Maximizing sexual signal transmission: use of multiple display sites by male houbara bustards

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Abstract
A good location of song or call posts and visual display sites of males is crucial for territory defence and mate attraction. These sites are typically located at prominent positions to ensure an efficient, long-distance sexual advertisement. If the purpose of display sites is to maximize visibility, a suitable strategy would be to use multiple display sites rather than just one site. We investigated this in the ground-displaying houbara bustard by using two recent technological advances that enabled us collecting high precision data, GSM/GPRS loggers provided with accelerometer and very high-resolution digital elevation models of the terrain. We found that 12 out of 20 marked males used two or three display sites instead of just one as previously assumed in this species. The most used display site had the largest viewshed and use of both alternative sites decreased in proportion to their decreasing viewsheds. The number of display sites was apparently determined by two factors. First, it was correlated with display intensity, suggesting that using multiple display sites may be a mechanism to increase sexual signal transmission in males that are dominant or in better condition. Second, supplementary display sites were not used when the principal display site already provided an excellent view of the surroundings, e.g. when it was located on a hilltop. These results confirmed that the function of secondary display sites is to supplement the viewshed provided by the principal display site, and so maximize sexual signal transmission.

Significance statement
Performing sexual display from just a single place is often not enough to reach all possible mates or competitors, so using multiple posts may be crucial for an effective sexual signal transmission. This is particularly important when the display is visual, and topographical barriers or vegetation may block the male’s line of view. Using last generation GSM/GPRS loggers equipped with accelerometers and very high-resolution digital elevation models of the terrain, we show how houbara bustard males, who perform a costly running display on the ground, have developed a complex display pattern that involves the use of various nearby display sites. These display sites are used in proportion to their visibilities, which shows that this multiple display site system has evolved to maximize the aggregated visual field of males and so increase their visibility to females and neighbour males.

Keywords African houbara bustard · Chlamydotis undulata fuertaventurae · Exploded lek · Sexual display · Visual signal

Introduction
Males of many animal species use specific sites to perform their territorial songs or sexual displays. The location of these sites must be subjected to strong selection, since they play a key role in achieving the two main functions of visual or vocal displays, namely territory defence and mate attraction (Andersson 1994; Kroodsma and Miller 1996; Bradbury and Vehrencamp 2011). In many lekking birds, elaborate visual displays have probably evolved to attract females located at large distances (Johnsgard 1994; Höglund and
Alatalo 1995). For example, males of some bustard species display white feathers that are visible over several kilometres in the open landscapes where these species live (Johnsgard 1994; Hellmich 1988, 2003; Jiguet and Bretagnolle 2001; Hallager and Lichtenberg 2007; Alonso et al. 2010a, 2012; Olea et al. 2010; Ziembicki 2010).

To maximize transmission of these visual and vocal signals, song or call posts and display sites are usually located at prominent locations within the male territory (Marten and Marler 1977; Hunter 1980; Collins 1981; Petit et al. 1988; Beck and George 2000; Delgado and Penteriani 2007; Alonso et al. 2012; Barrero et al. 2020). The fact that exactly the same locations are generally used year after year strongly suggests that their selection is associated to specific topographical and environmental features that maximize long-distance sexual advertisement (Johnsgard 1994; Höglund and Alatalo 1995; Delgado and Penteriani 2007; Alonso et al. 2012). On the other hand, their permanent location and conspicuousness may attract predators, and therefore a good visibility from these sites is not only important for sexual signal transmission but also to reduce predation risk (Bradbury et al. 1989; Wiley 1991; Balmford and Turyaho 1992; Gibson and Bachman 1992; Höglund and Alatalo 1995; Widemo 1997; Boyko et al. 2004; Morales et al. 2008).

