Seasonal Variation of LH, Sex Steroids, Body Mass, Molt, Display, and Laying in Two Subspecies of Houbara Bustard, Chlamydotis undulata macqueenii and Chlamydotis undulata undulata, Housed in Outdoor Cages under Natural Conditions

M. Saint Jalme,* J. Williams,† I. Mickaelian,* and P. Paillat*

*National Wildlife Research Center (National Commission for Wildlife Conservation and Developments), Taif, Saudi Arabia; and †INRA, Station de Recherches Avicoles, Centre de Recherches de Tours-Nouzilly, 37380 Nouzilly, France

Accepted November 22, 1995

Subspecies of the Houbara bustard are resident in North Africa (Chlamydotis undulata undulata) or are partial latitudinal migrants in Asia (Chlamydotis undulata macqueenii). Houbara breed in arid or semiarid zones, and the reproductive biology of wild Houbara is largely unknown. Body mass, molt, courtship display, laying, and plasma concentrations of LH, testosterone, and progesterone were measured in captive-bred birds of both subspecies, housed in outdoor cages under natural conditions, over a period of 1 year and 6 months, at Taif, Saudi Arabia (21° 15′ N). Captive Houbara bustards show a seasonal breeding pattern with a laying period from January to July. Males began displaying well in advance of any eggs laid and display long after the termination of laying. In females, gonadal activity and molt are largely exclusive; however, in males, slight overlap between sexual display and molt was observed. In females, seasonal variation of LH and progesterone was synchronous with laying activity. In males both testosterone and LH plasma concentrations were highest in January (testosterone ≈ 8 ng/ml; LH ≈ 3 ng/ml) at the beginning of the display period. This could correspond, in the wild, to the establishment of territories. Levels dropped significantly before the females started laying but stayed at an intermediate level throughout the breeding season (testosterone ≈ 3 ng/ml; LH ≈ 1.5 ng/ml). In the middle of August, during molt, and following heavy rainfall, LH and testosterone peaked (testosterone ≈ 2.3 ng/ml; LH ≈ 1.8 ng/ml), suggesting a possible impact of rainfall on Houbara gonadal activity. Houbara stopped laying before the maximum ambient temperature reached 32°C, indicating that high temperature could be a factor terminating laying activity. No major differences were found between the two subspecies in the timing or duration of the reproductive period; only the annual variation of the body mass varied slightly between the subspecies.

Populations of Houbara bustard (Chlamydotis undulata) have declined over their entire distribution, leading the IUCN to classify the species as vulnerable (IUCN, 1990). The nominate subspecies (Chlamydotis undulata undulata) is nonmigratory and inhabits the North African range. Chlamydotis undulata fuertaventurae lives only on the Canary Islands. Chlamydotis undulata macqueenii is a partial latitudinal migrant and occurs from the Sinai to western Mongolia (Cramp and Simmons, 1980). Concern over the threat of extinction of local populations was an important factor leading to...
The establishment of a captive breeding program in Taif (Saudi Arabia), with the aim of restoring wild populations. *Chlamydotis undulata undulata* and *C. undulata macqueenii* are captive-bred at Taif.

The Houbara bustard is adapted to desert environments with between 50 and 200 mm of annual rainfall, falling mainly in the winter (Mendelssohn et al., 1979; Coles and Collar, 1980; Mendelssohn, 1980; Haddane, 1985; Mian and Dasti, 1985). The mating system has been variously described as monogamous (Dementiev and Gladkov, 1968), polygamous, and promiscuous (Collins, 1984). The clutch is incubated by the female alone. The reproductive biology of wild Houbara is still largely unknown. Sexual maturity is thought to be reached after 2 years (Mendelssohn, 1983). In captivity, exceptionally, Houbara lay at 1 year old, around 25% lay at 2 years old, 65% at 3 years, and 85% at 4 years (Saint Jalme et al., 1994). *Chlamydotis undulata macqueenii* lays a single clutch of one to four eggs on alternate days, and *C. undulata undulata* lays a clutch of one to three eggs (Heim De Balzac and Mayaud, 1962; Etchecopar and Hue, 1978; Mendelssohn, 1980; Urban et al., 1986). A replacement clutch may be laid if the first is lost (Cramp and Simmons, 1980). Timing of nesting appears to vary across the breeding range, but is concentrated in the spring months, with laying occurring earlier in more southern and western localities (Dementiev and Gladkov, 1968; Mendelssohn, 1980; Lavee, 1988). In North Africa (*C. undulata undulata*), eggs are usually laid in March–April (Cramp and Simmons, 1980; P. Gaucher, personal communication), although according to Heim De Balzac and Mayaud (1962), egg laying can occur between January and June. In Israel (*C. undulata macqueenii*) eggs are found from the end of February into April (Mendelssohn, 1980), but males start to display in December (Lavee, 1988), and in the southern USSR from April to June (Dementiev and Gladkov, 1968).

