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ORIGINAL ARTICLE

Male territories and the lek-like mating system of MacQueen's Bustard *Chlamydotis macqueenii*

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Abstract Lekking is a promiscuous breeding system in which females visit groups of displaying males only for the purpose of mating. The spatial organization of these groups can range from tight aggregations of individuals, or leks, to loose clusters of males displaying on exploded-leks, and it can also include males seemingly displaying alone. As the distance between displaying males increases, it becomes possible for them to hold fixed territories and for females to select mates not for their genetic quality, as on true leks, but for the quality of the resource on their territory, i.e., resource-defense polygyny. Here, in a 2-year study of a breeding population of MacQueen's Bustard *Chlamydotis macqueenii* in southwest Kazakhstan, we used GPS and radio-tracking coupled with observation to understand male territoriality and the spatial distribution of sites, and we followed the breeding behavior of cryptic females using nest locations and genetic paternity analysis. We found that males were faithful throughout the season and across years to a small and exclusive territory centered on their display site. These sites were significantly overdispersed in space and thus we could not delimit any leks in a study area spanning 350 km^2. Females nested in the vicinity of male territories and sometimes inside them, but based on a sample of six resolved paternities, they did not favor the territory of their mate for nesting. This is inconsistent with the hypothesis of resource-based female choice and implies that the breeding system of MacQueen's Bustard can be treated as a special case of lekking, albeit without male aggregation. Six broods were fathered by at least five different males, which lends support to the hypothesis that overdispersion of male sites is related to variability in female mate choice, and thus low male mating-skew in a lekking system.

Keywords Bustard · Lek · Mate choice · Paternity analysis · Resource defense

Zusammenfassung

Territorien bildende Männchen und das Lek-ähnliche Paarungsverhalten der Asiatischen Kragentrappe *Chlamydotis macqueenii*

Lekking ist ein promiskuitives Brutverhalten, in dem Weibchen Gruppen von sich zur Schau stellenden Männchen besuchen, nur um sich zu Verpaaren. Die räumliche Aufteilung dieser Gruppen reicht von dichten Ansammlungen von Individuen (Leks), über lose Gruppen von Männchen ('exploded Leks') bis hin zu anscheinend allein zur Schau stellenden Männchen. Zunehmende Entfernung zwischen den Männchen macht es ihnen möglich feste Territorien zu verteidigen und erlaubt den Weibchen ihre Brutpartner nicht nach der genetischen Qualität zu wählen (wie bei echten Leks), sondern nach der Qualität der Ressourcen in ihrem Territorium (wie bei Polygynie mit Ressourcenverteidigung). In einer zweijährigen Studie an einer Brutpopulation der Asiatischen Kragentrappe *Chlamydotis macqueenii* im Südwesten Kasachstans wurden GPS- und Peilsender gemeinsam mit Beobachtungen genutzt, um das Territorialverhalten der Männchen und die räumliche Verteilung der Balzplätze zu verstehen. Darüber hinaus wurde das Brutverhalten der verborgenen Weibchen anhand

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von Neststandorten und genetischen Vaterschaftsanalysen untersucht. Ergebnisse zeigten, dass Männchen während der Saison und über Jahre hinweg einem kleinen Territorium treu blieben, das sich um einen zentralen Balzplatz erstreckte. Die Balzplätze zeigten signifikante Überdispersion in ihrer räumlichen Verteilung und daher konnten wir in unserem Studiengebiet (350 km^2) keine Leks abgrenzen. Weibchen nisteten in der Nähe von männlichen Territorien und manchmal auch darin, aber anhand von sechs zugeordneten Vaterschaften konnten wir erkennen, dass sie die Territorien ihrer Partner nicht bevorzugten. Dies widerspricht der Hypothese, dass Weibchen sich ihre Partner anhand der Ressourcen aussuchen und deutet an, dass das Brutverhalten der Asiatischen Kragentrappe als Spezialfall des Leks betrachtet werden kann, wenn auch ohne räumliche Ansammlungen von Männchen. Sechs Bruten wurden von mindestens fünf verschiedenen Männchen befruchtet, was untermauert, dass die Überdispersion von Männchen mit der Variabilität bei der Partnerwahl der Weibchen einhergeht, und ein geringes Ungleichgewicht im Paarungserfolg einzelner Männchen in einem Lek zur Folge hat.

