THE INFLUENCE OF PHOTOPERIOD ON MALE COURTSHIP
AND NEST-BUILDING IN THE RING DOVE,

STREPTOPELIA RISORIA

by

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MASTER OF SCIENCE
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We accept this thesis as conforming to the
required standard

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Date \(25/10/76\)
The aim of this study was to examine the influence of photoperiod on the hormonal induction of courtship and nest-building behaviour in the male ring dove (*Streptopelia risoria*). In the first experiment 24 intact males were divided into two groups and held on long (16L:8D) or short (8L:16D) photoregimes for five weeks. They were then paired with intact females and their behaviour recorded. Long day males exhibited significantly higher levels of bowing and nest-soliciting.

In the second experiment males were again held on long or short photoperiods. Half of each group received daily injections of testosterone propionate. Testosterone treatment eliminated differences in courtship between the two groups, but nest-building remained significantly higher in hormone-treated long day birds. The experiment was then repeated using TP-treated castrates. In this case courtship did not vary between long and short groups, although nest-building was still greater under the long photoregime.

These results indicate that photoperiod alters male courtship by stimulating endogenous androgen production. The influence on nest-building, however, appears to be least partially dependent upon some other mechanism.
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A. GENERAL INTRODUCTION AND BACKGROUND

In birds, as in other vertebrates, the endocrine system controls both physiological and behavioural changes occurring within the reproductive cycle. Gonadectomy has been shown to result in the virtual loss of reproductive activity in male and female birds of numerous species, including ducks (Collias, 1962), Japanese quail (Brody, 1969), feral pigeons (Columbia livia) (Erpino, 1969) and chickens (Young, 1961); while replacement therapy using homologous hormones (androgens in males, estrogens in females) reinstates the lost behaviour patterns (see van Tienhoven, 1968, for a review).

Extensive studies have been conducted concerning the hormonal control of reproduction in ring doves. Castration abolishes courtship in both males (Erickson & Lehrman, 1964) and females (Cheng, 1973). Pigeon testes, and presumably those of doves as well, contain androgens, estrogens, and progesterone (Hohne et al., 1967) and it is therefore possible that male courtship is controlled by any of these three steroids.

Investigations using castrates have shown that intramuscular injections and intracranial implants of testosterone propionate will restore courtship and nest-building, and that estradiol benzoate reinstates nest-oriented behaviours but not the more aggressive displays (see Table I). Progesterone alone will not induce any sexual behaviours, although it does stimulate incubation (Komisaruk, 1966). When given in
TABLE I The effects of intramuscular injections (im) and intracranial implants (ic) of estradiol benzoate (EB), progesterone (Prog), and testosterone propionate (TP) on courtship in castrated male doves. (CH, chasing; BC, bow-cooing; NS, nest-soliciting; NB, nest-building; ↓, suppression of androgen-induced behaviour; +, induction of the behaviour in castrates; −, failure of the hormone to induce the behaviour in castrates; plasma E, Prog T, plasma levels observed in intact doves)

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<td>plasma E</td>
<td>not detectable (&lt;25 pg/ml)</td>
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<td>plasma Prog</td>
<td>constant at 1.27 mg/ml</td>
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* castrates with ic TP implants
** intact males
conjunction with testosterone, either endogenous or exogenous, progesterone appears to antagonize the androgen, suppressing aggressive courtship (bow-cooing) (Komisaruk, 1966; Erickson et al., 1967).

Since estrogen has not been detected in the plasma of male doves by radioimmunoassay (Korenbrot et al., 1974) it appears that testosterone is primarily responsible for the control of male courtship and nesting activity. This is supported by the observations that testosterone is present in the plasma in increasing concentrations as the cycle progresses (Hutchinson & Katongole, 1975) and is accumulated in the cell nuclei of the hypothalamus and pituitary in castrates (Zigmond et al., 1972; Stern, 1972).

The hormonal induction of behaviour is not an isolated process, but an integral step in the integration of external stimuli and behaviour. The effects of various factors on sexual activity are mediated by the endocrine system, either through changes in hormone production or changes in the influence of hormones on behaviour.

