

7. Display behaviour of breeding male Asiatic houbara (*Chlamydotis [undulata] macqueenii*) in Saudi Arabia

Abstract

Male Asiatic houbara (*Chlamydotis [undulata] macqueenii*) give spectacular visual displays, which may function as truthful advertising of fitness, and allow females to choose suitable partners. I examined whether a pre-condition for female choice – variation in male display intensity – exists in a houbara population in Mahazat as-Sayd Reserve, west central Saudi Arabia. Five key behavioural components of displays from 12 known-age males were sampled regularly over three breeding seasons from 1996 to 1998. On 100 occasions, a total of 570 running displays, 497 inter-display periods, all occurrence of feather flashing displays and feeding, and the distance covered during displays, were recorded. In addition, previously unrecorded details on the pattern and timing of male displays, and interactions between displaying houbara and other houbara, and with other species were described. Males were ranked based on the intensity of each behaviour each year, and on a combined rank for all behaviours. Intensity of male display differed among males in all years for all behaviours except distance ran during displays in 1997. Some males consistently ranked highly for all behaviours and in all years, whereas other males gave long display runs with short inter-display periods, but covered very little distance. Two strategies for performing displays that vary in intensity are suggested. There was no clear relationship between display intensity and male age or experience: in some years, the youngest, most inexperienced males gave the most intense displays. I conclude that the prediction that males vary in their display intensity was supported, and this allows opportunities for future researchers to examine whether the highest ranked males gain more matings with females than do lower ranking males.

Introduction

Remarkably, male Asiatic houbara (*Chlamydotis [undulata] macqueenii*), one of the most cryptic of all birds, have one of the most conspicuous of breeding displays, and these displays are best described as dispersed lekking behaviour (Hoglund & Alatalo 1995, Chapter 8). During display runs they bob, twist and circle over hundreds of metres of open desert, and their usually drab grey and brown pelage gives way to long bright white neck and breast plumes held erect above the head (Cramp & Simmons 1980, del Hoyo *et al.*, 1996). More remarkably, although well described in captive and semi-captive birds (Mendelssohn 1980, Launay & Paillat 1990, Gaucher *et al.*, 1996), little is known about this spectacular display behaviour in the wild (del Hoyo *et al.*, 1996, and see Ponomareva 1983).

Patterns of display behaviour have been described for most bustards. In the 25 bustard species, male display is a breeding season activity that is mainly vocal (5 spp.), terrestrial (12 spp.), or aerial (8 spp.) in nature, involving leaps in the air (e.g., *Lissotis* spp., *Afrotis* spp.), convoluted feather displays (e.g., *Chlamydotis* spp., *Otis* spp., *Ardeotis* spp.) and/or vocalisations (e.g., *Eupodotis* spp.). The function of the display appears to be sexual among the Palearctic, Indian and Australian, but not African bustards, and is aimed at attracting females or advertising fitness. In African species, there is a tendency towards equal male and female investment in parental care, and male displays apparently have a territorial role (del Hoyo *et al.*, 1996). Amongst most non-African species, the function of male display still remains unclear. For example, the display of male houbara is suggested to have both territorial and sexual functions (Launay & Paillat 1990), but no studies have quantified wild houbara display behaviours to test this hypothesis.

Previous studies of displaying houbara have focused on describing the repertoire of behaviours observed from captive individuals (Mendelssohn 1980, Launay & Paillat 1990), from limited field studies (Ponomareva 1983, Lavee 1985, 1988, Launay & Loughland 1995), and from anecdotal accounts (e.g., Alekseev 1980, Goriup *et al.*, 1992, Symens 1988, Launay *et al.*, 1997, and see Johnsgard 1991). The pattern of display is genetically fixed. Males raised in isolation from other houbara are able to perform the complete display sequence upon maturity, and if displaying males are interrupted, they invariably recommence

the display from the beginning (Gaucher *et al.*, 1996). As described from captive birds, the display follows a standardised and ordered pattern of four phases. A further two phases are included if a female is present. The pattern starts with the male standing and turning slowly on or alongside a prominent feature before becoming extremely visible by raising his display feathers, lowering his head onto his back and running in zigzags and circles for distances up to several hundred metres (Fig. 7.1). After this running phase, the male will stop, sometimes repeatedly flashing neck plumes by raising and lowering his head and bill clapping several times. If no female is present the male stands, then enters the start phase again, repeating the sequence many times per hour. If a female is present, the male enters the final approach and mounting stages (Launay & Paillat 1990, Gaucher *et al.*, 1996).



Figure 7.1: Male houbara in typical posture during a display run. The erect white plumes almost completely block forward vision. Photo: NWRC collection.

Only adult males fully develop the plumage required for display. Females and juvenile males lack the filamentous breast and crest plumes used in displays, but both can give a weak running display with all the components of a male display, but lacking in visual effectiveness

(Launay & Paillat 1990; pers. obs.). Female display is usually associated with the onset of egg-laying, when testosterone levels briefly increase (Saint Jalme *et al.*, 1996a). From observations in captivity, males can display for long periods. Males in captivity in Taif, Saudi Arabia, frequently display for several hours per day, in both the morning and afternoon, from December to July (peaking in March and April).

In the wild, males display at dispersed leks and are usually within a few km of other males, but sometimes are in sites that are isolated from other males. Separation distances between males are large, and males within a lek may be a few hundred metres to 1-2 km apart, and rarely encounter one another during display runs (Chapter 8). Male houbara displays are highly visible, and for this normally cryptic species the contrast between display and non-display plumage and behaviours could not be more striking. Performing displays is costly for males. Displaying is energetically costly, as demonstrated within controlled captive environs with unlimited food, where males declined in mass over the breeding season (Saint Jalme *et al.*, 1996c, Saint Jalme & van Heezik 1996). In addition, displaying may increase predation risk, because the display feathers severely restrict the ability of males to see, while greatly increasing their conspicuousness. Theoretically, differences in display intensity of males should relate directly to differences in their body condition, i.e., healthy males in good condition should display at greater intensity and for longer periods, than males in poor condition. Therefore, displays should represent truth-in-advertising of fitness, with females selecting males based on components of male display behaviour. Measuring houbara body condition and determining mating success are difficult in the wild, but quantifying display behaviours that may indicate differences in body condition is feasible. If mate selection of males by females is based on assessment of male displays, then *ipso facto* male displays must vary between individuals, and these differences should be measurable. Alternatively, if male display intensity is uniform between males, then females cannot be selecting males based on display behaviour.