Introduction

Lekking is an uncommon breeding system classically defined by the conspicuous aggregations of displaying males that females visit only for the purpose of selecting a mate (Bradbury 1981; Höglund and Alatalo 1995). Because females may be free to select a mate from a large number of individuals displaying close to each other on a lek, it is thought that sexual selection is particularly intense, leading to the evolution of elaborate behavioral displays and morphological ornaments seen in males (Darwin 1871; Trail 1990; Andersson 1994). However, ornamented males performing sophisticated displays and not involved in parental care are also found in species where the criterion of male aggregation is less clearly validated: in these situations, the system has usually been described as exploded lekking, when breeding males are found in loose clusters of large and dispersed territories (Höglund and Alatalo 1995; Ligon 1999) and occasionally as solitarily display (Pruett-Jones and Pruett-Jones 1982; Emlen and Oring 1977; Foster 1983; Jiguet et al. 2000).

It has been suggested that a mating system such as this could apply to many members of the Bustards (Otididae), an old-world, understudied family of birds (Morales et al. 2001). In the few species that have received some attention male parental care appears absent, and males are thought to be displaying solitarily or in dispersed groups during the breeding season, but most studies are no more than reports on the observation of a few displaying males (references in Morales et al. 2001). The behavior of three species however, the Great Bustard (*Otis tarda*), Little Bustard (*Tetrax tetrax*), and African Houbara (*Chlamydotis undulata*) have been investigated in more depth: authors have usually described loose aggregations of males within a larger section of suitable habitat (Lett et al. 2000; Jiguet et al. 2000; Alonso et al. 2003; Hingrat and Saint Jalme 2005), home-ranges of breeding males have been reported in all three species using either radio-tracking and/or observation (Lett et al. 2000; Jiguet et al. 2000; Hingrat et al. 2004; Magaña 2007; Alonso et al. 2010) and females have been found to lay regularly or occasionally on “leks” and male territories (Morgado and Moreira 2000; Jiguet et al. 2002; Hingrat et al. 2004; Magaña et al. 2011).

Classical leks, in contrast to exploded leks or solitary courts, contain little resources of value to females other than the males themselves. Females therefore probably choose a mate based on their assessment of the genetic quality of the male, possibly using cues such as his display position on the lek (Hovi et al. 1994) or his display behavior (Gibson 1996). However, if males are separated from each other by large distances, the possibility arises that females may find resources on male territories (Bradbury 1981; Jiguet et al. 2002; Alonso et al. 2012). Females could choose to mate with a male controlling the best resource so that she will have increased likelihood of rearing her offspring successfully. If this were true, the mating system would be more akin to resource-defense polygyny than to lekking (Emlen and Oring 1977). One approach in considering this issue has been to compare resource quality in breeding male and female home-ranges (Jiguet et al. 2002; Hingrat et al. 2007). A different and more powerful approach would be to directly assess the overlap of breeding female home ranges or nest locations with the precise delimitations of the territories of their mates. This has not yet been possible, however, due to the complexities involved in monitoring the mate choice of cryptic females while at the same time tracking male movements.

MacQueen’s Bustard *Chlamydotis macqueenii* is a steppe and semi-desert dwelling bird distributed from Mongolia to the Arabian Peninsula. It is migratory in the northern part of its range (Combreau et al. 2001, 2011; Judas et al. 2006) and loosely gregarious outside the breeding season (Cramp and Simmons 1980). Its reproductive strategy has not been investigated in as much detail as that of its sister species the North African Houbara Bustard (Hingrat and Saint Jalme 2005; Hingrat et al. 2007).

Here we assess the mating system of MacQueen’s Bustard on a homogenous steppe-land in Western Kazakhstan with particular reference to the criteria used to classify lekking systems (Bradbury 1981). We use GPS satellite tracking to understand the organization of male territories at a small scale. We then test the spatial distribution of male sites at a large scale to evaluate the aggregation criterion. We finally test between the competing hypotheses of resource- versus display-based systems by following female breeding behavior using nest locations and genetic paternity analysis. We predict that in a resource-based system, females should nest on their mate's territory due to the high quality of the resources on his site. If female choice is not based on resources, then the nest need not necessarily be located on the mate's territory.

Methods

Study site

The study took place in a steppe-land in southwest Kazakhstan (43°N, 52°E, Fig. 1) known to host a migrant population of MacQueen's Bustard (Combreau et al. 2001; Judas et al. 2006). The landscape was undulating steppe interspersed by sabkhas (dried-up depressions covered with salt encrusted clay) and patches of rough and rocky ground. Xerophytic vegetation, mainly 20 cm high *Artemisia* and *Salsola* shrubs, covered the entire landscape a part from the sabkhas. The area was sparsely inhabited by livestock farmers.