Nothing is known about control of the timing of reproduction in the Houbara bustard. Some have suggested that rainfall is an important trigger for reproduction. According to Etchecopar and Hue (1978), breeding does not occur during dry years in Africa. In Israel most Houbara do not breed after winters with little or no rain (Mendelssohn, 1980). The aim of the present study is to further our understanding of the reproductive biology of the Houbara bustard. The annual reproductive cycle and changes in blood hormone levels in two sub-species of Houbara, over a complete year, are described. Changes in hormone titers are associated with laying and displaying activity, variation in body mass, molt, and weather conditions.

**MATERIALS AND METHODS**

**Localization of Study and Meteorological Data Collection**

The study was conducted between December 1991 and July 1993 at the National Wildlife Research Center (NWRC), Taif, Saudi Arabia (lat. 21°15’N, long. 40°41’E; altitude, 1450 m). The difference between shortest and longest day lengths at Taif is 2 hr and 40 min. A meteorological station installed at the NWRC provided records of air temperature and rainfall.

**Animals, Food, and Housing**

*Chlamydotis undulata macqueenii.* Twelve males and 12 females aged 4 years at the beginning of the study originated from eggs collected in 1987 in Baluchistan, around lat. 28°N.

*Chlamydotis undulata undulata.* Twelve males and 12 females aged 4 years at the beginning of the study originated from eggs collected in 1987 in Algeria, around lat. 33°N. Prior to the study (between August and December 1991), birds were housed in heterosexual groups (10 males and 10 females) in outdoor aviaries (30 × 10 m). On December 15, 1991, birds were transferred to individual outdoor cages (6 × 4 × 2.3 m). Each male was housed inside one cage and each female inside two communicating cages. A mesh panel at the back of one of the cages allowed each female to be in visual contact with one male. Food and water were provided *ad libitum* throughout the year. Birds chose between three qualities of poultry pellets with different protein levels (14, 28, and 35%), but the same energetic value. Fresh alfalfa growing in each cage was always available. Alfalfa plots measuring 4 × 1.7 m were watered by overhead sprinklers for 1 hr/day.

**Data Collection**

Females were checked twice a day, in the morning and in the evening, to collect the eggs and thus stimu-
late replacement clutches. Males exhibiting courtship displays were recorded daily. Blood (around 3 ml) was collected from unanesthetized birds twice a month, from a wing vein into an heparinized syringe. Samples were centrifuged within 2 hr of collection and plasma was frozen at −18°C. During blood sampling, body weights were measured and molts of primaries and secondaries were recorded.

Hormone Assay

Plasma LH was assayed in duplicate (50- or 100-μl samples) following Sharp et al. (1987), using fraction PRC-AE1-s-1 as labeled hormone and standard and antisemur LH 3-3. The mean intra assay coefficient of variation was 12.6% and the inter assay variation for the two assays needed for this study was 10.8%. Progesterone was assayed following solvent extraction of the 200-μl plasma aliquot (Duplaix et al., 1981). The mean intra assay coefficient of variation was 7.6% and the inter assay variation for the six assays needed for this study was 9.4%. Testosterone was assayed following solvent extraction of the 200-μl plasma aliquot (Driot et al., 1979). The mean intra assay coefficient of variation was 7.6% and the inter assay variation for the six assays needed for this study was 9.4%.

Statistics

For statistical analyses each week was classified from 1 (December 15–21, 1991) to 52 (second week of December 1992). To evaluate the statistical significance of seasonal variations of all parameters but one, calculations were done using Friedman’s nonparametric analysis of variance, followed by the Wilcoxon test to compare the values obtained for two sampling times. Comparisons between subspecies or sexes were made using the Mann–Whitney U test. As progesterone was assayed in only a few birds, at different times, statistical analysis was done using the Kruskal–Wallis ANOVA. Summary data are presented in the text as means ± SEM.