In this chapter, I determine whether a necessary precondition of female choice of displaying male houbara is met: that males differ in the intensity with which they display. Specifically, I compare male display behaviour of known individual males and test whether male houbara differ in (1) the time spent display running, (2) the time spent in standing between display runs, (3) the number of feather flashes given during displays, (4) the distance of their display

runs, and (5) the propensity to feed when on display grounds. Feeding while displaying may indicate that males did not have sufficient energy reserves to continue displaying. I also describe timing of displays, and interactions of displaying males with other houbara and other species during displays.

Methods

Displaying males were located using one of two methods. First, based on observations of one male in January 1996, males appeared to stop displaying each day at about 0900 hrs. To avoid interrupting their displays I located males after that time using radio-telemetry (Chapter 2), then backtracked along their footprints in sandy and loose gravel substrata to display arenas. Tracks in display arenas were unlike any tracks of feeding birds (see Maloney 2001), and consisted of running and walking tracks, circles, and sites where the displaying bird stood and turned. Latitude and longitude co-ordinates were recorded for these sites by GPS. I used two methods to confirm that a site was actually a display site. First, I scanned the display area on subsequent mornings from daylight, from a vantage point about 1 – 2 km away using a Swarowski Optic 30 x 75 binocular spotting scope to confirm the display. Second, I chose prominent rises 1 – 2 km from males (as identified from radio transmitter signals), and scanned the surrounding area throughout the day looking for display activity. Houbara were wary, and initial attempts to observe them from closer than 1 km resulted in males abandoning that day's display. During all scans, I tuned into the frequency of the male's radio-transmitter, and therefore, I knew the direction and activity of the male. Transmitter signals varied from even and continuous when the male stood motionless, to very erratic when the male was displaying, and I was frequently able to confirm visually that fluctuations in signal strength related to male activity. I recorded details from single males, and from those in leks (defined as two or males displaying within 2 km of each other within the same season).

I recorded details of three of the six display phases described by Launay & Paillat (1990). These were (1) "stand and watch" (c.f. alert standing (*Fig. 15*) and slow-motion walk (*Fig. 44*) of Launay & Paillat 1990) - when the male stands in an upright position, and slowly

turns on the spot, with all display feathers hidden; (2) “display running” (Fig. 67 of Launay & Paillat 1990) - when the male tucks his head onto his back, raises neck and breast feathers and runs in a straight line or erratically zigzags or circles, for distances of a few metres to more than a kilometre; and (3) “final phase” (Figs. 70 & 71 of Launay & Paillat 1990) - where the male stops running, then repeatedly extends his neck, bill claps and raises his head, briefly flashing white breast and neck feathers (and see Launay & Paillat 1990, Gaucher *et al.*, 1996 for further description). All of these phases were readily distinguishable from a distance. “Starting phase” behaviours (Figs. 65 & 66 of Launay & Paillat 1990) - when the male partially erects his neck and breast feathers but does not run - were difficult to observe, and these were recorded opportunistically. The remaining two display phases (“final approach” and “mounting behaviour”) occur when a displaying male is in the presence of a female. These behaviours were not recorded during this study.

For each display sequence (one “display run” and one “stand and watch” phase), I recorded the identity of the male, time of day, location, duration (secs) and distance (m) of the display run (defined as the shortest distance between start and finish of display run), the duration of the inter-display run phase (secs), the number of feather flashes in the final phase, the occurrence of feeding behaviour, and the location and behaviour of any other houbara in the vicinity of the displaying male (within approximately 2 – 5 km, the limit of radio-transmitter reception at ground level). One male aged over two years of age was particularly difficult to observe and was never confirmed displaying, and all one-year-old males gave only intermittent displays; these birds have been excluded from the analyses (Table 7.1).

There were 17 adult males in the population, of which 16 were seen displaying at least once over the three years from 1996 to 1998 (Table 7.1). From 12 of these males, I recorded 570 display runs and 497 inter-display periods during 100 sampling events on 58 days (Table 7.2), i.e., a mean of 5.7 display runs and 5 inter-display periods per sampling event. More display runs than inter-display periods were recorded because I sometimes left the arena immediately at the end of a display run. Because of deaths, recruitment, difficulties in observing birds, and erratic transmitter signals from some males, displays were recorded in all three years from only four males. Of the remaining eight males, three were observed only in 1996, four only in 1998, and one in both 1997 and 1998 (Table 7.1). Therefore, sampling sometimes included the same individual males among years, and thus data were not strictly

independent among years. However, because I was interested in the relative performance of males within each year, and not whether the behaviour of individual males varied among years, I included all samples and analysed data separately by year. I assumed that females were choosing males based on observations of one or more displays within a season, and not on knowledge of a particular male remembered over a number of years. Collection of data from each male varied because the topography of some display sites made my observations easier, not because they were the males within the population that displayed most intensively: as judged by the presence of display-running tracks, most males were displaying regularly throughout the season. Display runs were straight runs, zigzags or circles. I recorded distance as the straight-line length from the start to finish points of straight runs and zigzags, and as the maximum diameter of circles. Distances were estimated to the nearest 5 m (circles), 10 m (runs \leq 100 m), or 50 m (runs $>$ 100 m), by mapping display movements and comparing these to known distances generated from GPS co-ordinates. The total distance ran in circles was not recorded because it did not adequately measure horizontal movements. When displaying in circles, males started and finished at the same place, and therefore were likely to encounter fewer females and be visible from fewer places than when they ran in straight lines. Males were recorded as either feeding or not feeding during sample periods.

Kruskal-Wallis non-parametric one-way ANOVA's were used to test for differences among males, within years, in time display running, time in inter-display periods, the number of feather flashes given in the final phase, and in the distance covered during display runs. Males were ranked within years for each behaviour and for a combined rank for all behaviours, using a 0 – 3 (1996), 0 – 4 (1997) or 0 – 8 (1998) scale, where 0 is the most intense level. Maximum scale values varied depending on the number of males present in each year. Where data were missing for individual males within years, ranking values for the remaining males were weighted to provide even contributions to the combined rank value. The proportion of display observations in which each male fed or did not feed was compared using Chi-square tests of heterogeneity. In all tests, P values of $<$ 0.05 were considered significant.