General methodology

Fieldwork took place in April–May 2005–2006. We worked from dawn to mid-morning and from late afternoon to dusk, times of high bustard activity (Combreau and Launay 1996). We used circular observations to search for birds. These consisted of a 360° visual scan of the area using a telescope from a fixed and slightly elevated position (such as the roof of the car). We recorded the distance, bearing, sex, number of individuals, and behavior of each bustard sighted. Displaying males were highly conspicuous and usually spotted at distances of 500–3,000 m. Females were visually followed back to their nest and the eggs collected as part of the captive breeding program implemented at our institute (the National Avian Research Center of Abu Dhabi, UAE) to address the population decline of this species (Lawrence et al. 2008).

Spatial distribution of male display sites

In a sub-section of the area shown on Fig. 1 (i.e., the study zone), we refined the methods described above to precisely map the distribution of male display locations. Preliminary work was done in 2005, the mapping being re-assessed and

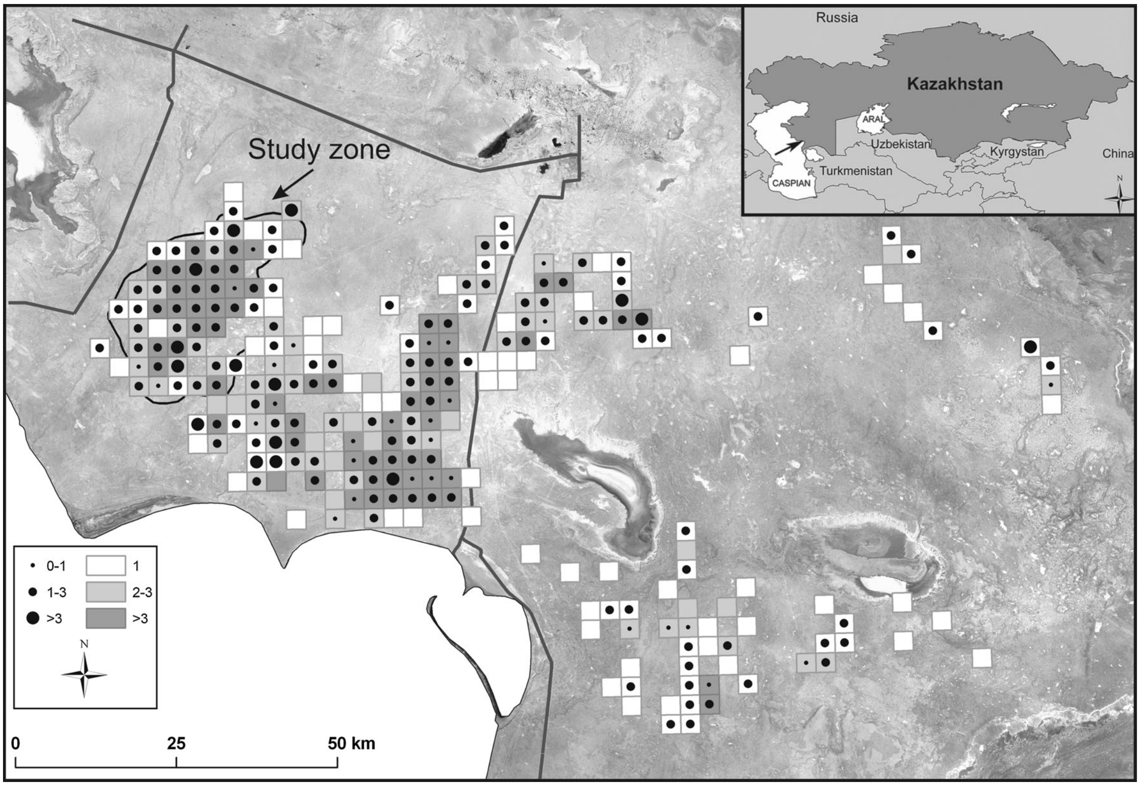

Fig. 1 Map of the region showing the density of displaying males as the mean number of individuals recorded per circular observation (*filled circles*) in 3-km^2 cells. Search effort is shown by the number of circular observations per cell (*shading*). Sabkhas and dirt tracks appear *white* and a tarmac road is drawn in as a *black line*

