A BEHAVIOURAL REPERTOIRE OF THE ADULT HOUBARA BUSTARD (CHLAMYDOTIS UNDULATA MACQUEENII)

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The Houbara bustard (Chlamydotis undulata, Order: Gruiformes, Suborder : Otides, Family : Otididae) is a medium sized desert bird which inhabits open or scrub-covered arid plains. Its distribution extends from the Canary Islands across North Africa to the Middle East and the USSR (Ali and Ripley, 1983; Cramps and Simmons, 1983; Dement'ev et al., 1951; Meinertzhagen, 1954; Heim de Balsac and Mayaud, 1962; Hüe and Etchecopar, 1970; Urban et al., 1986). Body length is in the order of 55-65 cm and wing-span in that of 135-170 cm, males being generally about 10 % larger than females. Plumage is typically described as being vermiculated or barred pale sand gray on the back, wings and tail with a white underbody (for greater detail see Cramps and Simmons, 1983 and the description of Chlamydotis undulata undulata given below). Sexual dimorphism in plumage is slight and females resemble males except in that the crown tuft and neck frills are less developed. Juvenile males and females resemble adult females (Cramps and Simmons, 1983). Seasonal variation in plumage appears to be absent (Cramps and Simmons, 1983). Three subspecies of the Houbara bustard are recognised. These are;

A North African race (*Chlamydotis undulata undulata*), which is distributed from Mauritania to Egypt. In this race, the hind neck and sides of the crown are sandy grey marked with black. A white tuft is present in the center of the crown. The back and upper tail coverts are a vermiculated sandy grey colour. The fore-neck and chest bib are white and frilled with long feathers, of which the uppermost are black and the lowest white with black tips. As is typical for the species, the rest of under body is white.

A Canary Islands race (Chlamydotis undulata fuertaventurae), which is smaller and much darker, on the upper parts of the body, than C. undulata undulata.

An Asian race (*Chlamydotis undulata macqueenii*), which is distributed from the Sinaï through Arabia to Pakistan, Afghanistan, Kazakhstan and Mongolia. This is the largest and palest in colour of the three subspecies. The tuft on the crown contains both black and white feathers. The neck frill contains more white feathers and the chest bib is grayer than is the case in the other two subspecies.

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In recent years, several authors have pointed out that wild populations of Houbara bustards are declining in all areas of their distribution (Alekseev, 1980; Collar, 1979; Haddane, 1985; Mansoori, 1985; Naseer Ahmed, 1985; Mirza 1985; Ponomavera 1979; Roberts, 1985; Shams, 1985). The decline of this species is due to multiple causes which include the extension of agricultural land, overgrazing by domestic animals and hunting (Lavee, 1985, 1988; Malik, 1985).

In order to conserve the Houbara bustard, field studies, designed to assess the major biological and ecological needs of the birds (Mian, 1984; Mian and Surahio, 1983; Suhario, 1985), have been carried out in parallel with the development of captive breeding programmes. Captive breeding programmes have been undertaken in Israel (Mendelssohn *et al.*, 1979), Dubaï (Platt, 1985) and, more recently, in Saudi-Arabia at the National Wildlife Research Center (N.W.R.C.). Such captive breeding programmes have been only partially successful. The need to improve the extent to which captive rearing conditions cater for the biological needs of Houbara bustards has led the N.W.R.C. to undertake more comprehensive behavioural studies of this species.

The practical problems associated with the study of desert birds in the wild are, without doubt, among the reasons why few attempts have been made to describe the behavioural repertoire of bustards. Preliminary observations for an ethogram of the Houbara bustard were made by Collins (1984), using *C. undulata fuertaventurae* as a model, and descriptions of male display have been published by Mendelssohn *et al.* (1979) and Ponomavera (1983). Relatedly, basic ethograms have been published for *Ardeotis australis* (Fitzherbert, 1979), *Tetrax tetrax* (Schulz, 1985, 1986), *Eupodotis melanogaster* (Schulz and Schulz, 1986) and *Otis tarda* (Hellmich, 1987).

In this paper we present a description of the behavioural repertoire of the adult Houbara bustard (*Chlamydotis undulata macqueenii*) which will hopefully contribute to further quantitative and comparative studies of the Otides sub-order.

MATERIALS AND METHODS

Study areas and observation methods

The behavioural repertoire of *Chlamydotis undulata macqueenii* described here was compiled from personal observations, sketches, photographs and films of free-living birds or birds kept in cages and enclosures at the N.W.R.C., supplemented by descriptions in the literature.