If the main purpose of display sites is to maximize visibility or sound transmission, the question arises whether a single location is enough or males could increase their viewshed by using more than just one display site. We investigated this issue in the Canarian houbara bustard Chlamydotis undulata fuertaventurae. The mating system of houbara bustards has been found to fit the definition of an exploded lek, with males displaying at distances of several hundred meters from each other, defending their display sites against other males (Collins 1984; Hingrat et al. 2004, 2008; Hingrat and Saint Jalme 2005; Alonso et al. 2012), and remaining faithful to them over the mating season and also between years (Abril-Colón et al. 2022). Their display is essentially visual and consists of fast circular runs with the head folded back, the white breast feathers fully spread out and the black throat feathers folded back onto the flanks. Each run lasts about 10–20 s, and during the peak display periods at dawn and dusk, they may reach frequencies of one run every 1–2 min. At the end of each circular run, the male usually performs 2–7 vocal sounds from a standing position with still erect and conspicuous white and black breast feathers (Heinze et al. 1978; Collins 1984; Hinz and Heiss 1989; Launay and Paillat 1990; Hellmich 2003; Cornec 2011, 2015; Cornec et al. 2014, 2015). Some authors have noticed that houbara males display at elevated points from which they have a good field of view and also minimize obstacles that could block transmission of their vocalizations (Hellmich 2003; Hingrat et al. 2008; Cornec 2015; Cornec et al. 2017). However, the importance of visibility as one of the main factors determining display site selection in this species has been investigated in detail only very recently (AU et al. unpubl. data).

While the common assumption is that each male has a single display site (Collins 1984; Hellmich 2003; Hingrat et al. 2004, 2008), in the present study, we describe for the first time the use of multiple display sites by houbara males. This was only possible by combining high-resolution topographic analyses with intensive monitoring of birds marked with GSM/GPRS data loggers, which recorded both, their display locations and their behaviour as determined through accelerometry. Our aim was to investigate the advantages houbara males may obtain by using multiple display sites, and whether they are faithful to each of these sites year after year. Our hypothesis was that, in case of multiple display sites, the principal display site, i.e. that used with highest frequency, should provide a higher viewshed than secondary, less used display sites, and that the function of these secondary display sites is to expand the viewshed to areas not visible from the principal display site. Specifically, we tested the following predictions derived from our main hypothesis: (1) the viewshed from the principal display site (hereafter, DS1) should be higher than that from alternative, less used display sites (hereafter, DS2 and DS3, in decreasing order of use), and the viewshed of these secondary display sites should correlate with their use by the displaying male, i.e. viewshed of DS2 > viewshed of DS3. (2) If males use secondary display sites only when they do not reach sufficient visibility from DS1, the viewshed from DS1 should be higher in males with only one display site than in males with multiple display sites; alternatively, some males might use only one display site due to topography constraints, e.g. when DS1 was in a very good location — e.g. a hilltop — and complementary display sites would not add any significant additional viewshed to that already provided by DS1. (3) By adding secondary display sites to DS1, a male would increase its total viewshed. (4) The accumulated viewshed of males with multiple display sites should be higher than that of males with just one display site, provided that visibility from DS1 is similar in both cases. (5) If selective pressures favouring the use of multiple display sites are strong, i.e. the male obtains clear benefits by using them, faithfulness to them should be expected in consecutive years; moreover, the order of use of these multiple sites should be the same year after year. (6) Dominant males, who presumably hold the best territories, should be expected to be more faithful to their DS1 than other males and should display proportionally more at their DS1 compared to other display sites. For the purpose of this study, we defined dominant males as those displaying more intensively.
Methods

Study area

The study was carried out in Lanzarote (Canary Islands, 29°02′N, 13°37′W; 846 km²), the main stronghold of the endangered Canary subspecies of African houbara Chlamydotis undulata fuertaventurae (Alonso et al. 2020). The Canary archipelago is located 140 km west of Morocco. The climate is subtropical-desert, with an average annual rainfall of 110 mm, concentrated in December–February and almost absent in June–August. Mean temperatures are 18 °C in winter and 25 °C in summer. The island has a volcanic origin, and today shows a weathered relief with a largely smoothed topography and a few mountain massifs. The dominant vegetation consists of xerophytic shrubland (Launaea arborescens, Salsola vermiculata, Lycium intricatum, Suaeda mollis, Euphorbia spp.), with some interspersed, once more extended but nowadays mostly abandoned farming areas.