Table 7.1: Type of observation of displays made from 1996 to 1998 in Mahazat as-Sayd Reserve. T = fresh tracks seen at display site, D = display seen but no data recorded, O = one or more display events seen and data recorded, NF = no display site found, Tx = transmitter was intermittently failing and this bird could not be followed in 1996 and 1997.

Permanent ring number	Male tx code	1996	1997	1998
H000155	4033	T, O	T	T
H000288	4060	-	NF	T, O
H000270	4282	-	NF	O
H000685	4933	-	-	D
H000228	5123	T, O	Dead	-
H000557	5124	-	D	NF
H000224	5177	T, O	T	T
H000263	5194	Tx	Tx	T, O
H000248	5260	NF	NF	NF
H000238	5282	T, O	T, O	T, O
H000691	5385	-	-	D
H000160	5411	D, O	D, O	O
H000161	5540	O	O	T, O
H000211	5547	D	D, O	T, O
H000214	5653	T	T	T
H000239	5674	O	O	D, O
H000233	5707	T	NF	O

Table 7.2: Male houbara display behaviours in Mahazat as-Sayd Reserve from 1996 to 1998: sample sizes for the number of males observed, number of sample periods, recorded behaviours, observation times and for other displays or tracks seen but where no details were recorded.

Year	1996	1997	1998	Total
Number of males observed	7	5	9	12*
Sample periods where displays recorded	39	19	42	100
Number of observation days	29	12	17	58
Number of running displays	261	88	221	570
Number of inter-display periods	226	77	194	497
Displays where distances ran recorded	158	77	204	439
Displays where feather flashes recorded	175	83	203	461
Sample periods for male feeding behaviour	39	19	42	100
Total time observing (mins)	2360	470	987	3817
Other displays seen, but no data collected	7	6	8	21
Fresh display tracks recorded	16	9	10	35

*displays recorded from 12 different individuals over the three years

Results

Display running and inter-display periods

Times spent display running and in inter-running periods were significantly different among males in all three years (Kruskal-Wallis tests Table 7.3, Fig. 7.2, Fig. 7.3). One male (tx5411) consistently displayed for the longest or second longest periods in all three years, whereas three males (txs: 5540, 5282, 4060) had the shortest display run and longest inter-run times in 1996 – 1998, respectively (Table 7.3). Male age was not consistently related to length of runs or inter-display periods. In 1998 the longest duration display runs, and the shortest inter-display times were given by two two-year-old birds (txs: 4060, 4282), whereas conversely, a four-year-old bird (in 1998) had the longest inter-display times in 1997 and 1998 (Table 7.4). Overall, time in the inter-run period was not significantly correlated with the time spent in the display run immediately prior to that period, in any year (Pearson's Rank Correlation, all three years, $r^2 < 0.003$, $P > 0.05$, $N = 261, 88, 220$, for 1996, 1997, 1998, respectively).

Table 7.3: Mean (+ 95 % C.I.) time, number or distance for display runs, inter-display periods, feather flashes and distances ran for male houbara in Mahazat as-Sayd Reserve from 1996 to 1998, and results of Kruskal-Wallis (H) tests. D.F. = (K-1), N = total number of observations from all males. NS = not significant at $P = 0.05$. For a detailed description of each behaviour, see methods section.

	Year	Mean	95 % C.I.	H	D.F., N	P
Display runs (secs)	1996	67.0	5.4	72.2	6, 261	<0.0001
	1997	75.8	10.1	13.6	4, 88	0.009
	1998	63.8	4.7	39.6	8, 221	<0.0001
Inter-display (secs)	1996	206.0	26.4	29.3	6, 226	0.0001
	1997	198.0	22.4	23.4	4, 77	0.0001
	1998	177.4	15.7	41.3	8, 194	<0.0001
Feather flashes (N)	1996	1.22	0.34	27.6	3, 175	<0.0001
	1997	1.88	0.36	15.9	4, 83	0.0032
	1998	1.68	0.24	28.8	8, 203	0.0003
Distance of run (m)	1996	45.2	16.2	20.5	5, 158	0.001
	1997	83.4	46.7	5.0	3, 77	NS
	1998	44.4	12.2	16.0	8, 204	0.042

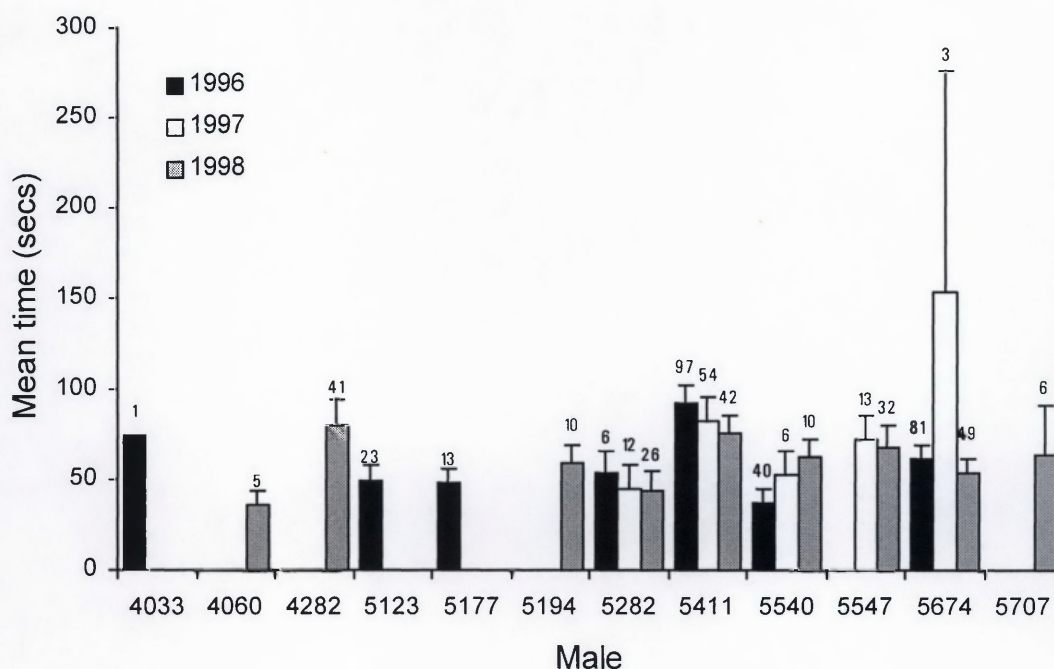


Figure 7.2: Mean (+ 95 % C.I.) time (secs) spent in display runs for individual male houbara displaying in Mahazat as-Sayd Reserve in each year. N values above bars. Missing bars indicate that the male was not sampled in that year (see Table 7.1). X-axis are transmitter frequencies.