RESULTS

Laying

In 1992, 83% (10/12) of female C. undulata macqueenii and 67% (8/12) of C. undulata undulata laid. Laying began on January 20 with a macqueenii (Fig. 1) and the last egg was laid by an undulata on June 29. The length of the laying period was 5 months, and the laying peak occurred at the end of March. There was no significant difference between the start of laying between the two subspecies, but macqueenii females finished laying on average 4 weeks earlier than undulata (P < 0.02). The mean duration of laying activity was 7 ± 1.2 weeks in macqueenii and 10 ± 1.4 weeks in undulata, but there were large individual variations (range, 1–18). In 1993, females started to lay 2 weeks earlier than in 1992 (P = 0.001), and laying activity was synchronous between the two subspecies.

When eggs were collected every day and females were not permitted to incubate, Houbara laid clutches of one to four eggs in macqueenii and of one to three eggs in undulata. There was no significant difference in the mean clutch size (undulata, 1.8; macqueenii, 1.9). Within a clutch, eggs were laid on alternate days. The average interval between clutches was 10 days in 1992 and 9 days in 1993, with no difference between the subspecies. The mean number of clutches laid by individuals of the two subspecies was very similar (between 4 and 5), with a maximum of 13 clutches laid in 1993. Significant seasonal variations in the clutch size or in the interclutch interval were not seen. Nevertheless, the first two individual clutches showed a tendency to be larger. The mean number of eggs laid by individual birds was between 7 and 11, with no significant differences between subspecies or years. The maximum number of eggs laid by a single female in one reproductive season was 26 for macqueenii and 19 for undulata. Again, large individual variations were observed (range, 1–26).

Grouping females of the two subspecies that laid in 1992 and 1993 (N = 15) gave a positive correlation in the date of start of laying between the two years (R = 0.66, P = 0.008). Thus females followed the same order when starting to lay in 1992 and in 1993. A positive correlation was also found between the two years in the duration of the laying activity (R = 0.51, P = 0.05).

Display

During the 1991–1992 reproductive season, males exhibited courtship displays from December to July. Displays started on average 10 weeks before laying (Fig. 3). The first displays were observed 3 days after the
FIG. 1. Comparison between female *Chlamydotis undulata macqueenii* (solid lines and solid histograms) and *Chlamydotis undulata undulata* (dashed line and hatched histograms), housed in outdoor cages under natural conditions, in (a) occurrence of molt (histograms) and annual variation in body mass (solid line and dashed line), (b) changes in number of laying females (solid line and dashed line), and onset of laying (histograms), and (c) changes in circulating LH and (d) progesterone. (e) Mean weekly maximum ambient temperatures (line) and rainfall in millimeters per week (histograms).

transfer of the birds into the individual cages. Seventy-one percent of the males started to display before the first female started laying, but the peak of display activity was synchronous with the peak of laying (Fig. 3). There was a large individual variation in the length of the display period (15 ± 3 weeks; range, 1–31 weeks, between December and July). No significant difference was seen between *macqueenii* and *undulata*. During August 1992, the display activity restarted in seven males (two *macqueenii* and five *undulata*). This period of display lasted between 1 and 3 weeks. During the 1992–1993 reproductive season, first displays were observed on the first week of October and males started to display on average 5 weeks earlier than in 1991–1992. The male that displayed the most, stopped courtship behavior for only 11 weeks in summer.

**Body Mass**

Houbara body mass varied seasonally in the two subspecies in both sexes (*P* < 0.001) (Figs. 1–3). Body mass
FIG. 2. Comparison between male *Chlamydotis undulata macqueenii* (solid lines and solid histograms) and *Chlamydotis undulata undulata* (dashed line and hatched histograms), housed in outdoor cages under natural conditions in (a) occurrence of molt (histograms) and annual variation in body mass (solid line and dashed line), (b) changes in number of displaying males (solid line and dashed line), and onset of display (histograms), and (c) changes in circulating LH and (d) testosterone. (e) Mean weekly maximum ambient temperatures (line) and rainfall in millimeters per week (histograms).

was least during the molt and greatest during the breeding period. The average annual body mass variation was larger in *macqueenii* (21% of the minimum weight) than in *undulata* (17%; *P* < 0.01), with no differences between males and females.