Data collection and processing

Between January 2017 and December 2018, we captured 20 houbara bustard males and equipped them with with backpack-mounted, solar-powered GSM/GPRS loggers (e-obs GmbH, Gruenwald, Germany), using a soft, elastic band as harness material. The weight of the logger (48 g) plus harness was 2.83% of the body weight (range 2.54–3.15). We caught the birds at display sites using nylon snares, a method that we selected as the most effective and harmless after considering various alternatives (Seddon et al. 1999, Y. Hingrat, pers. commun. April 2017). When waiting for the birds to be caught, the four members of the capture team remained at 300–500 m of the snares to be able to access the entangled birds by car as soon as possible. The head of the bird was covered with a soft cap to minimize capture stress during disentangling, measuring and tagging operations. All the process from capture to release lasted only 14 min (range 5–25). All males were considered to be adults, since none of them showed obvious immature characters. The sex was determined through their plumage features (Cramp and Simmons 1980; Gubin 1999) and confirmed by genetic analysis using DNA extracted from contour feathers plucked from the breast or flank (JL Hórreo et al. unpubl. data).

The loggers provided GPS locations of each bird at 5 min intervals from 05:00 to 23:00 h. They included an accelerometer (ACC) which recorded the acceleration of the transmitter on a 3D space and provided a 3D-graph representation of the bird’s movements. Data were automatically downloaded through the phone network and stored in Movebank database (https://www.movebank.org/). The loggers were programmed to register an intensive ACC-data recording schedule (interval: 10 s; byte count: 1188; sample rate: 16.7 Hz) for 1 h daily (07:30–08:30 h UTC), coinciding with the peak display period at dawn (Hinz and Heiss 1989; Hellmich 2003). This schedule resulted in an almost continuous activity recording (52.8 s/min).

To be able to identify the activities of houbara bustards from the ACC-graphs, we recorded with a chronometer the timing of all activities of 10 marked birds for variable periods (720 h in total) during the hour of intensive ACC-data recording. By comparing our timed field observations with the ACC graphs, we could identify the ACC patterns that corresponded to each activity. For this study, we were specifically interested in quantifying and locating circular display runs, since these are most frequently performed at fixed display sites, although a number of them are also performed at other sites within the territory (i.e. outside the fixed display sites used by each male; see Supplementary Figs. S1, S2). The selection of display runs of the 20 marked males was performed manually from the data stored in Movebank, through inspection of ACC graphs during the display season of the main study year (18 November 2018 to 29 March 2019 for 18 males; data for males 19 and 20 are from 2017 to 2018).

Linear display runs, which males often perform outside these fixed display sites when they see a female at reasonably close distance (i.e. <1 km), show a similar ACC-pattern, but last longer (up to >1 min) than circular display runs (mean = 16.09 s, SD = 7.03, n = 5495; JCA et al. unpubl. data). Thus, we excluded display runs lasting >30 s from the sample for analysis. Finally, only those display runs coinciding with the moment when the logger recorded a GPS location (every 5 min) were used in this study, since we needed display runs with known coordinates to establish very accurate display site locations for viewshed calculations. The final sample was 5682 circular display runs, which can be considered very representative, since it amounts 50.5% of all circular display runs performed by the 20 males during the hour of peak display activity (07:30–08:30) over the whole display season (15th November to 30th March) (unpublished data extracted from Movebank), and both series of number of display runs that used in this study and total number of runs performed by the males were highly correlated (r = 0.98, p < 0.001, n = 20 males).

Using ArcGIS Pro version 2.7.3 (ESRI, 2020), we plotted all display locations on a map, to find out where they were clustered and so identify the fixed display sites of each male. We then selected all display points included within a circle of 20 m radius centred around the mean coordinate of each of these clusters and defined the fixed display site as
the modal coordinate of all display coordinates within those circles. Modal coordinates of display runs represent fixed display sites better than mean coordinates because they are less sensitive to outlier values and GPS location errors of the loggers, which under the ideal conditions of our study area — clear sky, absence of tree vegetation — can be estimated at only 1.7 m for the e-obs loggers of third generation that we used (root mean-square location error (RMSE); Fleming et al. 2021). The standard deviation of location errors of e-obs 25 g loggers — slightly less accurate than the 48 g loggers — was estimated at 2.99 m by the manufacturers in a field test under similar conditions as in our study area (W. Heidrich, pers. commun.). For each male, a principal display site (DS1) was defined as the modal coordinate of the cluster containing the highest number of displays. In addition to DS1, many males had secondary display sites, of which a maximum of two (DS2, DS3) were defined for those males based on progressively decreasing numbers of clustered displays. We did a ground-truthing of the location of DS1 of all males through direct observation of displaying males and their footprints and circular tracks in the field and confirmed that GPS errors of display site modal locations were negligible.