For all 570 display runs and 497 inter-display periods, the mean (\pm 95 C.I.) time spent running was 67 ± 04 secs, and the mean time between runs was 2 mins 14 secs \pm 14 secs. The longest time spent on a single display run was 6 mins 04 secs, and the shortest time was just 3 secs. The longest inter-display period was 24 mins 07 secs, and the shortest 10 secs. Excluding observations of single display runs with no inter-display period, the mean (\pm 95 % C.I.) display-running rate (time display running as a proportion of total sample event observation time) for all males in all years was 17.8 ± 1.5 display runs per hour, i.e., one run every 3 mins 22 secs. The modal display rate was 16 runs per hour, and 80 % of runs were at a rate of 10 – 24 runs per hour. The maximum display rates recorded were 42.9 display runs per hour (i.e., a new display run beginning every 83 sec) by tx5411, and 41.7 runs per hour by tx5540, both in 1996. Minimum display rates were 4.9 runs per hour by tx5411, and 7.9 runs per hour by tx5123, again both in 1996.

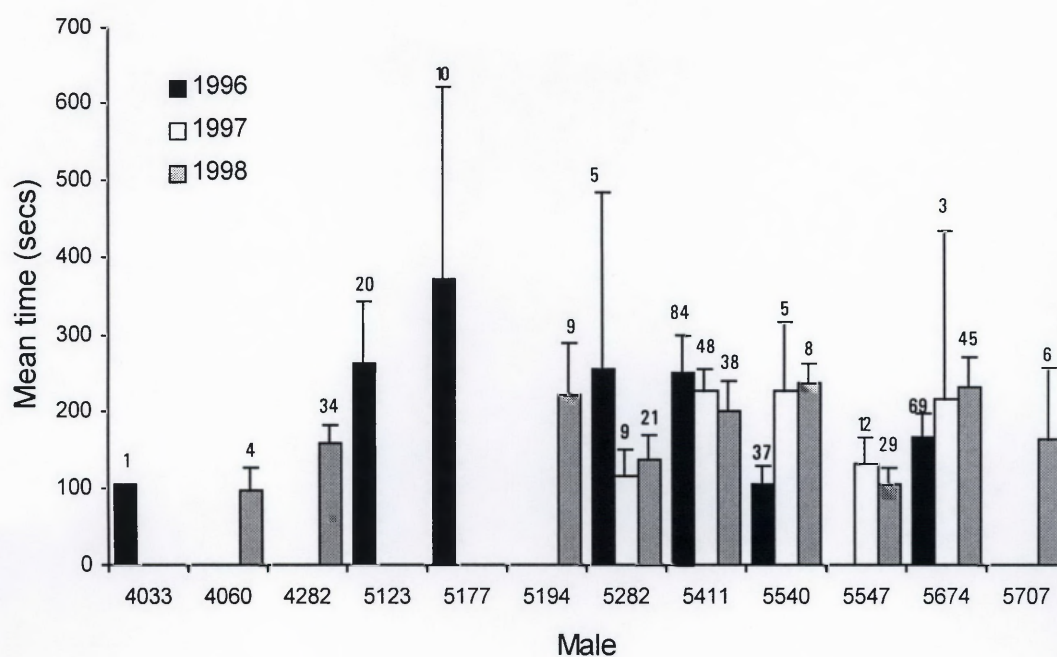


Figure 7.3: Mean (+95 % C.I.) time (secs) spent in inter-display periods for individual male houbara displaying in Mahazat as-Sayd Reserve in each year. N values above bars. Missing bars indicate that the male was not sampled in that year (see Table 7.1).

Number of feather flashes during final phase

Feather flashing was not reliably recorded from 14 display events in January or February 1996, or from some displays where light conditions were poor, and data from these periods were excluded from analyses. The numbers of feather flashes given by individual males were significantly different in all three years (Table 7.3, Fig. 7.4). Two males (txs: 5411, 5674) consistently gave more feather flashes than most other males, whereas one male (tx5282) gave the least number of flashes in two of the three years.

Overall, males gave 1.5 ± 0.2 (mean \pm 95 % C.I.) feather flashes in the final phase of 461 display runs from March 1996 to March 1998. The maximum number of feather flashes per display run was 13 and the modal number was three, with feather flashes occurring during 48 % of 461 display runs. In addition, I observed feather flashing during a previously undescribed situation, I called "standing flashes". During standing flashes, the male would stand in one place and repeatedly give flashes identical to the final phase of display running, without having a display run first. This behaviour was recorded on four occasions from four

different males, whereby, the four males stood, then entered the final phase 6, 1, 1 and 4 times, and gave 4 – 13, 8, 5 and 2 – 6 flashes respectively. For three of these males the standing flashes occurred in the midst of a bout of running displays, the other male was not seen display running before or after this display. No other houbara were in the vicinity of these males when they gave standing displays.

Table 7.4: Ranking index for each displaying male houbara from 1996 to 1998. Males are ordered by overall ranking per year, where 0 = the highest ranking of display intensity. Male ranking for feather flashes in 1996, and distance of display in 1996 and 1997 were weighted to account for missing data (nd) from some males. Weighting was achieved by assigning the top and bottom ranked males the highest and lowest score available in that year (e.g., 1996: 0 and 4), then apportioned remaining ranks evenly among the remaining males. For a detailed description of each behaviour, see methods section.