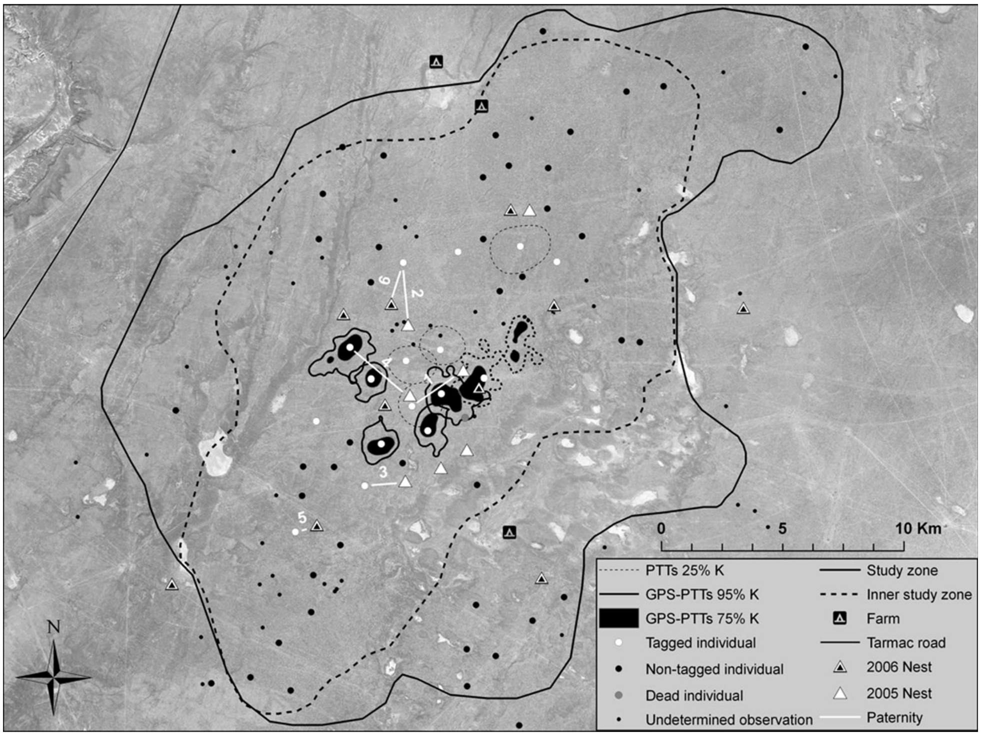

Fig. 2 Distribution of display sites in the study zone, home ranges of tagged males, nest locations, and paternity relationships

completed in 2006. When a displaying male was observed during a circular observation, we noted its location (distance and bearing) and guided a fieldworker to it using a two-way radio. A high concentration of droppings was usually found on the display site and the estimated distance from the observer to the bird was then compared to the known distance measured by GPS. Accurate estimation of distance was rapidly achieved in this way and we worked through the study zone to find as many display sites as possible. We marked a location as a habitual display site when both of the following conditions were met: more than 15 droppings were found and neighboring display sites were seen simultaneously occupied by a displaying male (i.e., on the same circular observation scan). When this was not the case, the sighting was recorded as an undetermined observation of a displaying male. The area was divided into the inner study zone where all display sites were mapped, and the periphery, where search effort was reduced, and therefore where most but possibly not all display sites were recorded (Fig. 2).

We tested the spatial distribution of male display sites using Ripley's K function (Ripley 1981; Haase 1995). Using the variance in all point-to-point distances as well as the mean, this function computes a $K(r)$ statistic from the data for a circle of radius r around each point. This enables an assessment of the point pattern for a range of spatial scales. K is then tested against the null hypothesis of complete spatial randomness using simulated random point patterns. Aggregation is identified when $K(\text{data}) > K(\text{random})$ and uniformity when $K(\text{data}) < K(\text{random})$. We computed K using the "spatstat" package for R (R Development Core Team 2011). We tested for departure from randomness at $p = 0.01$ by simulating 200 random point patterns using a Monte Carlo method and used Ripley's isotropic correction to account for edge effects (Baddeley and Turner 2005). We present the results in the form of $L(r)$, a normalized $K{:}L(r) = \sqrt{[K(r)/\pi]}$.

Male territoriality

We caught 13 males in the study zone in 2005 using dummy females lined with loop cord snares and placed on their display site. Six were equipped with 35-g solar-powered backpack satellite transmitters (Microwave Telemetry Inc., Columbia, MD, USA, hereafter referred to as PTTs) and seven with 18-g necklace radio transmitters (Holohil System Ltd, Ontario Canada). In late April 2006, seven males caught on neighboring display sites (of which one recaptured PTT) were fitted with 45-g solar-powered backpack satellite transmitters including a GPS device (Microwave Telemetry Inc., referred to as GPS-PTTs, on average 2.2 % of the male's weight). Unfortunately, one device was retrieved from a dead bird (probably poached) a few days following capture.