A major factor which is known to alter hormonal activity is photoperiod, which has been shown to control reproduction in numerous bird species (see reviews by Farner, 1970a & 1970b; Immelmann, 1971; Lofts & Murton, 1968; Wolfson, 1970). Long daylengths appear to stimulate development of the reproductive system by means of the pituitary-gonad axis. A change from short to long daylengths causes an increase in gonadal growth and a rise in plasma FSH, LH and testosterone levels in both immature (Follett, 1975) and mature (Follett, 1976) quail, and an initial increase in plasma LH and testis size in canaries (Nicholls, 1974).
Synthesis and release of gonadotropins in quail (Follett & Farner, 1966) and FSH levels in turkeys (Godden et al., 1975) are greater on long days than short.

These shifts in pituitary function seem to be controlled by the hypothalamus. Variations in the hypothalamic neurosecretory system have been observed in several bird species in response to changes in photoperiod (see Kobayshi & Wada, 1973; and van Tienhoven, 1968, for reviews) and lesions of the median eminence have been shown to abolish the photoperiodic response of the testes in ducks and white-crowned sparrows (van Tienhoven, 1968; Farner & Follett, 1966; Stetson, 1969).

Light-induced changes in testicular weight appear to be related to variations in testosterone secretion. In tree sparrows (Passer montanus) and green-winged teals (Anas crecca), for example, cycles of testis weight occurring under natural daylengths are paralleled by fluctuations in both total testosterone production and production per average testis weight (Lofts, 1975). It thus seems logical to assume that long photoperiods cause an increase in gonadotropin synthesis and release—possibly as a result of changes at the hypothalamic level—and that these in turn result in increased testis size and steroid production.

Since male courtship has been shown to depend upon the presence of gonadal hormones, photoperiodic effects on the hormonal control of male behaviour may be limited to changes in androgen levels as a result of stimulation of the hypothalamo-hypophyseal-gonad axis. This appears to be the case in the Japanese quail. In both males and females held on short days (8L:16D) sexual behaviour drops to the level
of long day (16L:8D) gonadectomized birds (Adkins, 1973; Adkins & Nock, 1976). Androgen treatment of either SD males or castrates causes an increase in sexual activity (Beach & Inman, 1965; Sachs, 1969) as does estrogen treatment of SD or ovariectomized LD females (Adkins & Adler, 1972; Adkins & Nock, 1976). Because the gonads seem to be nonfunctional in quail held on short days, and because no differences in behaviour were observed between SD and gonadectomized LD birds in response to hormone treatment, it has been concluded that in quail photoperiod functions solely via altered steroid concentrations (Sachs, 1969; Adkins & Nock, 1976).

Evidence does exist, however, indicating that in some species the effect of photoperiod cannot be entirely explained by changes in steroid levels. For example, castrated male sticklebacks which have been treated with methyl-testosterone are more likely to engage in nest-building activities if they have been held on long (16L:8D) rather than short (8L:16D) daylengths (Hoar, 1962).

In female domestic canaries, nest-building activity is greatly reduced by ovariectomy (Steel & Hinde, 1972). Estradiol injections will increase gathering in ovariectomized females exposed to long daylengths but have little effect under short photoperiods (Steel & Hinde, 1972; Hinde et al., 1974). Since gonadotropins are not directly involved (Hinde & Steel, 1975) it appears that photoperiod may be altering responsiveness to the exogenous estrogen.

Liley has found evidence of a similar effect in ring doves. Females held under long days (16L:8D) lay eggs in response to male courtship sooner
than females held under short days (8L:16D). In addition, LD birds engage in more nest-soliciting and nest-building (Liley, 1976). Treatment with estrogen and/or progesterone indicates that these behavioural differences persist even in the presence of high levels of exogenous hormone (Liley, in press). The birds used in this study were intact, however, and the endogenous hormone contribution was both unknown and uncontrolled.

All three of these studies indicate that photoperiod in some way alters the effectiveness of exogenous hormone treatment. In the absence of information concerning plasma and hypothalmic hormone levels it is impossible to determine the point at which photoperiod is having its effect.