Tx	Display runs	Inter-display period	Feather flashes	Distance of display	Overall rank	Age of male (yrs)
Criterion	<i>longest</i>	<i>Shortest</i>	<i>most</i>	<i>furthest</i>		
1996						
5411	0	3	2	0	0	3
4033	1	1	nd	3.6	1	3
5674	2	2	4	1.2	2	2
5540	6	0	0	4.8	3	2
5282	3	4	6	nd	4	2
5177	5	6	nd	2.4	5	2
5123	4	5	nd	6	6	2
1997						
5674	0	2	0	nd	0	3
5411	1	3	1	1.3	1	4
5282	4	0	4	0	2	3
5547	2	1	3	2.7	3	3
5540	3	4	2	4	4	3
1998						
4282	0	4	3	0	0	2
5547	2	1	2	4	1	4
5411	1	5	1	6	2	5
5282	7	2	4	1	3	4
5674	6	7	0	2	4=	4
5707	3	2	5	5	4=	4
4060	8	0	6	8	6	2
5540	4	8	8	3	7	4
5194	5	6	7	7	8	3

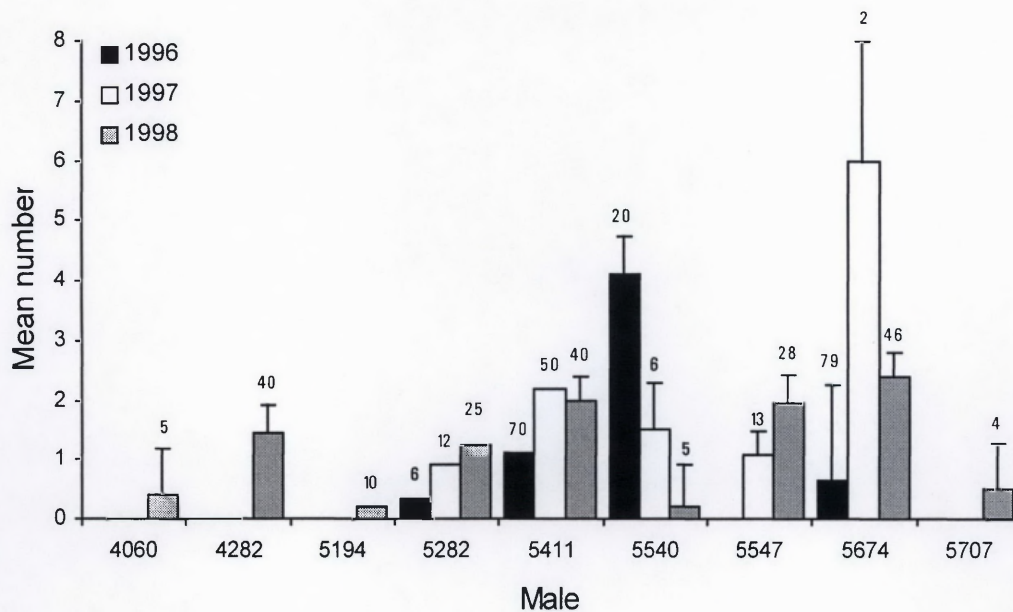


Figure 7.4: Mean (+ 95 % C.I.) number of feather flashes given in final phase of displays for individual male houbara displaying in Mahazat as-Sayd Reserve in each year. N values above bars. Missing bars indicate that the male was not sampled in that year (see Table 7.1). X-axis are transmitter frequencies.

Distances travelled during display runs

Males ran for significantly different distances during their display runs in 1996 and 1998, but not in 1997 (Kruskal Wallis tests, Table 7.3, Fig. 7.5). Ranking of males for distances ran in each year did not follow patterns for other behaviours recorded. Male 5411 ran the furthest and second furthest mean distances in 1996 and 1997, but in 1998 this male was only ranked sixth out of nine males, and had greatly reduced the length of its display runs (Fig. 7.5). Similarly, male tx5282, was one of the lowest ranking males in all other behaviours in all years, was the highest ranking male in 1997 and was second in 1998 for distance covered during display runs. The longest single run recorded was 1.2 km in a straight line (male tx5411, twice in 1997), and the longest cumulative distance over which a male displayed in one sample period was 2.2 km (tx5411 in 1997), and 2.1 km (tx5282 in 1998). On six other occasions males gave individual display runs that were 500 m or longer; tx5282 (0.8, 1.0 km), tx5674 (0.5, 0.5, 1.0 km), and tx5411 (0.5 km). Generally, the pattern for all males was to move mostly in circles and zigzags of less than 20 m diameter, inter-dispersed with

occasional longer weaving runs of many hundreds of metres. For all males combined, the mean (\pm 95 % C.I.) distance of each display run was 52 ± 12 m (N = 439). The modal distance was 10 m, with 82 % of runs covering 50 m or less.

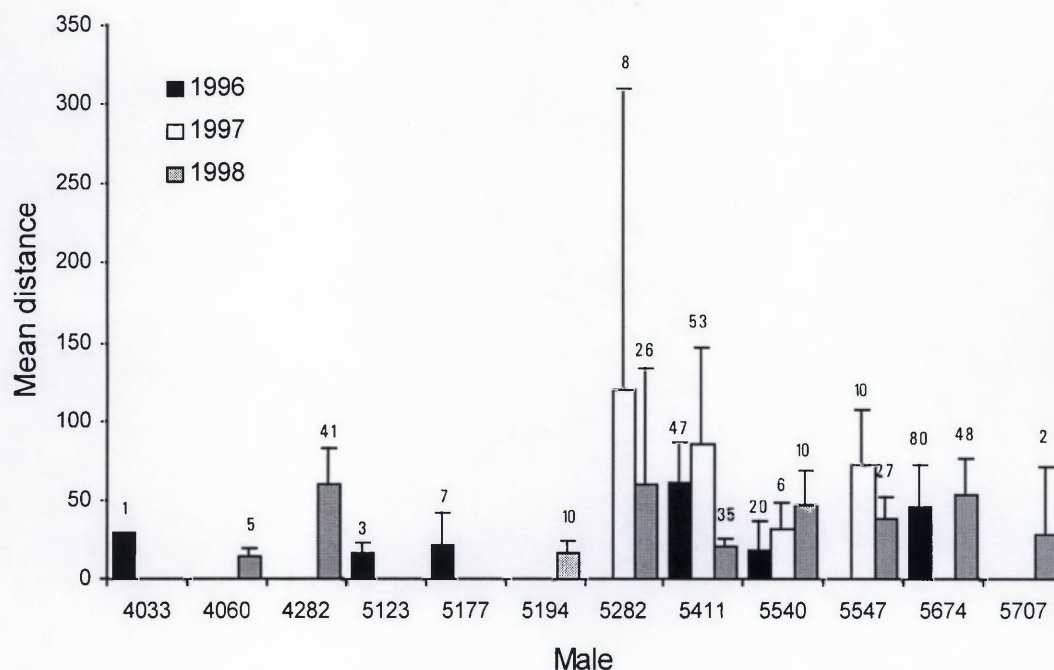


Figure 7.5: Mean (\pm 95 % C.I.) distance ran during displays for individual male houbara displaying in Mahazat as-Sayd Reserve in each year. N values above bars. Missing bars indicate that that male was not sampled in that year (see Table 7.1). X-axis are transmitter frequencies.

