected areas of greater habitat diversity than males, which may reflect differences in digestive capabilities for this sexually dimorphic avian herbivore (Demment & Van Soest 1985, Hassall *et al.* 2001). Another explanation is that the much smaller female may be more selective about habitat structure for reasons other than diet, such as thermoregulation (Belovsky & Slade 1986), predator avoidance (Whittingham & Evans 2004, Magaña *et al.* 2010), or ease of movement. In addition, habitat use was sex-specific in the breeding season, with males preferring short grassland areas more than females, probably for breeding displays.

Supplemental food was provided for two purposes: (1) to ease the transition of naïve captive-reared individuals into their new environment; (2) to reduce dispersal away from specifically managed release sites. When available, pelleted foods effectively replaced the forb fraction of the Great Bustard diet, suggesting that the manufactured pellets were an acceptable substitute for those plants in at least some important nutrient categories. By dispersal in December the birds' diet consisted almost exclusively of supplemental foods, augmented with barley grass and minor quantities of other plants, likely reflecting declining forage plant qualities in terms of abundance, diversity, and digestibility. This decline may have eventually triggered dispersal.

The nature and quantity of supplemental food provided may have been problematic. Because the young birds had been reared from hatching on a diet that included pellets, their caecal microbial community and the size, function and capacity of their caecum and small intestine may have varied from those of the conspecifics feeding entirely on the landscape (Moss & Parkinson 1972, Gross *et al.* 1985, Duke 1986). At dispersal, when pellet intake represented over two-thirds of the diet, these juvenile birds would have been physiologically less capable of extracting dietary nutrients than if we had begun decreasing pellet availability shortly after release (DeGouler *et al.* 1999, Sundu 2009). Second, with large quantities of artificial food available and consumed, released juveniles may have lacked some of the foraging behaviours necessary post-dispersal (Snyder *et al.* 1996, Galef & Giraldeau 2001, Schlossberg & Ward 2004, Champagnon *et al.* 2012, Riebel *et al.* 2012).

Mosaic management, which attempts to coordinate management across a group of farms rather than concentrating on individual farms, has been shown to be beneficial for other ground-nesting bird species (Schekkerman *et al.* 2008, Oosterveld *et al.* 2010). Studies on wild Great Bustard populations recommend the creation of arable and grassland habitat mosaics, providing a high diversity of food resources within a small area (Moreira *et al.* 2004, Palacin *et al.* 2012), and we suggest that this approach would be beneficial in the UK. This would be especially true for newly released juveniles if these habitat mosaics were not fenced, allowing different habitats to be accessed without flight. An assemblage of weedy plots and forb-rich, short sward grasslands interspersed among cereal crops, lucerne, and oil-seed rape with a volunteer barley grass understory available at various phenological stages (staggered planting dates) would provide maximum nutritional choice. Heavily grazed pastures are nutritionally barren and can contribute to Great Bustard declines (Carranza & Hildago de Trucios 1993). The inclusion of some clover, insect mixes, and some standing grain tillers would add to the diversity and potential nutrient options. Bordering the agricultural plots with short weedy grass field margins, perhaps 4–8 m wide, would ensure ease of movement, food access, roosting sites, and invertebrate and seed bank genetic reservoirs (Robinson & Sutherland 2002).

Currently in the UK, habitat management for wildlife in agricultural areas falls under Environmental Stewardship schemes, now being developed into the New Environmental Land Management Scheme.

Management of habitat mosaics created and managed specifically for Great Bustards could fall under this scheme because they could potentially support a wide range of other farmland birds, such as Stone-curlew, Lapwing, and Corn Bunting (Kleijn *et al.* 2006). Reversion of fields within the agricultural landscape to semi-natural grassland has been difficult to justify to landowners on an economic basis under current Environmental Stewardship schemes (A. Taylor, pers. comm.), despite being extremely helpful to a broad array of flora and fauna (Carvell *et al.* 2006, Baker *et al.* 2012). However, even small areas of semi-natural grassland in suitable areas for Great Bustards would be beneficial (Moreno *et al.* 2010).

In conclusion, it is often difficult to judge how released individuals will utilize their new environment during re-introduction schemes, particularly where the habitat may have changed since the species was present. Here, we show the value of monitoring the diet and habitat use of released individuals to support adaptive project management, which may be critical for improving reintroduction success.

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