The purpose of the present study was to examine what Hinde and Steel (1975) refer to as the dual role of photoperiod, as it relates to the reproductive behaviour of male ring doves. In other words, an attempt has been made to discover the effect of daylength, and to then determine whether this effect is the result of photic stimulation of the pituitary-gonad axis resulting in increased steroid levels, alteration of the effectiveness of hormones in inducing reproductive behaviour, or a combination of the two. Of particular interest is the question of whether the hormonal induction of behaviour is a relatively stable process or one which fluctuates as a result of interaction with the environment or endogenous physiological changes.

The first problem to be considered was the actual effect of daylength on intact males. Ring doves have been domesticated for a long period of time, and their presumed ancestors inhabit regions close to the equator where annual variations in daylength are small (Goodwin, 1967; Vaurie, 1961; Parkes, 1973). It has therefore been suggested that they are unresponsive
to photoperiod (van Tienhoven, 1968). Certainly the effect is not nearly so dramatic as that seen in many temperate species, but evidence does exist suggesting that reproductive activity declines during periods of short daylength.

Whitman (1919) noted that the intervals between laying increased in late fall and winter. Goodwin (1952) states that his doves, which were held at semi-liberty in England, usually bred from late February or March to early September. In Australia birds kept in outdoor aviaries ceased breeding in May and began again in July (Davies, 1974a). Although this indicates that ring doves stop breeding during periods of short daylength, it must be recognized that corresponding low temperatures could be the controlling factor.

Liley (1976) found that in winter long daylengths were associated with significantly higher levels of female courtship and egg production than short daylengths. And finally, preliminary results reported by Hutchison (1976) suggest that males held on 6L:18D for 30 days exhibit much lower levels of aggressive courtship than do males held on 14L:10D.

In the first experiment, then, male doves held on long or short photoperiods were paired with receptive females during 20 minute tests and their behaviour compared. The second and third experiments examined the interaction between daylength and exogenous testosterone. Intact (Exp. II) or castrated (Exp. III) males received daily injections of testosterone propionate (TP) for 5 weeks while being held on the two light cycles. During the 2 weeks following the treatment period each male was paired with a female for 6½ hours/day, and observed at various times throughout the day.
B. GENERAL METHODS

1. Experimental Animals

All of the experimental subjects were the offspring of ten breeding pairs of ring doves (Streptopelia risoria) obtained from Rutgers University in the spring of 1974. At between three and four weeks of age the young were removed from their parents and held in large indoor/outdoor aviaries in mixed groups ranging from 40 to 80 birds. Between 8 and 14 months of age they were sexed by exploratory laparotomy and banded.

2. Experience Prior to Testing

The reproductive experience of individuals was unknown; undoubtedly most mature birds had taken part in some degree of courtship, although the absence of nesting sites prevented the successful hatching of eggs and subsequent participation in parental activities. However, since their ages varied—and possibly their state of reproductive development—all birds were allowed to breed in the laboratory before being used. Pairs were placed in cages containing nesting material (pine needles or string) and a nest bowl, and were allowed to build a nest and lay two eggs, which were then checked to insure that they were fertile. Following this initial breeding experience the birds were returned to the aviaries until needed.

3. Housing and Maintenance

Aviaries: The doves were held in three aviaries, each consisting of a long room (6.2x3.6x2.4 m) connected to an enclosed outside area (3.8x3.9x2.3 m).

Holding Cages: Experimental birds were held in small isolation
cages made of aluminum and wire mesh. Each cage measured 43x43x43 cm and was equipped with a perch, water tube and feeder (see fig. 1).

Experimental Cages: During experiments the birds were placed in aluminium cages measuring 120x45x65 cm. Each cage was fitted with an opaque partition dividing it into halves, 2 perches, 2 water dishes, and a feeder. A glass nest bowl was suspended 15 cm above the floor on the left side. In experiments II and III two of the eight cages had 10 cm wide shelves attached to the ends 30 cm above the floor instead of perches.

C. A SYNOPSIS OF COURTSHIP AND NEST-BUILDING BEHAVIOUR

The courtship behaviour of ring doves has been discussed at length by several authors (see Lovari & Hutchinson, 1975; Liley, 1976; Miller & Miller, 1958; Hutchinson, 1970a). The following is a brief summary of the activities recorded in this study.