Occurrence of feeding when on display site

Of the 12 males observed displaying, five did not feed during displays, and four fed on only one occasion. The remaining three males (txs: 5282, 5411, 5674) fed on 4 – 9 occasions, representing 27 – 39 % of observations (Table 7.5). For all males combined, feeding occurred significantly more often in 1996, when males fed during 19 of 39 (48 %) sample events, than in later years ($\chi^2 = 17.4$, D.F. = 2, $P = 0.0002$).

Table 7.5: Number of sample periods per year and totals for all three years combined, in which individual male houbara fed or did not feed in Mahazat as-Sayd Reserve from 1996 to 1998. Male numbers are unique transmitter frequencies.

Male Tx	1996		1997		1998		Total No	Total Yes	Sample periods
	No	Yes	No	Yes	No	Yes			
4033	1						1	0	1
4060					1		1	0	1
4282					6	1	6	1	7
5123	3	1					3	1	4
5177	2						2	0	2
5194					2		2	0	2
5282	1		1	2	5	2	7	4	11
5411	7	8	9	1	8		24	9	33
5540	2	1	2		2		6	1	7
5547			3		4	1	7	1	8
5674	4	9	1		9		14	9	23
5707					1		1	0	1
Totals	20	19	16	3	38	4	74	26	100

Ranking of males over all three study years

Examination of variation in ranks across years between males was possible for only four males (txs: 5282, 5411, 5540, and 5674) for whom data was collected in each of the three years (Table 7.4). Of these males, tx5411 and tx5674 were usually ranked higher than tx5282 and tx5540 based on each of the behaviours and times measured in each year, indicating that some males may consistently give more intense displays over several years.

Length of time spent on the start phase

Duration of the start phase was recorded on 21 occasions, from four males (txs: 5177, 5411, 5540, and 5674). Males spent 29.6 ± 11.9 secs (mean \pm 95 % C.I., range = 4 – 99 secs) in the start phase. There were too few observations to examine differences between males among years in this behaviour.

Daily and seasonal timing of displays

The earliest date that display runs were observed was 20 January in 1996, and 3 February in 1997. The latest date in each year was 30 April in 1996, and 1 April in 1997. No displays or display tracks were seen outside of these periods. Start and finish dates of displaying were not recorded in 1998, but I observed display running from 4 February to 24 March.

Males displayed from first light for up to three hours, and again from two hours before sunset until it was dark (Fig. 7.6). I scanned known display sites repeatedly, and regularly tracked males throughout the reserve during the day, but I never saw males start displaying after 0930 or before 1600 hrs (local daylight time) or found tracks that indicated that they did so. In the morning, the earliest display start time was by tx5411, at 0543 hrs on 16 April 1996, and the latest finish was by tx5177, at 1013 hrs on 30 January 1996. In the evening, the earliest start time was by tx5540 at 1620 hrs on 10 February 1996, and the latest finish time was by tx5411 at 1845 hrs on 22 February 1997. I was unable to observe males displaying at night.

On 13 occasions I observed males actually arriving at their display arena and beginning to display, and on 27 occasions I watched males leaving the display arena after displaying. On other occasions, the male was already present, or I could not confirm that the male had not been displaying elsewhere, or I ceased observations before the male left the display ground. Mean time from arrival of the male at the arena to first display was 23.3 mins (N = 13, S.D. = 32.7), and mean time to leave the arena after the last display was 38.8 mins (N = 27, S.D. = 49.4). On arrival, males walked quickly with neck extended (low-head walking, *Fig. 47* of Launay & Paillat 1990) until reaching the edge of a patch of vegetation, or a prominent feature such as a low bush or rocky outcrop, where they stood in an erect posture, slowly turning either their head or body. After finishing their last display males either assumed a hunched posture with neck extended and parallel to the ground and quickly ran (low-head running, *Fig. 48* of Launay & Paillat 1990) along vegetation lines away from the display arena, or they remained in the area feeding.

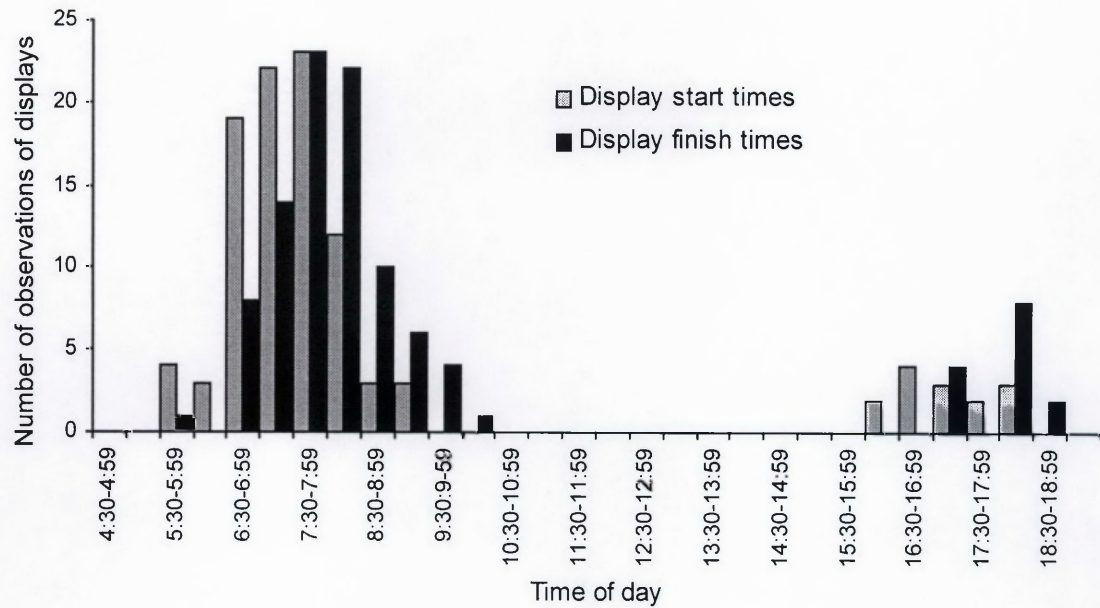


Figure 7.6: Daily timing of male houbara displays in Mahazat as-Sayd Reserve from 1996 to 1998 (N = 100, all years combined). Sunrise varied from 0558 hrs in mid-April to 0628 hrs in mid-February, and sunset from 1811 hrs in mid-February to 1838 hrs in mid-April.