Most of the personal observations described were of eleven adult semicaptive birds (6 males and 5 females) living in a large (100 ha) scrub covered enclosure during the period between January and June, 1989. All of these birds were individually marked with colour leg bands. Observations were made with a Questar telescope which allowed detailed observations of individuals up to one kilometer away. A total of 420 hours of observation was made of this group of birds. All observations were carried out from a 40 meter high rock located within the enclosure. In addition to the direct observations a 4 hour long video-recording was also made in order to allow more detailed descriptions of certain behaviour

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patterns. The remaining personal observations described were of birds kept in cages measuring 5×6 meters. Twenty of these cages were equipped with video-monitoring systems, which allowed birds to be observed, without disturbing them, from a separate room. Direct observations were also made of birds kept in cages without video-monitoring systems.

The behavioural repertoire presented in this paper is purely qualitative and no attempt is made to describe possible diurnal or seasonal variations in behaviour. The descriptions cover the most common postures and behaviour patterns shown by adult Houbara bustards. Approximately eighty behaviour patterns are described. Only those behaviour patterns seen during our own study are described in detail. However, descriptions of other behaviour patterns given in the literature are also referred to in the text.

Classification and nomenclature of behaviour patterns

The organisation of the paper and the terminology used broadly follows that used in Hellmich's (1987) ethogram of the Great bustard (*Otis tarda*). In giving names to particular behaviour patterns we have deliberately avoided those which imply some form of function for the behaviour. The decision to do this was made firstly, because in many cases the function of the behaviour patterns described could not be determined with certainty and secondly, because certain behaviour patterns appeared to have multiple functions. However, where possible, we have followed the terminology used by McFarland (1987) for descriptions of comfort behaviour and the terminology of Morris (1956) for descriptions of feather posture.

RESULTS

All the behaviour patterns observed were grouped into one of eight different categories. These categories were ;

- Resting behaviour : all behaviour and postures shown when the birds were quiescent, with the exception of sleeping.

- Comfort behaviour : all activities associated with body maintenance and care of the plumage.

- Locomotion.
- Feeding behaviour.
- Social behaviour.
- Sexual behaviour.
- Incubation and parental care behaviour.
- Miscellaneous behaviour patterns.

Descriptions of behaviour patterns

1. Resting behaviour (Plates 1a; 1b)

Resting behaviour was observed at all times of day in both males and females. Resting behaviour could be divided into three types or classes. These were ; sitting, crouching and standing.



Plate 1a. — Resting behaviour of adult Houbara bustards. Figs: 1: Neck-short sitting posture, 2: Head- up sitting posture, 3: Alert sitting posture, 4: Head-up crouching, 5: Neck-short crouching, 6: Alert crouching, 7: Neck-short standing, 8: Neck-short ruffled standing, 9: Neck-short ruffled and fan tailed standing, 10: Head-up standing, 11: Head-up ruffled standing, 12: Head-up ruffled and fanned standing.

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1.1. Sitting (Plate 1a; Figs 1, 2, 3)

Three distinct sitting postures were discernable. The differences between these postures primarily involved the position of the neck.

In the *neck-short sitting posture* (Plate 1a; Fig. 1) the neck is folded back against the body such that the head rests on the upper part of the back parallel to the ground and slightly above the level of the shoulders. This posture differs from the squatting posture described by Collins (1984) and from the low-head incubating posture described below. In these latter two postures, the head is held slightly above and forward of shoulder level.

In the *head-up sitting posture* (Plate 1a; Fig. 2) the posture of the body is identical to that in the neck-short sitting posture but the neck is partially extended and slightly curved back over the body. The head is held parallel to the ground.

In the *alert sitting posture* (Plate 1a; Fig. 3) the neck is fully extended and held at right-angles to the body. The head is orientated upwards and is frequently held slightly to the left or right of the line of the body.

1.2. Crouching or heel-standing (Plate 1a; Figs 4, 5, 6)

During crouching, the keel and ventral region are held above ground level and the bird rests on the upper extremities of the shanks and the points of the digits. The shanks are held parallel to the ground and at right-angles to the hocks. As was the case for sitting, three distinct crouching postures were discernable; *neck-short crouching* (Plate 1a; Fig. 5) *head-up crouching* (Plate 1a; Fig. 4) and *alert crouching* (Plate 1a; Fig. 6). The differences between these postures involved the variations in the position of the neck described for the sitting postures. Crouching was observed most frequently when the ambient temperature was in excess of 30° C.