We then calculated the area visible from each display site as the number of pixels that could be seen from it, i.e. with no other pixel blocking the visual line between the display site and the focal pixel, within a circular buffer around the display site (see the two scales defined below). Analyses were carried out by using a high-resolution digital elevation model (DEM) of 2 m pixel size obtained from LIDAR imaging at the Canary Islands Spatial Data Infrastructure (SDI) (https://www.idecanarias.es). This GIS analysis determines the raster surface locations visible to each observer, or in other words, identifies whether the observer (i.e. the displaying male in DS1 to DS3) is visible from each raster surface location (Law and Collins 2019). The visibility of each cell centre is determined by comparing the altitude angle to the cell centre with the altitude angle to the local horizon. The local horizon is computed by considering the intervening terrain between the point of observation and the current cell centre. If the point lies above the local horizon, it is considered visible. To account for the height of a male and a female (or male) observing it, we added an offset height of 0.3 m to specify an offset to the display site and to all other pixels in the visibility analysis. An example of the areas visible to a male houbara from two display sites is shown in Supplementary Fig. S3.

We made all calculations for two different buffers, a long-range and short-range visibility area, to account respectively for the maximum distance from which a displaying male would be seen by other houbaras (long-range), and for the visibility of the displaying male within its territory. In the case of long-range buffer areas, we set the limit at 3000 m radius from each fixed display site (DS1–DS3) based on published visual acuity values of birds (Hodos 1993) and estimates from experts for other bustard species (G. Martin, pers. commun.; Alonso et al. 2012). Field trials showed that a displaying male houbara bustard can be seen by the human eye at approximately 1–1.5 km (personal observation). Considering for birds a potential acuity of 2.5 times that of the human eye (Hodos 1993), a displaying male would certainly be seen at 3 km by a female (potential mate) and by another male (potential competitor). To check prediction (1) taking a different approach from that based on calculating different long-range viewsheds for each display site (DS1–DS3), we also calculated the accumulated visibility that resulted from successively adding to the viewshed of DS1 the viewsheds of the two secondary display sites (DS2, DS3), but within the same buffer of 3000 m around the principal display site. As for the short-range viewshed, we set the limit at 467 m, the mean radius of a circle of the same surface as a male territory during the peak display season (JCA et al. unpubl. data; based on 95% kernel density estimates of the areas used by our males in January–February).

To examine whether males use the same display sites year after year, we used a sample of 1–2 additional breeding seasons (2019–2020, 2020–2021) for which we had radiotracking data of marked males. We used the accelerometer sequences of display runs identified manually for the main breeding season (2018–2019) to train the model of the phyton-based application AcceleRater (Resheff et al. 2014), and obtain display runs automatically for these 1–2 additional breeding seasons. Among various model types available in AcceleRater, we found that random forest was the best one, with 93.03% correct classification ($SD = 0.44SD$), which means that all behaviours were identified with more than 90% accuracy. Once all display runs had been quantified and located on a map, we checked whether their modal values for each male coincided or not with DS1–DS3 of the main study year. To minimize observer bias, blinded methods were used when all behavioural data were recorded and/or analysed. Display location maps, viewshed maps and viewshed calculations are given in Online Resource 1.

**Statistical analyses**

We used Wilcoxon matched-pairs signed-rank tests to assess differences in visibility between display sites of males. Because not all males had the same number of display sites, these tests were carried out separately for all pairs of display sites with data for the same males in both display sites (e.g. DS1 vs DS2, DS2 vs DS3, DS1 vs DS3, etc.). We used Spearman’s rank correlations to assess relationships between number of display runs and number of display sites of males, percentage use of their principal display site, and percentage display runs in locations outside fixed display sites, and
Pearson’s coefficient to test the correlation between number of displays of each male in the sample used in this study and total number of displays downloaded from Movebank, after log-transformation of both variables. Finally, we used Kruskal–Wallis tests to examine differences in visibility from DS1 between males with only one display site and those with multiple display sites, and to check for differences in accumulated visibility from all display sites and number of display sites. All analyses were performed using Statistica v. 7 (Statsoft, Tulsa, OK, USA).