Interactions with other individuals

Six species other than houbara were recorded very near displaying houbara males. Brown-necked ravens (*Corvus ruficollis*) were recorded disrupting male display runs six times as they flew by. On each occasion the male houbara ceased displaying, and either crouched low and hid (N = 5) or stood in the open (N = 1) until the raven had passed. Two males did not resume displaying, whereas other males resumed displaying 2 – 12 mins later. One hoopoe lark (*Alaemon alaudipes*) attacked and chased a displaying male houbara for more than 20 m, with the male continuing to display. Sand gazelle (*Gazella subgutturosa*) and Oryx (*Oryx leucoryx*) were observed within 100 m of displaying males four times without eliciting any obvious change in behaviour from the displaying bird. Two Rueppell's foxes (*Vulpes rueppelli*), one red fox (*V. vulpes*) and one *V. spp.* were seen 20 – 100 m from displaying males, but showed no sign of hunting behaviour towards houbara. However, the male houbara reacted to the presence of foxes on all four occasions - twice by stopping, standing and watching, once by running and hiding, and once by crouching and hiding. Males did not resume displaying that day after these interactions with foxes.

Interactions between displaying males and other houbara on display sites were recorded on 12 occasions. Interactions were between breeding-age females ($N = 3$), neighbouring males ($N = 6$ males) and one-year-old immature houbara ($N = 3$), and are summarised in Table 7.6. Resident displaying males pursued or followed most intruding males from their display sites, but in contrast, gave running displays to all three females and one immature. However, females always left the display site quickly, and no copulations were observed.

Table 7.6: Number and % occurrence of interactions between resident displaying males and immature or adult male and female houbara intruding on display sites.

Age/sex of intruder	Behaviour of displaying male	N	% occurrence
(A) Behaviour of displaying male towards intruder			
Immatures ($N = 3$)	Chase immature, not displaying	1	33
	No reaction	1	33
	Running display towards immature	1	33
Adult females ($N = 3$)	Running display towards female	3	100
Adult males ($N = 6$)	Chase male, not displaying	5	83
	Head up but no other response	1	17
(B) Behaviour of intruder towards displaying male			
Immature ($N = 3$)	Threat posture, then leave area	1	33
	Leave area in fast walk, head down	2	67
Adult females ($N = 3$)	Threat posture, then leave area in fast walk, head down	1	33
	Leave area in fast walk, head down	2	67
Adult males ($N = 6$)	Leave area in fast walk, head down	2	33
	Fly from area	4	67

Discussion

These results provide the first comprehensive account of display activities of individual male houbara. Males differed from each other in the intensity of their display for all four behaviours I measured. Generally, males that display-ran for the longest periods also had the shortest inter-display times and gave the most feather flashes in the final stage. Together, males with these characteristics appeared to be displaying more intensely than those running for less time, spent longer between display runs, and gave fewer flashes. I therefore conclude, that individual males do differ in their display intensity and that these differences have the potential to allow females to discriminate between males. However, the distances that some males ran during displays did not fit with the pattern of intensity of other behaviours given by these males. One male in particular (tx5282) was ranked lower than most males for all other behaviours, but gave some of the longest display runs. Possibly then, there are several strategies that males can use to advertise their fitness and some males may spend more time standing, watching and/or covering greater distances in single runs, rather than undertaking many display runs with few short pauses. These data provide the basis for future studies that should focus on mating success of the males relative to the intensity of their display or the strategy they choose to use.

Male display intensity did not appear to be closely linked to male age and experience during the relatively short period of this study. Except for the lack of regular displaying by immature one-year-old males, there was no clear relationship between male age and display intensity, i.e., the oldest males in the population did not always have the most intense displays. On the contrary, I have shown that at least one two-year-old male in 1998 displayed more intensely than did most four- and five-year-old males, and that some of the oldest males gave the lowest intensity displays. It is unknown whether this result is typical for the species: age structure and details of display behaviour are unknown for all other wild houbara populations.

Only one other study has recorded aspects of use of feather displays in wild houbara. In Russia, Ponomareva (1983) recorded duration of feather displays during the start phase of up to one minute in wild houbara. This was similar to the 99 sec maximum time I recorded. In Mahazat as-Sayd Reserve the start phase usually took less than 30 sec and appeared to be a

stage leading to the intense display running that always followed. By comparison, feather displays during the final phase, including head movements and bill-clapping, were sometimes given as standing flashes, in the absence of display running, and in these instances up to 13 feather flashes were recorded, well above the mode of three feather flashes recorded in normal final phase displays in this study, and the two to three flashes recorded by Launay & Paillat (1990). Feather flashes in the final phase of displays are spectacular in their own right, even from a distance the bird appears to pulse as white feathers are displayed then retracted. This flashing display is similar to the display used by houbara when approaching a female (Launay & Paillat 1990, Gaucher *et al.*, 1996), and may indicate a higher motivational state of the male. However, when standing flashes occurred in Mahazat as-Sayd Reserve, no females (or males) were near the displaying male (i.e. within approximately 1 km). Altogether then, because males invest much of their time and energy into display activities for many months, and based on the differences in male display behaviour I report here, it seems likely that females are using such feather displays as a mechanism for selecting fit males. Other studies that have shown that female selection is based on differences in male plumage details (e.g., wing spotting in buff-breasted sandpiper, *Tryngites subruficollis*, Lanctot *et al.*, 1998; red breast streaking in yellow warblers, *Dendroica petechia*, Yezerinac & Weatherhead 1997), rather than on differences in male behaviours. Plumage differences have not been measured in individual houbara, but do not vary markedly (pers. obs.). I consider that the large differences in display behaviour among males described in this chapter give more opportunities for females to readily assess male fitness, than do subtle differences in plumage.