1.3. Standing (Plate 1a; Figs 7, 8, 9, 10, 11; Plate 1b, 13, 14, 15)

Standing birds adopted one of at least eight different postures. The major differences between these postures involved the position of the neck and tail and the degree of pilo-erection.

In the *neck-short standing posture* (Plate 1a; Fig. 7) the position of the head and neck are similar to those in the neck-short sitting posture and the body plumage is relaxed.

In the *neck-short ruffled standing posture* (Plate 1a; Fig. 8) the position of the head and neck are the same as above but the body plumage is ruffled.

In the neck-short ruffled and fan tailed standing posture (Plate 1a; Fig. 9) the position of the head and neck are the same as above, the body plumage is ruffled and the tail feathers are fanned vertically. When a bird adopts this posture the dark coloured bars on the tail feathers are clearly visible. The neck-short ruffled and fanned standing posture was most frequently seen after rain had fallen and was rarely seen when the ambient temperature was high. The vertical fanning of the tail feathers, characteristic of this posture, was observed in other situations (see below) but never in the absence of ruffling of the body feathers.

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The *head-up standing posture* (Plate 1a; Fig. 10) is identical to the neck-short standing posture, except in that the neck is partially extended.

The *head-up ruffled standing posture* (Plate 1a; Fig. 11) is similar to the neck-short ruffled standing posture, except in that the neck is partially extended.

The *head-up ruffled and fanned standing posture* (Plate 1a; Fig. 2) is also identical to the neck-short ruffled and tail fanned standing posture, except in that the neck is partially extended.

In the *head-up horizontal fan tail standing posture* (Plate 1b; Fig. 13) the neck is extended, the body plumage sleeked and the tail feathers fanned horizontally. This was the least frequently observed of all standing postures and was seen only when one bird was approached by another, which implies that it may have some social function.

In the *wet weather standing posture* (Plate 1b; Fig. 14) the neck is drawn back against the body so that the head lies on top of the body between the wings; the middle to lower part of the neck is thus thrust forward and, on some occasions, is used as a support for the bill. The plumage is sleeked and the body held high above the legs. Birds adopting the wet weather standing posture invariably orientated themselves towards the prevailing wind.



Plate 1b. — Resting behaviour of adult Houbara bustards. Figs : 13 : Head-up horizontal fan tail standing, 14 : Wet weather standing, 15 : Alert standing.

In the *alert standing posture* (Plate 1b; Fig. 15) the keel is raised, the neck fully extended and the head orientated upwards in line with the body. The bird then remains immobile in this position. On occasion, this posture was adopted by all the birds observed, irrespective of their preceding postures or behaviour.

One striking aspect of the standing behaviour of birds in groups was the fact that, irrespective of the posture adopted, all individuals faced in the same direction vis à vis the prevailing wind and sought the protection of shrubs and bushes; the result of this being that, when viewed from up wind, only the heads of the birds were visible.

2. Comfort behaviour (Plates 2, 3, 4)

Comfort behaviour was defined according to McFarland (1987) and thus included all behaviour related to care of the plumage and skin, together with

thermo-regulatory behaviour. According to Collins (1984) comfort behaviour occupies a large proportion of the time budget, and, although most frequent in the early morning and late afternoon, is seen at all times of day. Comfort behaviour was divided into eight categories. These were ; *preening, stretching, scratching, shaking, ruffling, flapping, sand-bathing* and *sun-bathing*.

2.1. Preening (1)

Preening behaviour is shown by sitting and standing birds. Preening, which principally involves stroking and arranging, is almost invariably performed with the beak closed. The regions of the body which are preened preferentially are the breast (Plate 2; Fig. 16, standing and Fig. 24, sitting), the neck (Plate 2; Figs 17 & 18, standing and Fig. 25, sitting) and the tail (Plate 2; Fig. 23, standing and Fig. 28, sitting). Birds did not appear to preen themselves in any systematic fashion and preening bouts were frequently interrupted before the birds had preened all parts of their bodies. In total thirteen different preening activities were recognised. Most, but not all, of these activities are performed by sitting and standing birds.

In *breast preening* (Plate 2; Fig. 16, standing and Plate 3; Fig. 24, sitting) the feathers of the breast region are arranged by horizontal movements of the beak.

In *neck preening* (Plate 2; Figs 17 & 18 and Plate 3; Fig. 25) the bird is standing or sitting and manipulates the feathers of the upper (Figs 17 & 18) or lower part of the throat (Fig. 25).