Results

Display intensities at different display sites

Eight of the 20 marked males used a single display site (DS1), 5 used two (DS1, DS2) and 7 used three (DS1, DS2, DS3) (Table S1). All display sites used by a male were relatively close to each other (108.9 m, $SD = 61.0$, range $= 30.3–233.1$; Supplementary Table S1). The typical distribution in cases of three display sites was a triangle, with similar distances between DS1, DS2 and DS3 (Supplementary Table S1, Supplementary Fig. S1). In addition to these fixed display sites, males sometimes displayed at other locations within their territories. This usually occurred when a female entered the territory. The male normally walked towards her and performed both, linear and circular display runs at different points outside the fixed display sites, attempting to induce her to copulation. Males displaying more intensively performed more displays at locations outside fixed display sites ($r_S = 0.67, p < 0.01, n = 20$, Fig. 1a). However, the proportion of these displays outside fixed sites decreased with display intensity ($r_S = -0.75, p < 0.01, n = 20$; Fig. 1b), while the proportion of displays at the principal display site increased ($r_S = 0.63, p < 0.01, n = 20$; Fig. 2). These results indicate that sexually more active males made a higher proportional use of their fixed display sites, and particularly of their principal display site.

Visibilities from each display site

From the principal display site (DS1), males could see 20.0% of the surface around them in the long-range scale, and 47.5% in the short-range scale (Table 1). In the long-range scale, the viewshed from the principal display (DS1) was a 20.3% higher than that from DS2 and a 27.9% higher than that from DS3. The viewshed was also higher from DS2 than from DS3 (Table 1). These differences were significant ($Z = 3.14, p = 0.002, n = 19$ pairs, Wilcoxon matched-pairs signed-rank test comparing DS1 vs DS2 or DS3; $Z = 3.06, p = 0.002, n = 26$ pairs including also the comparison DS2 vs DS3). In the short-range scale, the differences in

![Fig. 1](image1.png) Correlation of total number of displays with number (a) and percentage (b) of displays performed outside fixed display sites (DS1, DS2, DS3) in 20 houbara bustard males

![Fig. 2](image2.png) Correlation of total number of displays with percentage of displays performed at the principal display site (DS1) in 20 houbara bustard males
viewshed followed the same pattern (DS1 > DS2, DS1 > DS3, DS2 > DS3) but did not reach significance (Z = 0.72, p = 0.47, n = 19 pairs). Wilcoxon matched-pairs signed-rank test comparing DS1 vs DS2 or DS3; Z = 1.46, p = 0.14, n = 26 pairs including also the comparison DS2 vs DS3. These results show that houbara males used alternative display sites in proportion to the long-range viewsheds from each of them (Fig. 3), showing a similar but less marked relationship with the short-range viewsheds.

As for the second approach of our viewshed analysis, i.e. using the accumulated viewsheds, each male had from all its display sites within the long-range (3000 m) buffer centred on each display site, excluding (a) all display runs performed at locations outside fixed display sites (other locations), and including (b) display runs at locations where males with display sites (DS1 and DS2) but did not reach significance (Z = 0.72, p = 0.47, n = 19 pairs).