**Females.** Body mass of *macqueenii* females began to increase significantly between the first two measurements (*P* < 0.005), in the second half of December 1991. Increase in body mass was significant until the middle of February (February 8–18; *P* = 0.05). In *undulata*, the average body mass began to increase significantly 2 weeks later (December 15–January 16; *P* < 0.05), and continued to increase until the beginning of March (February 8–March 9; *P* < 0.05). Individual body masses were maximal at the beginning of laying. In 1992 maximal masses were reached on average between the third week of February and the first week of March, with no significant differences between the two subspecies.

For the females of the two subspecies, body mass
started to decrease significantly between March 9 and March 29 (macqueenii: $P < 0.005$; undulata: $P < 0.05$), and continued to decrease until the middle of April (macqueenii: $P < 0.01$; undulata: $P < 0.05$). Minimal masses were recorded, on average, in the middle of May ($22 \pm 2$) at the beginning of the molt in macqueenii and 2 months later (in the middle of July) in undulata ($31 \pm 3$), in the middle of the molt ($P < 0.03$). Nevertheless, a significant decrease in body mass was observed in both subspecies between June and July, when all females stopped laying. Body mass of macqueenii females began to increase significantly between the end of July and the middle of September ($P < 0.05$). Increased body mass was significant only between October and November in undulata. From November 1992 to June 1993, body mass variation was synchronous in the two subspecies; maxima were reached on average in the third week of February.

**Males.** Seasonal variation in male body mass was synchronous for the two subspecies during the first 6 months (Fig. 2). Body mass increased abruptly during the second fortnight of December ($P < 0.005$). Males

**FIG. 3.** Comparison between male (dashed line and hatched histograms) and female (solid lines and solid histograms) Chlamydotis undulata, housed in outdoor cages under natural conditions, in (a) annual variation in body mass, (b) occurrence of molt, (c) changes in number of laying females (solid line) and in number of displaying males (dashed line), and onset of laying (solid histograms) and onset of displays (hatched histograms), and (d) changes in circulating LH. (e) Mean weekly maximum ambient temperatures (line) and rainfall in millimeters per week (histograms).
reached their maximum body mass on average at the end of January, about 1 month before the females ($P < 0.001$). Body mass decreased significantly in *macqueenii* during the first fortnight of February ($P < 0.01$). It then stabilized for 1 month corresponding to the period of maximum display and the laying peak. Body mass began to fall again between the middle of March and the middle of April ($P < 0.05$, for the two subspecies), synchronously with the females. Even though males stopped displaying several weeks after the females stopped laying, minimal body masses for males and females were recorded in the middle of May for *macqueenii* and the end of July for *undulata* ($P < 0.01$). In *macqueenii*, the first significant increase in body weight was recorded between May and June ($P < 0.05$). Body mass then stabilized and another significant increase was recorded only between September and October ($P < 0.005$), at the same time as in *undulata* ($P < 0.01$). In 1992–1993, body mass was at a maximum on average 7 weeks earlier than in 1991–1992, at the beginning of December in *macqueenii*, and 2 weeks later in *undulata* ($P < 0.05$); more than 2 months before the females ($P < 0.001$). Maximum body mass was synchronous with the start of display for both years.

**Molt**

Molt started on average 2 weeks after the females stopped laying. There was a correlation ($n = 18$, $R = 0.64$, $P < 0.005$) between the last week of laying and the first week of molt. Molt began in the first week of May (20 ± 0.6) for *macqueenii* and lasted until the second week of September (40 ± 1.4). Molt began 4 weeks later in *undulata* (24 ± 1.2; $P < 0.03$) and also lasted for 4 weeks (44 ± 1.2; not significant). The mean duration of the molt was the same in the two subspecies, at around 20 weeks.

In males, there was no significant difference in the timing and duration of the molt between the two subspecies. Males began molting at the end of April and finished their molt in the middle of September. The mean duration of the molt was 22 weeks. No relationship between molting and displaying was apparent. Males continued displaying long after they started molting. In *macqueenii*, timing and duration of the molt were the same in males and females.

In both sexes, the molt started alongside a greatly reduced body mass. In *undulata*, body mass remained low until the end of the molt, whereas in *macqueenii*, body mass gradually increased from the beginning of the molt.