Wing preening (Plate 2; Figs 19 & 20 and Plate 3; Fig. 26) is directed towards both the interior and exterior surfaces of the wing. When the inner surface of the wing is preened the tectrices and secondaries are preferentially manipulated. When the outer surface of the wing is preened the upper tectrices are preferentially manipulated. In the figures, birds are shown preening the inner surface of the wing when standing and the outer surface of the wing when sitting. However, the fact that the bird is standing or sitting does not influence which surface of the wing is preened.

In *leg plumage preening* (Plate 2; Fig. 21) the feathers of the *pteralyla cruralis* are manipulated (see King and McLelland, 1984).

Back preening (Plate 2; Fig. 22 and Plate 3; Fig. 27) involves the care of the feathers of the *pteralylae cruralis* and *femoralis*. As in breast preening, care of these feathers primarily involves left to right and right to left horizontal movements of the beak.

Tail preening (Plate 2; Fig. 23 and Plate 3; Fig. 28) was the most frequent preening activity observed. Tail preening movements follow a strict sequence. The base of the tail is preened with lateral movements of the beak, the beak is then placed between two rectrices and moved outwards towards their tips. This sequence of movements is then repeated.

2.2. Stretching

Stretching movements are only infrequently seen, but on those occasions when they are seen the most frequently observed are; *leg-stretching, wing-stretching* and *body-stretching*.

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⁽¹⁾ The Houbara bustard does not possess a uropygial or preen gland. The descriptions of preening given thus refer to the manipulation of the plumage and not to the oiling of the feathers.







Plate 2. — Comfort behaviour of adult Houbara bustards. I. Preening. Figs : 16 : Breast preening, 17, 18 : Neck-preening, 19, 20 : Wing preening, 21 : Leg plumage preening, 22 : Back preening, 23 : Tail preening.

In *unilateral wing and leg-stretching* (Plate 3; Fig. 29), the wing and leg of one side of the body are extended out and back from the body. The leg is totally obscured by the wing. The toes are stretched outwards in the same plane as the leg.

In *unilateral wing-stretching* (Plate 3; Fig. 30), the leg is not always obscured by the wing and the wing is extended more perpendicularly with respect to the body than is the case in unilateral wing and leg-stretching.

In *body-stretching* (Plate 3; Fig. 31), the wings are partially extended and raised above and slightly forwards of the body. The body is orientated down-



Plate 3. — Comfort behaviour of adult Houbara bustards. II. Preening, stretching and scratching. Figs: 24: Breast preening, 25: Neck-preening, 26: Wing preening, 27: Back preening, 28: Tail preening, 29: Wing and leg stretching, 30: Wing stretching, 31: Body-stretching, 32: Neck stretching, 33: Scratching.

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wards, sometimes to such an extent that the radius-metacarpal joint touches the floor.

Neck stretching (Plate 3; Fig. 32) differs from the initial phases of the male courtship display (see below) in that, although the lateral feathers of the neck are raised, those of the crown are sleeked. Furthermore, neck stretching is shown by both males and females.

2.3. Scratching, shaking, ruffling and flapping

Scratching (Plate 3; Fig. 33). In this figure the bird is shown scratching the neck. This behaviour can be shown using either foot and may equally well be directed to the back of the head.

Shaking, ruffling and flapping. As is the case in C. undulata fuertaventurae (Collins, 1984), shaking, ruffling and flapping were invariably shown after bouts of preening behaviour.

In *shaking* (Plate 4; Fig. 34), the body is rotated slightly about its axis and only the folded wings are moved up and down.

In *ruffling* (Plate 4; Fig. 35), all parts of the body are moved. Ruffling frequently follows a bout of neck stretching; at the end of the neck stretching bout the feathers of the anterior part of the body are raised and the body is shaken about its longitudinal axis. This shaking movement passes as a wave from the anterior to the posterior end of the body. The feathers of the tail are slightly fanned in the vertical plane.

Wing-flapping (Plate 4; Fig. 35) begins in a way similar to body-stretching; however the wings are flapped and the body gradually brought upwards into the vertical plane.

2.4. Dust-bathing

Dust baths are usually taken in small dust or sand filled depressions in the ground. Three forms of dust-bathing behaviour were observed.

In *body dusting* (Plate 4; Figs 37, 38), the bird sits with the posterior part of the body slightly raised and kicks up a cloud of dust. The left and right feet are kicked out alternately.

Dust-bathing frequently follows on from a bout of body-dusting. The bird lies on its side with its neck resting on the ground and kicks dust over its body. The left and right feet are kicked out alternately.