1. Chasing and Pecking

When a pair of ring doves is first placed together the male usually rushes towards the female, his head held low and his rump feathers ruffled. If she flees he continues to chase her, frequently pecking her on the head and neck. This display is usually accompanied by a 'kah' or 'laughing' call.

2. Bow-Cooing

Chasing rapidly gives way to the 'bow-coo' in which the male stretches his neck upward, then bows forward with his bill pointing towards the ground, uttering a characteristic cooing sound. The underlying motivation of the bow-coo has been the subject of considerable speculation
Fig. 1 Isolation and experimental cages.
(see Lovari & Hutchinson, 1975; Davies, 1974b; Goodwin, 1956a; Lofts & Murton, 1973), but it is generally agreed to be indicative of a mixture of aggressive and sexual tendencies.

3. Male Nest-Soliciting

Following repeated bow-coos the male usually moves to a corner of the cage or to the nest bowl and begins nest-soliciting; standing or squatting in an oblique position, his head close to the ground, he vibrates both wings simultaneously, intermittently uttering 'nest-coos'. Various forms of this behaviour occur, including oblique posturing in the absence of either cooing or wing-flipping, or both. In the following tests nest-soliciting was defined by the presence of both the oblique stance and wing-flipping.

4. Female Nest-Soliciting

Soliciting by the male appears to attract the female--she eventually approaches him and begins to spend more and more time in his vicinity, often engaging in allopreening. After a period which may vary from a few minutes to several days the female also begins to nest-solicit. Initially this elicits an aggressive response from the male, who pecks at her head and neck. Nest-soliciting by the female is also variable; wing-flips and/or nest coos in the absence of the oblique posture being common. For this reason it was identified simply by the occurrence of wing-flipping at the nest.

5. Nest-Building

As the female becomes firmly attached to the nest site male soliciting gives way to nest-building. Building is a co-operative effort:
following varying amounts of time spent picking up and dropping nesting material (handling), the male carries a piece to the female, who remains at the nest. She takes the material from the male and tucks it beneath her. However, this division of labour is not strict (see White, 1975a) and females may occasionally pick up material and carry it to the nest.

6. Copulatory Behaviours

Behaviours associated with copulation usually occur during the afternoon. The female approaches the male and pecks gently at the base of his bill, while rhythmically flipping her wings (begging). The male then takes her bill in his and appears to regurgitate food, which she swallows (billing). After one or several bouts of begging and billing the female crouches, her upper wings extended. This is followed either by a repetition of the above sequence, or by mounting and copulation.

Crouching may also occur shortly after a pair is placed together, in response to chasing and bowing by the male. In such cases begging and billing are absent and the crouch is rarely followed by mounting. Cheng (1973a) calls this form of crouching an 'aggressive crouch' as it may be accompanied by 'kah' calls. But similar female behaviour is also seen during vigorous attacks by the male (cf. 'cringing' in pigeons (Akerman, 1966)) and the 'flight stance' in doves ((Miller & Miller, 1957)), both of which are classified as escape responses.), and appears to inhibit both chasing and pecking by the male. In this context the early crouch appears to serve as an appeasement display rather than an aggressive behaviour, which could also explain its appearance in response to bow-cooing and chasing at the beginning of an encounter.
EXPERIMENTS I & Ia - THE EFFECT OF PHOTOPERIOD
ON COURTSHIP IN INTACT MALES

A. INTRODUCTION

As was mentioned earlier, there has been no detailed study examining the effect of daylength on the behaviour of male ring doves. The present study was undertaken in order to measure differences in courtship between individuals held on different photoperiods. Male doves were exposed to long or short light cycles for five weeks. They were then tested by pairing them for 20 minutes with a female which had been held on an intermediate light cycle. Each male was given three tests at two-day intervals.

B. METHODS

1. Subjects

The subjects were 24 mature male doves which had been treated as described in section IB. They were moved from the aviaries into holding cages on July 7, 1975 (one bird became ill and was replaced on July 12). Twelve mature females used as stimulus birds were moved into the laboratory on July 28.