GPS-PTTs enabled precise estimation of home-ranges: they have an accuracy of 5–10 m and were set to record a location every 2 h (making 89 % of fixes attempted between the date they were deployed and late July). Home-ranges were computed as 95 and 75 % fixed kernel probability densities with a smoothing parameter set at 200 m (Worton 1989). The resulting distributions enabled an additional assessment of display site location independent of our field observations.

We assessed site fidelity within and between seasons with data from PTTs and radio-tracked birds. However, unlike GPS-PTTs, location accuracy makes home range estimation difficult for PTT data. Testing PTT devices on a fixed location prior to their use in Kazakhstan resulted in the majority of locations in best quality Argos classes 1–3 being accurate to 700 m, but more than 10 % of points were inaccurate by 2–10 km ($n = 203$). Yet the distribution of locations was centered on the test spot, and we therefore expected a similar pattern for males faithful to a particular site. We then compared PTT home range sizes between early (mid-March to end-April) and late spring (end-April to mid-June). This comparison is valid because PTT accuracy does not vary with date and the 50 % kernels computed discarded substantially erroneous locations.

Paternity analysis

We found seven nests in the study zone in 2005 and ten in 2006. The female was caught on all but one. A blood sample was taken from the brachial vein of all trapped females and tagged males in both years. Chicks were blood sampled at 1 month of age. This was licensed under CITES permits 00KZ000609 and 05FEA27, no birds being harmed by handling.

We used Qiagen DNA Blood and Tissue kits to extract DNA and 17 microsatellite loci were amplified using fluorescent primers: loci A2, A10, A21, A22, A29, A106, A120, A204, A205, A210, D12, D110, D118, D119 (Chbel et al. 2002), O26 (Lieckfeldt et al. 2001) and O27, O38 (Pitra et al. 2004). PCR mixtures contained 0.5 U DNA Polymerase (Solis Biodyne), 80 mM Tris–HCl (pH 9.5), 20 mM $(NH_4)_2SO_4$, 2.5 mM $MgCl_2$, 200 μM dNTPs, 2 μl BSA (2 mg/ml), 10 pmol of each primer and approximately 100 ng of DNA. PCR cycling was: initial denaturation (94 °C: 4 min), 30 cycles (94 °C: 30 s, 50 °C: 30 s, 72 °C: 45 s) and final extension (72 °C: 30 min). PCR products were separated on an automated 3130xl Genetic Analyzer, scored, and analyzed using GENEMAPPER 3.7 (Applied Biosystems).

Genotype frequencies deviated significantly from Hardy–Weinberg equilibrium at two loci (Table 1). Both loci O27 and D110 showed a high estimated frequency of null alleles but only O27 was involved in a number of mother-offspring allele mismatches. Due to this and D110 having high polymorphic information content, we only excluded O27 from paternity analysis. The probability that this set of markers would not exclude an unrelated male from paternity was 0.0006 if the genotype of the mother was known and 0.02 if not. We checked for labeling errors and estimated the genotyping error by comparing mother-offspring allelic profiles. We then performed likelihood-based paternity assignment using Cervus 3.0 (Marshall et al. 1998). Simulation required for calculation of critical values used in assessing paternity probabilities was run with the following parameters: 10,000 cycles, a proportion of 0.99 loci typed, a genotyping error of 0.03 and a reproductively active male population of 500, a maximum estimate based on a density of 0.14 fixed males per km^2 obtained from this study. Substantially varying this latter

Table 1 Marker-specific characteristics calculated using Cervus

Locus	Alleles	H_O[a]	H_E[a]	PIC[b]	NEP1[c]	NEP2[c]	HWE[d]	F[e]
A21	10	0.371	0.369	0.358	0.924	0.778	NS	0.000
A22	6	0.586	0.661	0.593	0.766	0.613	NS	0.056
A29	5	0.407	0.412	0.358	0.914	0.802	NS	0.001
A106	9	0.701	0.683	0.632	0.729	0.56	NS	0.000
A120	7	0.497	0.548	0.507	0.837	0.673	NS	0.069
A210	7	0.517	0.574	0.533	0.814	0.647	NS	0.040
D110	8	0.55	0.715	0.676	0.686	0.506	<0.05	0.132
D118	9	0.676	0.736	0.695	0.667	0.487	NS	0.037
A2	5	0.569	0.634	0.576	0.786	0.625	NS	0.055
A10	5	0.566	0.579	0.495	0.827	0.702	NS	0.012
A205	7	0.725	0.735	0.683	0.688	0.515	NS	0.005
D119	9	0.71	0.754	0.717	0.635	0.456	NS	0.030
O38	9	0.563	0.61	0.543	0.799	0.652	NS	0.051
A204	3	0.472	0.472	0.375	0.889	0.804	NS	0.000
D12	4	0.206	0.227	0.216	0.974	0.881	NS	0.058
O26	6	0.614	0.623	0.561	0.792	0.638	NS	0.002
O27	4	0.182	0.224	0.214	0.975	0.882	<0.05	0.130