### Table 1 Comparison of viewsheds from principal and secondary display sites of 20 male houbara bustards

|                | DS1                  | %      | n   | DS2                  | %      | n   | DS3                  | %      | n   | Difference in % |
|----------------|----------------------|--------|-----|----------------------|--------|-----|----------------------|--------|-----|-----------------|
| **Long-range viewshed (3000 m):** |                      |        |     |                      |        |     |                      |        |     |                 |
| Overall mean   | 1,335,619 ± 635,576  | 20.0   | 20  | 1,108,349 ± 453,481  | 17.3   | 12  | 1,063,139 ± 392,733  | 15.8   | 7   | 20.3            |
| DS1 vs DS2     |                      |        |     | 1,333,005 ± 621,556 | 20.5   | 12  | 1,108,349 ± 453,481  | 17.3   | 12  | 3.2             |
| DS1 vs DS3     |                      |        |     | 1,359,417 ± 568,382 | 20.0   | 7   | 1,063,139 ± 392,733  | 15.8   | 7   | 17.0            |
| DS2 vs DS3     |                      |        |     | 1,077,163 ± 378,325 | 16.0   | 7   | 1,063,139 ± 392,733  | 15.8   | 7   | 1.3             |
| **Short-range viewshed (467 m):** |                      |        |     |                      |        |     |                      |        |     |                 |
| Overall mean   | 81,282 ± 25,614      | 47.5   | 20  | 74,763 ± 20,041      | 43.7   | 12  | 66,419 ± 24,247      | 38.8   | 7   | 2.7             |
| DS1 vs DS2     |                      |        |     | 76,778 ± 23,670      | 44.8   | 12  | 74,763 ± 20,041      | 43.7   | 12  | 2.7             |
| DS1 vs DS3     |                      |        |     | 69,861 ± 28,892      | 40.8   | 7   | 66,419 ± 24,247      | 38.8   | 7   | 9.0             |
| DS2 vs DS3     |                      |        |     | 73,984 ± 25,123      | 43.2   | 7   | 66,419 ± 24,247      | 38.8   | 7   | 11.4            |

Figures are numbers of 2 × 2 m pixels visible ± SD, and the % these pixels represent compared to total numbers of pixels in a circle of, respectively, 3000 m (long-range viewshed) and 467 m radius (short-range viewshed) around the display site. **DS1**, principal display site; **DS2, DS3**, secondary display sites in descending order of use. For each pair of display sites compared, the difference in % means the percentage gain in viewshed from the display site with higher visibility compared to the display site with lower visibility. **n** Sample sizes vary from 20 to 7 because of the 20 males, 8 had one display site, 5 had two and 7 had three display sites.
around DS1, the percent terrain visible of that accumulated viewshed was the highest from DS1 and decreased progressively when the male moved to DS2 and DS3 (94.0%, 79.1% and 70.3%, respectively; Supplementary Table S2). Pairwise comparisons showed that these viewshed differences were significant ($Z = 2.78$, $p = 0.005$, $n = 19$ pairs, Wilcoxon matched-pairs signed-rank test comparing DS1 vs DS2 or DS3; $Z = 2.86$, $p = 0.004$, $n = 26$ pairs, including also comparison DS2 vs DS3). Using the sample of males with three display sites to quantify how additional locations contribute to increase viewshed, we found that the $1376 \times 10^3$ pixels visible from DS1 increased to $1473 \times 10^3$ pixels with the addition of pixels visible only from DS2 (a 3.8% increase in viewshed), and to $1478 \times 10^3$ pixels with the addition of DS3 (an additional 3.5% increase in viewshed; Fig. 4). Expressed as percentages of their total accumulated viewshed from all display sites of each male, these figures correspond to 87.7% visible only from DS1, 91.6% from DS1 + DS2 and 95.1% from DS1 + DS2 + DS3.

### One vs several display sites

Males displaying more intensively used a higher number of display sites ($H = 8.363$, $p = 0.015$, $df = 2$, $n = 20$, Kruskal–Wallis test; Fig. 5). The number of display sites is also apparently associated to the topography of the display site location (Supplementary Table S3). As expected from prediction 2, all five males displaying on top of hills used only one display site, since there was no alternative location offering a better view or providing additional viewshed. In contrast, males displaying on plateaus or terraces tended to use three display sites (Supplementary Table S3).

The total long-range viewshed of the 12 males with multiple display sites was 9% higher than that of the 8 males with only one display site ($1,377,848$ pixels, $SD = 611,322$, $n = 12$; $1,265,665$ pixels, $SD = 722,865$, $n = 8$, respectively), although the difference did not reach significance ($Z = -0.86$, $p = 0.38$, Mann–Whitney U test).

Finally, long-range and short-range viewsheds from DS1 were respectively 2.3% and 14.7% higher in males with just one display site compared to those with multiple display sites. These differences increased to 25.4% and 20.9% after excluding the 6 males that displayed less intensively and therefore, as expected from Figs. 1 and 2, used DS1 less (<30% display runs) and displayed more at locations outside fixed sites (>60% display runs; males 2, 6, 11, 14, 15 and 19). However, none of these differences were significant ($p > 0.40$), probably due to the small sample sizes.