A high proportion of males' time at their arenas was spent displaying, and that display was rigidly performed. Deviations from the sequence of stand alert - display run - stop - feather flash - stand alert occurred only when another houbara was present on the arena, when the male was disturbed (e.g., by passing predators), or occasionally when males gave standing flashes. Display running is likely to be energetically demanding and with several hours per day taken up with display, males may lose weight as the breeding season progresses (Saint Jalme *et al.*, 1994). This is compounded because displaying coincided with peak morning and evening feeding periods when insect activity was greatest (Combreau & Launay 1996), and males may have difficulty allocating sufficient time to each of these tasks. In captivity, males decline in weight over four months of breeding and do not start to increase in weight

until mid-May, at the end of the display period (Saint Jalme *et al.*, 1994). Rapid weight loss may explain the increased occurrence of feeding at display grounds in 1996 compared to later years. The young age and lack of experience of males in 1996 may have contributed to this difference, but equally young and inexperienced males (e.g., txs: 4060, 4282) in 1998 did not frequently feed on the display grounds. More likely, males in Mahazat as-Sayd Reserve in 1996 were in poorer condition than in later years. The reserve was drier and warmer, and spring rains arrived later in 1996 than in 1997 or 1998 (see Chapter 4, Appendix 1), and female houbara either failed to nest, or nested later in the 1996 breeding season (Chapter 4). Quantitative data on food supplies during this period are not available, but I suggest that reduced food availability brought on by low rainfall in spring 1996 may have led to males increasing feeding activity during displays. During that time males apparently compensated for reduced food availability by increased feeding, without reducing the rate of or time spent on display runs, and without sampling or shifting to new display grounds (see Chapter 8).

Male houbara display from mid-January to April each breeding season, and this was the same period over which females nested (Chapter 4). I observed displays during every morning and most evening visits I made to display grounds from February to April for most males, and although I could not record display activity on days when I was not present, it is likely that most males displayed on a daily basis over this period. Males in a captive population housed 220 km south west of Mahazat as-Sayd Reserve, with unlimited food, displayed daily from December to July, with a peak from February to April, and some males displayed almost year round (Saint Jalme *et al.*, 1994, Saint Jalme *et al.*, 1996c). Exact periods of displays are unknown for other populations. In Central Asia, displays apparently commence soon after the arrival of migrating males to breeding grounds in early spring (Dement'ev & Gladstov 1951, Aleskeev 1980). In China, displays were found in June and July, being late spring/summer (Yang *et al.*, 2002). In Saudi Arabia, three males were recorded display running in open lava fields in Harrat al-Harrah reserve in March 1990 (Goriup *et al.*, 1992). However, despite frequent observations at the same sites in following years no further displays were seen in the area (P. Seddon pers. comm.).

It is unknown whether males display at night. Where I was able to determine males arriving at a display site in the early morning, and leaving at night, display runs commenced soon

after first light, and with three exceptions, ceased immediately before total darkness. The exceptions were when males continued to display when it was too dark for my observations, but monitoring fluctuations of their transmitter signals indicated that display activity ceased shortly after dark. Houbara are known to feed on moonlit nights (Anegay 1994, Combreau & Launay 1996), and display activity on moonlit nights is certainly possible, but increased risk of predation from nocturnal predators such as foxes (*Vulpes spp.*), cats (*Felis spp.*) and eagle owls (*Bubo bubo*) may make night displaying risky, and would presumably also make it difficult for females to see males displaying.

I was unable to determine whether houbara display intensity was related to mating success. Determining mating success through direct observation is difficult for this species. Females spent very little time in association with males, and despite many hours of observation, male-female encounters were extremely rare, and none that I witnessed resulted in copulation. On two of three occasions when males and females were together, the females appeared uninterested in the males. However, these females were potentially receptive: none had a nest at the time of the interactions but all had bred or would later breed in the season, and up to 78 % of eggs were fertile (Chapter 4). Therefore, matings and presumably mate choice was occurring regularly. The scarcity of interactions may have been because the population size was low (N = a maximum of 36 adult birds), and therefore the probability of encounter was likely to be low. Alternatively, males and females may be meeting and mating at sites away from the display grounds, at night, or for very brief periods during the day (mating of the closely related *C. u. fuertaventurae* may take as little as one minute in the wild, Collins 1984). Females may need to learn the whereabouts of traditional lek arenas at which to find males (see Chapter 8), and because arenas in Mahazat as-Sayd Reserve are new and therefore lack long-term traditional use, females may not know where to locate males. My approach in this study was to find and observe males, and thereby observe encounters with females whenever they arrived at display sites. I suggest that a better method of detecting copulations, and developing greater understanding of male-female interactions would be achieved by closely following females, in conjunction with DNA analysis of adults and young to show paternity. DNA sampling is possible: for adults by taking blood samples before each bird's release, and for chicks by catching them after hatching.

One other explanation of the function of male display - territory defence (Launay & Paillat 1990) - was not supported by my data. In this study, males were frequently located within 1-2 km of other males, yet male-male encounters were almost as rare as those with females, indicating that males are not encountering each other often. Displaying males interacted with other males on six occasions. In all cases, the males were neighbours. However, contrary to anecdotal reports from others (e.g., Dement'ev & Gladstov 1951, F. Launay pers. comm. in Saint Jalme *et al.*, 1996c), I recorded few aggressive encounters, and those recorded were all in March and April, well after the establishment of display "territories" or arenas, and well after the period when testosterone levels peak in males at the beginning of the breeding season (in January, Saint Jalme *et al.*, 1996c). At least three of the interactions I observed occurred when neighbouring males that had ceased regularly displaying for the season were feeding near to the arena of an actively displaying male, i.e., one of the males no longer had a requirement for a display-based territory. However, it is possible that aggressive interactions were occurring at other times of year, perhaps even during the pre-breeding period. Males formed small groups at this time, and it is possible that by the time these males moved to display arenas a dominance hierarchy was already in place. Also, with more opportunity to interact over longer time periods, males in sedentary populations, such as in Mahazat as-Sayd Reserve, may not be as aggressive as those in the migrating populations reported in Dement'ev & Gladstov (1951). Further, if male display had a territorial purpose, then males should display near to territory boundaries with other males. This was not the case and males displayed centrally within a display arena, usually in complete visual isolation from other males. In addition, I have shown elsewhere (Chapter 8) that males were not displaying in, or defending, sites where females nested or spent a lot of time, and therefore, male displays are not a mechanism for defence against, or of, females whose home ranges overlap with male display sites.