[a] Observed (H_O) and expected heterozygosity (H_E)

[b] Polymorphic information content

[c] Non-exclusion probabilities knowing only the genotype of only the candidate parent (NEP1) or the genotype of one known and one candidate parent (NEP2)

[d] χ^2 test of departure from Hardy–Weinberg equilibrium (HWE) using a Bonferroni correction

[e] Frequency of null alleles

parameter did not affect the results. We accepted a male as father when the best candidate was assigned paternity above the 80 % confidence level (Slate et al. 2000).

Results

Male territoriality

Out of the 13 males caught in 2005, one PTT died during migration and two radio-tagged birds were not found again in the region in 2006 (i.e., presumably died or did not return to the area). All other birds reoccupied in 2006 the site they were caught on in 2005 ($n = 10$). Tagged birds were faithful to their trapping location within a season ($n = 18$) and the size of 50 % kernels of PTTs did not differ between early and late spring (paired t test: $t_3 = 0.9$, $p = 0.4$). Both GPS-PTTs in 2006 and PTTs in 2005–2006 showed locations centered and concentrated on the display site independently identified from observation and droppings ($n = 10$, Fig. 2). Males remained on this site until early to mid June before gradually making movements away from it.

The 95 % kernel distributions of GPS-PTT locations taken between late-April and mid-June ranged from 1.9 to 3.5 km^2 across individuals (Fig. 2). However, birds were usually found in much smaller areas over this period, ranging from 0.4 to 1.1 km^2 (75 % kernels) and non-overlapping with those of neighbors. There was moderate overlap between 95 % kernels of two pairs of neighbors (see Fig. 2) but we found no significant variation of distance between these neighbors with time of day (ANOVA: $F_{11,221} = 0.8$, $p = 0.7$, $F_{11,244} = 0.3$, $p = 0.98$), indicating that they were constantly separate from each other.

Spatial distribution of display sites

We identified 60 display sites in 2006 in a study zone that covered 350 km^2 (Fig. 2). Mean nearest-neighbor distance (±SE) in the inner study zone was 1,446 ± 50 m ($n = 49$, range 760–2,810 m). The distribution of male sites was overdispersed, significantly departing from a random distribution for r values slightly larger than 1 km (Fig. 3a, $p < 0.01$). At larger spatial scales the distribution was random, reflecting the absence of male sites from rough ground and sabkhas in the southwest and southeast sections of the study zone. A test that included undetermined observations showed that the distribution was marginally overdispersed and statistically departing from random at similar values of r ($p = 0.05$, but the distribution was not statistically different from a random pattern at $p = 0.01$), and the distribution tended towards aggregation for increasing values of r (Fig. 3b).