In *neck dusting* (Plate 4; Fig. 39), the bird rests on its shanks with the tail and rear end of the body held high in the air. The neck rests on the ground and is frequently rotated so as to be rubbed in the dust.

2.5. Sun-bathing

Like McFarland (1987) we have classified sun-bathing as a comfort behaviour.

Wing-spread sunning (Plate 4; Fig. 40). In the figure the bird is shown sitting with only one wing extended. However, the behaviour may also be shown with both wings extended. This behaviour, which appears to have a thermoregulatory



Plate 4. — Comfort behaviour of adult Houbara bustards. III. Figs: 34 : Shaking, 35 : Ruffling, 36 : Flapping, 37, 38 : Body dusting, 39 : Neck dusting, 40 : Wing spread sunning.

function, was seen only when the ambient temperature exceeded 30° C; it never had a duration of more than 5 minutes and was frequently accompanied by guttural fluttering (panting).

3. Locomotion

Although the Houbara bustard is capable of long and sustained periods of flight, it is essentially ground dwelling and appears to prefer running or walking

as a means of locomotion (1). If frightened, the birds do not fly but run quickly and seek cover. During the daytime, movements from one area to another are slow, discrete and frequently interrupted by bouts of resting behaviour.

3.1. Running and walking

During our observations, we recorded nine types of running or walking. However, this list should not be considered as exhaustive.

Walking (Plate 5, Fig. 41). This was the most frequently observed form of locomotion. The gait is slow; body stance does not vary and the neck is held upright at right angles to the body.

Nod-walking (Plate 5, Figs 42 & 43). This is also a frequently observed form of walking. The only differences between this form of locomotion and walking are the jerky back and forward movements of the head.

Slow motion walking (Plate 5, Fig. 44). As its name implies, slow motion walking is walking with an extremely slow gait. Step pace is so reduced that the bird spends periods of time standing on one leg with the other leg folded against the body.

Low head walking (Plate 5, Fig. 47). The gait is similar to that in walking and nod-walking. The neck is extended out in front of the body and slightly curved, so as to be held in line with the shoulders. This mode of locomotion is principally employed when crossing areas of ground which are devoid of cover.

Alert walking (Plate 5, Fig. 49). The gait is somewhat more rapid than in slow motion walking. The neck is slightly lowered but the head is held high and orientated to one side or the other.

Trotting (Plate 5, Fig. 45). The speed of movement is intermediate between running and walking. Body stance does not vary and the neck is held upright at right angles to the body.

Nod-trotting (Plate 5, Fig. 46). Identical to trotting except in that the head and neck are jerked backwards (see nod-walking).

Low head running (Plate 5, Fig. 48). The bird moves very rapidly with its neck extended and its head held low. This form of running is principally used when the birds are in flight from some form of danger and is the most common of all flight reactions. According to Mian (1988), the flight distance of the Houbara is in excess of 500 m. The birds direct their runs so as to dodge between and hide behind available sources of cover.

3.2. Flying

As mentioned above Houbara bustards fly only rarely, preferring walking and running as a means of locomotion. However, this should not be taken as an indication that the bird is a poor flier or is incapable of sustained flight. Flying usually appears to commence with a short take-off run (Plate 6, Figs 50 & 51),

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⁽¹⁾ The foot of the Houbara is anisodactyl in that there are three forward pointing toes but lacks a hallux. The toes are lobed, in a fashion similar to, but less extreme than, that observed in the Great crested grebe (*Podiceps cristatus*). The claws resemble those of the Ostrich (*Stuthio camelus*) in that they are strong and flattened.







Plate 5. — Locomotion behaviour of adult Houbara bustards. I. Walking & running. Figs: 41 :
Walking, 42, 43 : Nod-walking, 44 : Slow-motion walking, 45 : Trotting, 46 : Nod-trotting, 47 :
Low-head walking, 48 : Low-head running, 49 : Alert walking.

although Collins (1984) has reported seeing birds take off from a stationary standing posture. In flight (Plate 5, Figs 52 & 53) the neck is extended and the wings are slightly kinked about the carpal joint. Wing action is slow, the wing strokes being made through a relatively shallow angle both above and below the horizontal.

4. Feeding behaviour

Houbara bustards of the subspecies *macqueeni* are opportunist feeders. However, there is some controversy concerning the proportions of the diet





Plate 6. — Locomotion behaviour of adult Houbara bustards. II. Flying. Figs : 50, 51 : Take-off run, 52, 53 : Flying.

represented by plant (1) and animal (2) material (Heim de Balsac and Mayaud, 1962; Cramps and Simmons, 1983; Collin, 1984; Mirza, 1985).