### Interannual fidelity to display sites

Sixteen of 17 males (94%) for which we had data from more than 1 year used the same display sites in consecutive years (the only exception was male 2, who moved its DS1 200 m; Supplementary Table 4). Among 7 males with three sites in 2018–2019 (males 3, 7, 8, 9, 10, 11 and 12), four repeatedly used exactly the same three locations in other years (males 7, 8, 9, 10), and two males repeatedly used two locations (males 11, 12). Interestingly, the proportional use of these multiple display sites was the same in consecutive years, i.e. DS1 > DS2 > DS3. The repeated use was recorded either in both subsequent years (male 7) or just in one of them (2020–2021), probably because the breeding season 2019–2020 was too dry (see Supplementary Table 5) and most males reduced their display rate considerably (see...
Supplementary Table 6), using no fixed display site (male 8), or just two of the three original display sites (males 9, 10). Male 12 repeated DS1 in both years, and DS3 in one of them; Supplementary Table 4.

In addition to this noteworthy fidelity to multiple display sites, there were two marked males and a non-marked male who used the display sites of dead males. The two marked ones were males 11 and 13 (Supplementary Table 4). Male 11 moved to the territory of male 16 after this male’s death and displayed exactly at the same 3 display sites (DS1, DS2 and DS3) that male 16 had used in 2018–2019, remarkably using them in the same order of preference as its predecessor. In 2019–2020, a dry year when all males showed a lower display intensity, male 11 used only DS1 and DS2 but not DS3. As for male 13, in 2018–2019, it used the DS1 of a male we had marked in the previous years but not included in this study. The third case was male 20, who died in July 2018 and its DS1 was taken by a non-marked male (Supplementary Table 4).

Discussion

We found that more than half of houbara males used multiple display sites instead of just one as was previously assumed in this species. This finding was only possible thanks to the use of two very recent technological advances, which enabled us to obtain high precision data rarely achieved before in similar studies. First, the last generation GSM/GPRS loggers provided with accelerometer, which made it possible to record and identify a large sample of display runs of each male and register their locations with an unprecedented accuracy (Boyd et al. 2004; Cagnacci et al. 2010; Nathan et al. 2012; Brown et al. 2013). Second, spatial analyses have been carried out using a very high-resolution DEM obtained from LIDAR information (Neumann et al. 2015; Sharma et al. 2021), which has become available only recently, making it possible to obtain very accurate viewsheds of the surroundings of displaying males (Alonso et al. 2012; Aben et al. 2018; Sahraoui et al. 2018; Zong et al. 2021).

It is known that birds or mammals that defend their territories by means of vocalizations may use more than just one song or call post to, and that multiple posts tend to be at high or conspicuous points and aggregated near the most used core areas (Murie and Harris 1978; Whitten 1982; Kroodsma and Miller 1996; Delgado and Penteriani 2007). However, to our knowledge, this study represents the first detailed analysis of how birds maximize signal transmission using multiple display sites.

The principal display site used by male houbaras had the largest viewshed compared to alternative sites, and the proportional use of the different display sites was correlated with the viewshed these locations offered, confirming that selection of multiple display sites is adjusted with high precision to the benefits obtained. The increase in viewshed gained by adding secondary display sites is admittedly small (7.33% when adding DS2 + DS3), but the effect is statistically significant at least in the long-range scale. This suggests that houbara males try to maximize signal transmission during displays and that by switching to multiple display sites, they may potentially increase the number of by-standing female partners.

The alternative display sites of a male were certainly very close to each other, but the 108.9 m ($SD = 61$) mean distance between them represents a considerable proportion of the average radius of a male territory during the display period (467 m). Such distance was enough for the male to have a slightly different perspective of its surroundings, adding a small but significant fraction of visible terrain to the viewshed obtained from its main display site. That additional viewshed surely contributed to optimize the display efficiency by reaching more potential mates and competitors and controlling possible approaching predators. On the other hand, a much longer distance between the main and supplementary display sites would prevent males from economically moving between them without incurring the risk of territorial intrusion by neighbours.