**Hormones**

**Luteinizing hormone.** In both sexes and both subspecies there was an annual pattern of LH titers with maximum levels in winter and spring, and nadirs during summer and autumn (females: $P < 0.001$; male *macqueenii*: $P < 0.01$; male *undulata*: $P < 0.001$) (Figs. 1–3). One small peak of LH was also recorded in the middle of August for both sexes in the two subspecies. The pattern of the winter–spring variation appeared to be bimodal. A significant increase in LH was recorded on December 31 in males (*macqueenii*: $P < 0.01$; *undulata*: $P < 0.05$), 15 days before the females (January 16, $P < 0.05$). A decrease in LH titers then occurred between February 2 and February 18 (*macqueenii* males and females: $P < 0.05$; *undulata* males: $P < 0.05$). The following increase, between the middle of February and the beginning of March, was significant only in females (*macqueenii*: $P < 0.005$; *undulata*: $P < 0.01$). The amplitude of the first peak was greater than that of the second peak for males ($P < 0.05$) but smaller for females ($P < 0.05$). Decreased LH titers occurred significantly between the first and third weeks of May in *undulata* males, and in *macqueenii* females ($P < 0.05$). The decrease was significant only in the middle of June in *macqueenii* males and in *undulata* females. A significantly increased LH was recorded between the middle of July and the middle of August (*undulata* females and males: $P < 0.005$; *macqueenii* females: $P < 0.005$; *macqueenii* males: $P < 0.05$). This was followed by a decrease of similar amplitude between August and September (*undulata* females: $P < 0.01$; *undulata* males: $P < 0.05$; *macqueenii* males: $P < 0.05$). This summer peak of LH was recorded less than 1 week after significant rainfall between August 11 and 15 (66 mm). During winter 1992, the first significant increase in LH was recorded in *macqueenii* males between November 15 and December 13 ($P < 0.05$), while day length was still decreasing. The increased LH was significant at the end of December in *undulata* males and females ($P < 0.05$) and only at the end of January in *macqueenii* females ($P < 0.05$). Average maximum levels of LH were higher in females than in males, whereas the minima were higher in males than in females. Differences were sig-
nificant only for the minima between *macqueenii* males and females (*P* < 0.05). Significant positive correlations were found between the mean plasma LH concentration and the percentage of laying females (Spearman rank correlation test: *macqueenii*, *r* = 0.76, *P* < 0.01; *undulata*, *r* = 0.8, *P* < 0.01).

Testosterone. Plasma levels of testosterone seasonally varied (*P* < 0.001 in both subspecies). Testosterone varied in males of the two subspecies in the same way as LH levels. Testosterone titers began to increase between December 15 and 31 for both subspecies (*P* < 0.05); maxima were reached in January. As with LH, a significant decrease was recorded at the beginning of February (*P* < 0.05). Testosterone stayed at a relatively high level during March and decreased again between April 14 and May 5 (*P* < 0.05). A peak occurred in the middle of August (*P* < 0.05), and then significantly increased from the middle of November to the middle of December (*P* < 0.05). Significant positive correlations were found between the mean plasma testosterone concentration and the percentage of displaying males (Spearman rank correlation test: *macqueenii*, *r* = 0.68, *P* < 0.01; *undulata*, *r* = 0.65, *P* < 0.01).

Progesterone. As for the other parameters, progesterone showed seasonal variations (*P* < 0.05, for both subspecies). Levels were elevated during the laying period and lower during the remainder of the year. There were no measurements in August. The level of progesterone reached the minimum at the end of May for both subspecies.

**DISCUSSION**

Captive Houbara bustards show a seasonal breeding pattern with a laying period extending from February to June, with some clutches laid as early as January and as late as July. Differences in the timing of laying between the two subspecies were observed only in 1992. In 1993 laying by the two subspecies was synchronous. The differences observed in 1992 are considered to reflect individual variation. In Baluchistan laying occurred in March–April with a maximum of 15 days’ variation between the years (P. Paillat, personal communication). The laying peak was recorded during the first fortnight of April. The same laying dates were recorded in Algeria in 1986 and 1987 (P. Gaucher, personal communication). Females started to molt 2 weeks after the end of laying. As *undulata*, in 1992, finished laying later than *macqueenii*, this could explain the shift in the start of molt. Laying never occurred between July and December, the molting period. In contrast, males continued displaying far after the beginning of the molt. In the majority of bird species, gonadal activity and molt are separate events in the annual cycle, and are ergonically incompatible (Farner and Wingfield, 1980). Overlap between molt and gonadal activity could be an adaptation of irregular opportunistic breeders (Serventy, 1971). In Houbara, there is an overlap between molt and sexual display in males. In females, however, gonadal activity and molt were mutually exclusive.