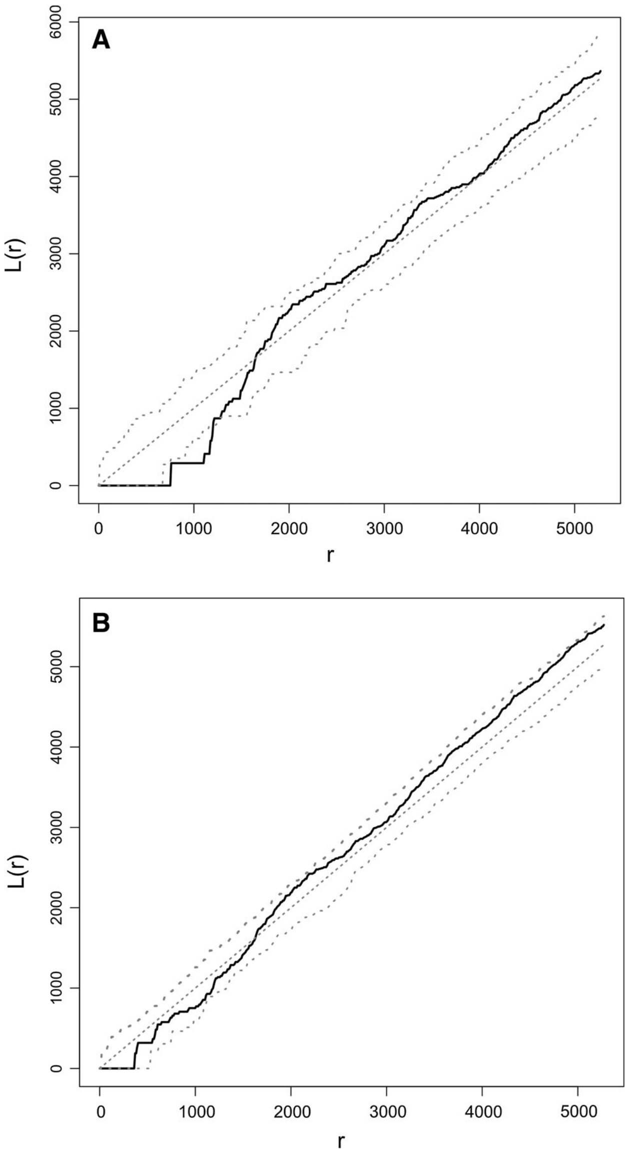

Fig. 3 Comparisons of random patterns and observed distributions of display sites (**a**) and display sites as well as undetermined observations (**b**), using Ripley's L as a function of distance (r) in meters in the inner study zone. The *black line* is the observed statistic and *grey dotted lines* represent distributions at complete spatial randomness as well as the *upper/lower* critical limits of a Monte Carlo test ($p = 0.01$) of departure from randomness (see "Methods")

At the regional level, we found displaying males in just about all the areas surveyed except for rocky ground and sabkhas. Densities of displaying males were similar in the study zone and elsewhere (Fig. 1).

Paternity analysis

Five males were identified as fathers from six different broods (Table 2; Fig. 2) and all but one sired all chicks within a brood. In that brood of four, we identified the father of two chicks with confidence >80 % but this individual was not the best candidate father for the other two chicks. It is likely that we did not sample the male that sired these.

Based on the area of 75 and 95 % kernels of the largest GPS-PTT home-range in 2006 approximated to a disk, we constructed two model disks centered on the father's site, representing core and maximum home-range. These had a radius of 600 and 1,060 m, respectively. Nests for which paternity was resolved were located at an average of 2,125 ± 339 m from the father's display site (Table 2), with only one nest being within the modeled 95 % home range of the father. Including nests at which the father was not genotyped, the distance between nest and father, or nearest possible father (i.e., not genotyped), was 1,925 ± 229 m and only two out of 15 nests were within 1,060 m of his site. The average distance to the nearest male site, however, was only 1,127 ± 103 m and six out of 15 nests were within the modeled 95 % kernel home range of a male that was not the father of the brood.

Discussion

All males equipped with a tracking device occupied a territory throughout the breeding season and were faithful to it between years. Data from satellite-tracked individuals strongly suggested that this territory did not overlap with those of neighbors and that a habitual display site was located in its centre. Males only abandoned their territory at the end of the mating season to range through other males' former territories. This use of an exclusive territory on which males live as well as display seems similar to what has been described in the Little Bustard in less detail, yet substantially different from the descriptions of Great Bustard leks (Jiguet et al. 2000; Morales et al. 2001).

Display sites were uniformly distributed in our large study zone extending over 350 km^2 (Figs. 2, 3) and although displaying males were absent from rocky terrain and sabkhas, they were found throughout our survey area at the regional scale (Fig. 1). This tended to suggest that the study zone was part of a continuum rather than an isolated congregation of male territories. The spatial distribution of bustard male sites shown here thus does not adhere to lekking's main criterion, i.e., aggregation of males (Bradbury 1981; Höglund and Alatalo 1995). The distribution is more uniform than the apparently random spatial organization of some male forest grouse (Ellison 1971; Lewis 1985). It also differs markedly from the weakly aggregated distributions found in other bustard species (Jiguet et al. 2000; Hingrat and Saint Jalme 2005) or the spatial associations due to habitat characteristics (Delgado et al. 2010). Upon including undetermined sightings of displaying males (Fig. 3b), overdispersion was only marginally significant and the spatial pattern tended towards aggregation at higher spatial scales (>4,000 m inter-male distances). However, these undetermined sightings were not display sites: they consisted of individual sightings of a displaying male at one point in time with no evidence of a display site—despite intensive labor to find one. They could be floaters (Gross 1996) or fixed males having a large territory or having temporarily left their main display site due to a variety of possible reasons such as disturbance or the presence of a female (both observation and GPS tracking have shown that this does happen during the breeding period).