Whatever the food source sought, feeding always commences with *foraging* behaviour (Plate 7; Fig. 54). During foraging the body is orientated slightly downwards, the neck bent backwards on itself and the beak pointed downwards. The bird walks slowly but more rapidly than in slow motion walking.

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⁽¹⁾ For example, the fruits and leaves of Lycium and Salsola species.

⁽²⁾ Predominantly beetles (Tenebrionidae) and ants (Formicidae).





Plate 7. — Feeding behaviour of adult Houbara bustards. Figs: 54: Foraging, 55: Picking, 56: Sticking, 57: Chasing, 58: Flying prey catching, 59: Large prey handling.

When the food source is plant material, the bird adopts the *picking posture* (Plate 7; Fig. 55). The pecking movements made in this posture are very precise, each peck resulting in the taking of one food item.

Sticking behaviour (Plate 7; Fig. 56). This behaviour was observed when birds were taking ants from swarms on the ground. However, the same behaviour may also be used to remove insects from crevices or burrows and to remove particles of sand and gravel which obscure a prey item.

Chasing behaviour (Plate 7; Fig. 57). During this behaviour pattern, the animal runs with its neck extended so as to be held almost parallel to the ground, accelerates rapidly towards the prey item (usually an insect) and seizes it by means of a springing movement of the body. Chasing behaviour only occurs over short distances.

Flying prey catching behaviour (Plate 7; Fig. 58). This behaviour pattern is shown when birds attempt to catch flying insects. This behaviour is sometimes accompanied by jumping movements.

When tackling large animal prey (such as scorpions) the birds invariably adopt the *large prey handling posture* (Plate 7; Fig. 59).

5. Social behaviour

The social behaviour and structure of wild populations of Macqueen's Houbara bustard (C. undulata macqueeni) are virtually unknown, due to the

practical problems of studying this species in the wild. During the course of our observations we observed two behaviour patterns which clearly had some social function and were always directed towards conspecifics. Other behaviour patterns which appeared to have some social function are described later in the text. The two behaviour patterns with clear social functions were aggressive chasing and threatening.

Aggressive chasing (Plate 8; Fig. 60) was shown by both males and females when foraging and by females during nest-site selection. However, whether or not aggressive chasing was used in the formation or defence of territories could not be determined. At the start of a bout of aggressive chasing the head is lowered, the body plumage slightly fluffed, the tail raised and the body rocked backwards and forwards. This sequence of behaviour patterns is followed by the bird launching itself towards its opponent and chasing it over a distance of several meters with the head and neck held down and forwards. At the end of a chase the bird usually adopts a standing posture.





Plate 8. — Social behaviour of adult Houbara bustards. Figs : 60 : Aggressive chasing, 61, 62, 63, 64 : Threatening.

Threatening (Plate 8; Figs 61, 62, 63 & 64) was also shown by both males and females and was directed to members of the same and opposite sexes. On some occasions two animals were seen to threaten each other simultaneously. The postures adopted during threatening appear to be the same as those shown in the crouching display described by Collins (1984) and the collective display described

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by Ponomareva (1983). Threatening was seen when individuals were surprised by the sudden arrival of a conspecific and when males were displaying. In respect of this last situation, on one occasion a female which was being displayed to threatened the displaying male, and on three occasions a displaying male was threatened by other males which were in close proximity.

As shown in the figures (Plate 8; Figs 61, 62, 63 & 64), the postures shown during threatening principally involve lowering and spreading of the wings, fanning of the tail, ruffling of the plumage and forward projection of the neck. Once having adopted a threat posture the individual jumps towards the animal or animals being threatened. Bouts of threatening are usually terminated by the animal which is threatening pirouetting or by the flight of one or more of the protagonists. Physical contact between individuals was never observed after threatening behaviour.

6. Reproductive behaviour

The most spectacular aspect of the behaviour of the Houbara bustard is, without doubt, the male courtship display. The courtship display of *C. undulata undulata* has been described in both wild and captive birds, that of *C. undulata macqueenii* has been described by Mendelssohn *et al.* (1979) and Ponomareva (1983) and that of *C. undulata fuertaventurae* by Collins (1984). During the course of our own observations we have seen male display in *C. undulata macqueenii* in both captive and semi-captive males. On two occasions elements of male display behaviour were also seen in two captive females.