The spring plasma concentrations of LH, testosterone, and progesterone showed changes similar to those of other species. In females, variation of LH and progesterone was synchronous with laying activity, and high titers of these two hormones were synchronous with the laying peak. As in other species of birds, the onset of ovarian development should be associated with an increase in the concentration of plasma LH. The concentration of plasma progesterone is known to increase when the largest ovarian follicle is fully developed and hence the baseline concentration of plasma progesterone could be an indicator of the presence of a mature ovarian follicle (Sharp, 1980). In *macqueenii*, minimum LH concentrations were higher in males than in females. The same differences have been observed in domestic hens, quail, and red grouse. This difference is believed to arise because the estrogens secreted by the ovary exert a greater negative feedback action on LH release than do androgens secreted by the testes (Sharp, 1980).

In males, the spring peak of LH and testosterone seems to be bimodal. Both testosterone and LH plasma concentrations were highest in January at the beginning of the display period, during the pre-egg phase, when body masses were also maximal. Levels dropped significantly before the females started laying but stayed at an intermediate level throughout the laying period. In three species of birds in the Sonoran desert (*Toxostoma curvivestre*, *Campylorhynchus brunneicapillus*, and *Amphispiza bilineata*) that exhibited a prolonged breeding season (over 6 months), the highest concentrations of LH and testosterone in males are associated with the early part of the annual breeding cycle. Maximum
testosterone concentrations decrease after the begin-
ning of the season even though the gonads remain ac-
tive and multiple nesting is common (Vleck, 1993). This
pattern of testosterone secretion is associated primarily
with male–male interaction and with heightened levels of
aggression (Wingfield et al., 1990). In many bird spe-
cies the onset of the courtship display coincides with the
period of fastest maturation of the testis (Balthazart,
1983). Testosterone regulates the expression of repro-
ductive behaviors, both sexual and aggressive (Wing-
field et al., 1990). In a theoretical approach, Wingfield
et al. (1990) explained the diversity of temporal patterns
of testosterone secretion in male birds as a function of
the degree of male–male aggression and paternal
behavior. A nonbreeding baseline testosterone level in-
creases to a breeding season baseline stimulated by en-
vironmental cues. These levels are sufficient for sper-
matogenesis and the expression of reproductive behav-
iors. However, the testosterone level may increase
above baseline to the maximum level achieved under
physiological conditions. As male–male aggression de-
creases and parental care increases, the period of high
circulating level of testosterone should become shorter
and the amplitude of the increase less. Males of poly-
gyne species may have higher levels of testosterone
for longer periods during the breeding season than do
males of monogamous species. This is the case in Tetrao
urogallus with an exploded lek system (Wingfield et al.,
1990) or in the European quail (Saint Jalme et al., 1986)
with a mating system of successive monogamy.

Following the model of Wingfield, the seasonal pat-
tern of testosterone recorded in captive Houbara could
indicate a territorially monogamous species with patern-
al investment, whereas the evidence suggests that the
mating system of the Houbara is polygynous, or promis-
cuous, with no participation of the male in incubation
or rearing of the chicks. The male courtship display of
the Houbara is spectacular and classified as a running
display (Mendelssohn et al., 1979; Ponomavera, 1983;
Collins, 1984; Launay and Paillat, 1990; Gaucher et al.,
1996). It is possible that the displays of male have both
territorial and sexual function (Launay and Paillat,
1990). In Uzbekistan in spring (F. Launay, personal
communication), males established territories at the be-
coming of March, soon after their arrival on the breed-
ing ground. During this time aggressive behavior be-
tween males was common, and became rarer despite the
fact that males displayed on their territories
throughout the breeding period. The first peak of tes-
tosterone in male Houbara could correspond to the es-
tablishment of territories, which was observed in wild
populations. The medium level of testosterone recorded
over the remainder of the breeding season is sufficient
to maintain courtship behavior and spermatogenesis
(Saint Jalme et al., 1994). The decreased body mass dur-
ing the breeding season could be explained by the en-
ergic cost of displaying. Males displayed for several
hours each day. It is possible that high plasma levels of
testosterone and the resulting increase in activity
associated with displays are energetically expensive.