Table 2 Resolved paternities

ID	Year nest found	Year father caught	Distance nest-site (m)	Offspring sired and confidence interval	
				95 %	80 %
1	2005	2005	2,550	3/4	1/4
2	2005	2005	2,650	1/3	2/3
3	2005	2005	1,650	2/2	–
4	2005	2006	3,200	3/3	–
5	2006	2006	900	1/2	1/2
6	2006	2005	1,800	–	2/4

Females nested in the vicinity of male territories, usually just outside, but sometimes inside the areas defined as territories in this study. They did not favor the territory of their mate, regularly nesting on the territory of a male that sired none of their offspring. Although this result stems from only a small sample of six resolved paternities, it does not fit with the hypothesis of resource-based female mate-choice (Emlen and Oring 1977). Rather, it implies that mate choice would operate as on leks, where it is thought that females select a mate only for his genetic quality (Höglund and Alatalo 1995). While this study is the first to genetically link the nest site to the location of the father's territory in a bustard species, female bustards in other species have also been observed nesting on or in the vicinity of male display sites (Jiguet et al. 2000; Hingrat and Saint Jalme 2005; Magaña et al. 2011). The evidence presently available suggests therefore that in MacQueen's Bustard, and possibly in others, although resources may be present and used by females on male territories, males do not appear to use these resources to attract females. Central Asian steppes are rich of a variety of plants, reptiles, and invertebrates homogenously distributed over very large acreages. In Xinjiang, Western China, male displaying sites tend to host lower plant species richness and plant density than random sites (Weikang et al. 2002), suggesting that females may find more resource attractive habitat away from displaying sites. Moreover, the male display could potentially raise the interest of predators and nesting in the vicinity would likely pose a danger for the nest and chicks.

The population of MacQueen's Bustard studied here fits all the criteria of a lekking species, except for the uniform spatial architecture of male territories; the breeding system can thus only be described as lek-like. In the African Houbara, authors describe weak aggregations, i.e., exploded leks. It is important to point out that the distances between neighboring displaying sites measured in this study were twice as large as those observed in African Houbara in Morocco (Hingrat and Saint Jalme 2005). Such large inter-male distances, a consequence of landscape features, availability of elevated points used for display, population density, as well as species-specific characteristics, may render these exploded leks invisible. In reports where the study area was too small to thoroughly evaluate the level of aggregation, an exploded lek may not necessarily have become apparent at a larger scale (Blackford 1963; Ellison 1971; Payne and Payne 1977; Beehler and Pruett-Jones 1983; Lett et al. 2000; Andreev et al. 2001).

The absence of a lek per se in an otherwise lek-like system is an unusual finding. Yet theoretical models of the evolution of lekking could provide some elements of explanation. In Bradbury's original model of female preference, males aggregate only if they gain more matings by doing so than by displaying solitarily (Bradbury 1981). If this is not the case, they would tend to disperse for ecological reasons. According to the hotshot model, leks are formed by males aggregating around a high-quality male, with overdispersion as a prediction when female choice is variable (Beehler and Foster 1988). Our data does not appear to suggest the present of hotshots given that six broods were sired by at least five different males. We acknowledge that our sample of resolved paternities is very limited, but it is corroborated by the absence of male reproductive skew recently reported in the African Houbara in Morocco (Lesobre et al. 2010). It is not impossible therefore that non-aggregation could be linked to low male-mating skew due to variable female mate-choice. We could speculate that there may not be sufficient variation in the fixed males' quality for females to strongly favor particular phenotypes, hence the absence of a lek, but that fixed males may be more attractive to females than non-fixed males, and thus that floaters may display next to fixed males in an attempt to gain matings. Other possible explanations for a uniform distribution of males could lie in the homogenous distribution of food resource on the steppe allowing large inter-individual distances without compromising on habitat quality, or could be related to the effects of copulation disruption from neighbors (Foster 1983), or population density (Langbein and Thirgood 1989; Höglund and Stöhr 1997).

It is becoming clear that the model of lek evolution supported differs with the species studied, e.g., female traffic in sage grouse *Centrocercus urophasianus* and ochre-bellied flycatcher *Myonectes oleaginus* (Gibson 1996; Westcott 1997), and hotshot males in black grouse *Tetrao tetrix* and great snipe *Gallinago media* (Hovi et al. 1994; Saether et al. 2005). Some authors have even argued that these models may be operating simultaneously at different spatial scales (Jiguet and Bretagnolle 2006). Settings such as those described in this study should enable novel tests of these models, enabling an evaluation of hypotheses pertaining to the absence of male aggregation. In particular, comparative studies of male spacing within and between species that include data on density, resource availability and mating-skew would be particularly informative.

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