Our results suggest that the use of single instead of multiple display sites may be probably determined by at least two factors. One of them is display intensity, the influence of which could be exerted by two mechanisms: first, by the differences in display intensity among individuals, which largely depend on male quality. Indeed, male condition has been found to correlate with display intensity in several bustard species including houbaras (Jiguet and Bretagnolle 2001, 2014; Alonso et al. 2010a, b; Chargé et al. 2010, 2013). The number of display sites used was correlated with display intensity, so if we admit that display intensity is a reliable indicator of male quality, houbara males using more display sites would be those that are more dominant or in better condition. The second relevant mechanism has to do with the differences in display intensity between years in the whole population. We observed a marked reduction in the overall display intensity in dry years, and specifically regarding multiple display sites, our results show that the use of secondary display sites was often suppressed in years with lower rainfall, when males concentrated their reduced display effort in the principal display sites.

A second factor regulating the number of display sites was the relief of the terrain. We found that when the principal display site was in a very good location, e.g. a hilltop from which the male has a better view of the surroundings, males used just one display site, most likely because supplementary locations would necessarily be at a lower altitude and thus would obviously not increase the viewshed from the principal site. Males displaying on hillsides, with a limited
view hill upwards, or on terraces or plateaus, with a quite horizontal and therefore limited line of view in at least some directions, tended to use two or three display sites.

Finally, some displays were performed outside fixed display sites, at locations irregularly distributed within the male territory and generally not far from the main display site. Although we cannot completely discard that these displays may also contribute to complete a male’s viewshed, there is an alternative plausible explanation. These displays often occurred when a female approached and the male tried to induce her to copulation by displaying close to her (Hellmich 2003; JCA et al. pers. obs.). If this was the main reason for displaying outside fixed sites, we should have expected that sexually more active males would have performed a higher proportion of their displays at these non-fixed sites, since vigorously displaying males are precisely those one would expect to attract more females. Our results show the opposite, i.e. that males displaying more intensively tended to display less outside fixed display sites, and use proportionally more their main display site. The most plausible interpretation of this relationship is that more sexually active males, which are probably dominant, more experienced individuals or in better physical condition, might hold better display sites, and particularly better principal display sites. In support of this interpretation, we know that competition for display sites is high, not only as deduced from the relatively frequent aggressive encounters among neighbour males (JCA et al. pers. obs.) but also as suggested by the three cases when we observed a rapid access of new males to a display site left vacant after the death of its owner. The occupation of display sites of dead males is a common phenomenon in many species and has been also reported for houbaras in Morocco (P. McCormick, cited in Hellmich 1998, page 46) but never verified with marked birds.

In sum, the results confirmed most of our predictions and thus validated the main hypothesis, namely that the function of secondary display sites is to expand the viewshed to areas not visible from the principal display site. We do not discard, however, that when deciding how many display sites to use males could take into account some of the additional factors related to conspecifics and terrain structure, such as for example vegetation and stone cover that may affect the selection of the primary site (AU et al. unpubl. data). Our study has shown that houbara bustard males maximize sexual signal dissemination by using multiple display sites, and we suggest that this behaviour may be more widespread than is currently believed. Future studies should investigate whether other species, particularly those living in open habitats, use similar mechanisms to optimize visual or acoustic signal transmission during sexual display.

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**Author contribution** JCA conceived the study, obtained the funding, analysed the data and wrote the manuscript, JCA, IA-C, CP and AU did the fieldwork. JMA-M did the GIS analyses and obtained the viewsheds. All authors revised, edited and approved the final version of the manuscript.

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**Data availability** Datasets generated during and/or analysed during the current study are included as Online Resources in Supplementary Material with the manuscript.

Capture, handling and marking houbara bustards were authorized and conducted under permissions issued by regional authorities (Viceconsejería de Medio Ambiente, Gobierno de Canarias, license 2015/10584). The weight of the logger plus harness material was below the commonly accepted limit of 5% of the weight of the birds. We did not observe any stress signs or behavioural alteration of the birds from marking. The methods used comply with the Spanish guidelines for ethical use in animal research.

**Declarations**

**Competing interests** The authors declare no competing interests.

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