The start of courtship behaviour is characterised by the male partially erecting the white feathers which cover the sides of the neck (Plate 9; Figs 65 & 66) and fully erecting the feathers of the crest. In C. undulata macqueenii the erect crest feathers fall over the beak. The duration of this phase of the display is variable and, according to Ponomareva (1983), may last for as long as one minute. Displays are frequently terminated at the end of this phase; the feathers of the crest and neck being gradually returned to the relaxed position. If the display is continued, the white neck feathers are further erected and reach the level of the beak. The neck is then drawn back and up in a fashion such that the head rests on the back between the wings. This last movement results in the feathers of the neck being drawn up above the level of the beak with their tips falling backwards over the head. The body is held in the horizontal plane and the folded wings drawn upwards such that their upper edges are above the level of the back. The animal then begins to make exaggerated high stepping movements, at first on the spot and then in one direction or another at an ever increasing speed. We have called this phase of the display display running (Plate 9; Fig. 67). Bouts of display running are of variable duration (9 s to 1 min 24 s in our observations) and are interspersed with periods of inactivity (4 s to 26 s) during which the bird assumes its original posture. The distance covered during display running may be as great as several hundred meters; the direction of running being erratic with frequent back tracking. Display running is terminated abruptly; the bird stops moving, orientates its body down and forwards, extends its neck and simultaneously claps its bill and raises its head (Plate 9; Figs 68 and 69). The bill clapping and head raising movements may be repeated two or three times in succession. The bird then re-adopts its original posture (sometimes waiting for more than a minute before relaxing the feathers of the crest and neck) or recommences display



Plate 9. — Reproductive behaviour of adult Houbara bustards. Figs : 65, 66 : Starting phase, 67 : Running phase, 68, 69 : Final phase, 70, 71 : Final approach.

running. During the course of our observations of semi-captive birds we noted that individual animals tended to display in different areas, that displays sometimes occurred in the apparent absence of any other bird, that displays occurred when males and females or only females were present and that displays were sometimes directed at particular females. In the latter case, the male usually followed the female over several tens of meters.

If a female is receptive to a male, display running is followed by *final* approach and mounting behaviour. A description of the mating behaviour of the Houbara bustard was made by Collins (1984) for *C. undulata fuertaventurae*. If at the end of a display run, a female has remained within a distance of 2 to 3 meters of the male, the male extends his neck and advances towards the female whilst clapping his beak and waving his head and upper body from side to side (Plate 9; Figs 70 & 71). If the female moves away, the male may recommence display running. If the female crouches, the male continues to approach and straddles over the female whilst continuing to clap his beak. Once positioned over the female, the male begins to peck at the back of her head and the base of her beak. Copulation occurs very quickly (within 9 s according to Collins, 1984) and the female moves away from the male immediately afterwards. After copulation the male progressively returns its plumage to the normal relaxed posture.

7. Incubation and parental care behaviour

Incubation is performed, exclusively by the female, over a period of approximately 23 days. The nest is a simple scrape in the ground and is usually located in the open. The two postures most frequently adopted by incubating females are shown in Figs 72 & 73 of Plate 10.

Parental care behaviour (Plate 10; Figs 74 & 75). During the two weeks following hatching the chicks are fed almost exclusively on insects (in particular Tenebrionidae). The mother feeds the chicks by presenting them with insects in the manner shown in Figs 74 & 75 of Plate 10. The female presents the insects at the height of the chicks beaks and at the same time gives a muted call. This call, which resembles a low intensity grunt, appears to attract the chicks to the females beak.

8. Miscellaneous behaviour patterns

This category of behaviour patterns artificially groups together an number of behaviour patterns such as *defecation* (Plate 11; Fig. 83) and *settling down* (Plate 11; Fig. 82) — which require little description or explanation, a *predator defence posture* (Plate 11; Fig. 84) and two behaviour patterns with possible but unconfirmed social functions.

The predator defence posture was seen on several occasions when the birds were overflown by low flying Brown necked ravens (*Corvus ruficolis*). This posture differs from a threat posture in that the neck is extended upwards and the extended wings are held parallel to the body.

The two behaviour patterns observed with possible social functions were *tail-lifting* (Plate 11; Figs 76, 77 & 78) and *head-jerking* (Plate 11; Figs 79, 80 & 81). Tail lifting, which was performed by both standing and sitting birds, consists of rhythmic lifting and fanning of the tail feathers up to an angle of 90° with the



Plate 10. — Incubation and parental care behaviour of adult Houbara bustards. Figs : 72 : Low head incubating, 73 : Incubating, 74, 75 : Parental care.

body. In head-jerking, which was only performed by standing birds, the bird extended its neck and moved its head back and forth over the upper back and breast in a jerky fashion.