In the middle of August, in both sexes LH exhibited
a small but significant peak. This increase was synchro-

nous with a temporary restart in displaying activity
for 30% of the males. The summer peak of LH was
accompanied by a corresponding increase in gonadal
steroids at least in males (not measured in females),
suggesting that gonads were responsive to gonadotro-
phin stimulation. After the postnuptial molt, several
species (Pekins, Rouen duck, wild mallards, lesser snow
goose, willow ptarmigan, herring gull, white stork, and
house sparrow) were shown by August/September to
display a transient resumption of LH and testosterone
and the amplitude of the increase less. Males of poly-
gyne species may have higher levels of testosterone
secretion, generally together with a partial recovery of
sexual behavior (Jallageas and Assenmacher, 1979;
Hegner and Wingfield, 1986; Hall et al., 1987). It has
been suggested that the physiological basis of gonadal
recrudescence in the autumn is a recovery of photosen-
sitivity at a time when day length is still long enough
to stimulate gonadal development (Hegner and Wing-
field, 1986). This recrudescence of gonadal activity dur-
ing summer in Houbara followed heavy rainfall that
occurred less than 1 week before the blood was sam-
ped. In contrast to the above-cited species, this gonadal
recrudescence occurred during the molt period, sug-
gesting that rainfall could have triggered these hor-
monal peaks as for birds of the Sonoran desert, which
begin breeding in the late winter and which could have
a short period of nesting in summer following rains
(Vleck, 1993). Nevertheless, the hormonal increase was
not followed by laying activity. In Australian desert
species, unseasonal midsummer rains will induce
breeding only when breeding during the previous
spring was inhibited by drought (Keast, 1968). Mea-
surements of LH and testosterone during a second an-
nual cycle with no rainfall during summer will be nec-
essary to verify this hypothesis.
Given that the sheer complexity of environmental information makes it difficult to separate the effects of one environmental cue from another, information collected on the subject during annual cycles is limited. The breeding range of Houbara is characterized by semidesert habitat, in which the occurrence of rain is seasonally predictable. Throughout the Houbara breeding range, the optimal conditions for reproduction appear to occur in winter and spring (Serventy, 1971; Grenot, 1974; Mendelssohn et al., 1979; Haddane, 1985; Mian and Dasti, 1985; Yom-Tov and Tchernov, 1988). The proximate factor synchronizing gonadal development in Houbara could therefore have evolved independently of rains. The latitude of the breeding range (25–40° N) is not incompatible with a photoinduction of gonadal development. Such a photoperiodic response has been described in many species of tropical and equatorial birds (Gwinner and Dittami, 1985; Tewary and Dixit, 1986). Nevertheless, our evidence for the possible action of photoperiod as a synchronizer of Houbara reproductive activity is limited. Although the data presented in this article do not support any hypothesis about the impact of temperature on the reproductive cycle of Houbara, 6 years of observation on captive Houbara suggest that in captive Houbara high temperature could be the major factor terminating laying activity. Detrimental effects of high temperature on gonadal activity have been demonstrated in many species (for review see Ricklefs and Hainesworth, 1968; Wingfield, 1980; Simons and Martin, 1990).

The fact that no major difference was observed between the two subspecies, macqueenii and undulata, is not surprising. Even if the African subspecies is considered to be sedentary or nomadic, and the Asian subspecies more as a migrant or partial migrant, birds of the two subspecies originated from populations breeding at the same latitude. Populations of macqueenii breeding in Baluchistan, the southern part of the species range, are probably sedentary, sympatric with migrant populations in winter.

ACKNOWLEDGMENTS

The authors thank the National Commission for Wildlife Conservation and Development of Saudi Arabia and its Managing Director, HRH Prince Saud Al Faisal and Secretary General Prof. A. Abuzinada, for their support and confidence throughout the project. Special thanks goes to Jacques Renaud General Manager of N.W.R.C. The authors also thank Abdul Rahman Khoja for smoothing the administrative path.

REFERENCES


Copyright © 1986 by Academic Press, Inc. All rights of reproduction in any form reserved.