DISCUSSION AND CONCLUSIONS

The behavioural repertoire presented here, although by no means exhaustive, can be used to compare certain of the behaviour patterns shown by Houbara

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Plate 11. — Miscellaneous behaviour patterns of adult Houbara bustards. Figs: 76, 77, 78: Tail lifting, 79, 80, 81: Head jerking, 82: Settling down, 83: Defecation, 84: Defence posture.

bustards with those already described for other species of the sub-order Otides. The resting behaviour patterns shown by the Houbara appear to be very similar to those of the Great Bustard (*Otis tarda*) described by Hellmich (1987). The threat postures of the Houbara are identical to those of *Tetrax tetrax* (Cramps and Simmons, 1983) and the Great Bustard (Hellmich, 1987). However, in this context it is pertinent to point out that the Houbara bustard appears to have far fewer threat displays than the Great Bustard (see Hellmich, 1987). This difference may be indicative of the Houbara having a less hierarchical social structure than the Great Bustard.

The descriptions of male display behaviour given here are only in partial agreement with those given by Géroudet (1974) for C. undulata undulata, by Collins (1984) for C. undulata fuertaventurae, and by Mendelssohn et al. (1979) and Ponomareva (1983) for C. undulata macqueenii. Our observations at the N.W.R.C., where it is possible to observe both C. undulata undulata and C. undulata macqueenii, lead us to believe that many aspects of male display behaviour are different in these two subspecies. Ponomareva (1983) states that macqueenii males display at particular sites (arenas). In our experience this is true for C. undulata undulata but not for C. undulata macqueenii. The differences between the descriptions of aspects of male display behaviour given here and those given elsewhere in the literature can be explained in at least two ways. Firstly, most existing studies of Houbara bustards have been carried out on unmarked birds; this makes localisation of the exact display sites of particular males difficult. Secondly, it is possible that the displays of male macqueeni Bustards have multiple functions. During our observations we saw males display in proximity to other males and/or females without interacting with or displaying to the other birds, males direct their displays to other males as well as females and, on one occasion, two males displayed simultaneously at the same site with an inter bird distance of less than 10 meters. These observations are more consistent with male display behaviour having both territorial and sexual functions, than with it being a simple manifestation of lek behaviour.

In conclusion much remains to be learnt about the behavioural ecology and reproductive behaviour of *C. undulata macqueenii*. Further studies of this species are urgently required if captive breeding populations are to be successful and wild populations to be maintained. Such investigations will also be of value in comparative studies of reproductive biology within the sub-order Otides.

SUMMARY

The Houbara Bustard (Chlamydotis undulata) is declining throughout its range. Captive breeding programmes, which are essential to the conservation of this species, require detailed knowledge of the behaviour of the birds. At the present time this knowledge is largely lacking. This paper describes the behavioural repertoire of adult Houbara bustards of the subspecies macqueenii (C. undulata macquenii). A total of eighty behaviour patterns are described and illustrated. These behaviour patterns are divided into eight groups; incubation and parental care, resting behaviour, comfort behaviour, feeding behaviour, locomotion, sexual behaviour, social behaviour and miscellaneous behaviour patterns. Particular attention is paid to the display behaviour of males. It is suggested that the display behaviour of males of the sub-species macqueenii differs from that of the other two subspecies (C. undulata undulata and C. undulata fuertaventurae).

RÉSUMÉ

Le déclin de l'Outarde Houbara sur l'ensemble de son aire de distribution nécessite la mise en place de programmes de sauvegarde de cette espèce. Ceci a rendu indispensable l'étude détaillée du comportement de cet oiseau, jusqu'alors pratiquement inconnu. Nous présentons ici un éthogramme des adultes de la sous-espèce *macqueenii (C. undulata macqueenii)*. Quatre vingt comportements sont représentés et décrits. Ces comportements ont été regroupés en huit catégories : Comportements de repos, de confort, locomoteur, d'alimentation, sociaux, sexuels, d'incubation et de soins aux jeunes, ainsi que quelques comportements à finalité non évidente.

Une attention particulière est prêtée aux parades sexuelles des mâles, dont l'aspect et le déroulement semble indiquer une différence vis à vis de celles des mâles des deux autres sous-espèces (C. undulata undulata and C. undulata fuertaventurae).

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