2. Maintenance

The 24 experimental birds were divided between two rooms, each of which had controlled lighting. Each room contained a rack of 12 holding cages in which individuals were visually isolated. There was no apparent
transfer of sound between the two rooms. Lighting was supplied by two 40 watt fluorescent tubes mounted 1.7 m in front of each rack of cages. The average light intensity in the centre of the cages was 390 lux (range: 350-425 lux). One room was placed on a light schedule of 16L:8D (light: 8:00 - 24:00), the other on 8L:16D (light: 8:00 - 16:00). Food and water were available at all times. The temperatures in the two rooms varied widely, with the short day room averaging 1° C above the long day room (LD room: 21± 3° C; SD room: 22± 3° C).

The stimulus females were held in groups of four in test cages, visually isolated from any males, for 3 weeks. The cages were illuminated by fluorescent lights on a 14.5L:9.5D cycle.

3. Experimental Procedure

The males were held on 16L:8D (L) or 8L:16D (S) light schedules for 5 weeks. Testing began on August 18, and continued for 9 days. A male and female were placed on either side of a partitioned test cage in one of the two holding rooms, and allowed to adjust for half an hour. Each cage was supplied with a nest bowl and 50 pieces of string, approximately 12 cm long. At the end of the adjustment period the partition was removed and a record made of the ensuing courtship. After 20 minutes the partition was replaced and the male returned to his holding cage.

The birds being tested were visually isolated from those in the holding cages, but sound transferred freely between them. In order to balance the auditory stimuli received by the isolated males the room in which the tests were performed was alternated, even though auditory
stimulation, which has a marked effect on the female reproductive system (Lott & Brody, 1965; Lott et al., 1967; Lehrman & Friedman, 1969) does not appear to affect the breeding behaviour of males (Nottebohm & Nottebohm, 1971).

Each male was given three tests at intervals of three days. Eight males, four from each of the two rooms, were tested every day, between 9:00 and 13:00. Due to limited space each female was used for two consecutive days (a total of 8 trials, 4 with LD males and 4 with SD males). The females had been separated from any males for 3 weeks prior to testing, while being held on a constant light cycle in order to minimize differences in responsiveness. Because the order of testing was varied so that each male was paired with 3 different females it is assumed that females provided the males from the two experimental groups with a relatively 'constant' stimulus.

4. Behavioural Recordings

The following behaviours were recorded on a 20 channel Esterline Angus event recorder at a chart speed of 3in/min.:

1. chasing
2. pecking
3. bow-cooing
4. male nest-soliciting
5. begging
6. billing
7. crouching
8. mount/copulation
9. male nest-building
10. female nest-soliciting
11. female nest-building
C. RESULTS AND DISCUSSION

Of the behaviours recorded only the five listed in Table II were observed in the majority of birds. This is not surprising as copulatory and nesting activities occur during more advanced stages of the reproductive cycle.

Courtship does appear to be influenced by photoperiod; L birds showed higher levels of both bow-cooing and male nest-soliciting. Aggressive behaviour did not differ significantly between the two groups.

The behaviour of the females seemed to relate more closely to the individual involved than to the type of male encountered. Three females accounted for two-thirds of the tests in which female nest-soliciting was observed, while three others did not display soliciting with any males.

D. SUPPLEMENTARY EXPERIMENT Ia

1. Introduction

Although the previous experiment gave a good indication that day-lengths affected male courtship, it dealt only with responses occurring during the first 20 minutes of an encounter. In order to gain some idea as to whether or not the observed differences between the two groups persist over a longer time interval, experiment I was followed by a supplementary test covering a 3-day period.

2. Materials and Methods

Upon completion of experiment I all of the males were retained in their holding cages. At 8:30 on the following day 24 experimentally naive females were moved from the aviary and one female placed in each cage, along
TABLE II  Summary of the courtship displayed by intact males held on long or short photoregimes. Chasing, male soliciting and female soliciting are based on the number of seconds spent performing the given activity per 20 minute test; pecks and bow-coos are based on the number of events per 20 minute test.

<table>
<thead>
<tr>
<th></th>
<th>SHORT PHOTOPERIOD n=12</th>
<th>LONG PHOTOPERIOD n=12</th>
<th>p*</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>range</td>
<td>mean</td>
</tr>
<tr>
<td>chasing</td>
<td>28</td>
<td>(0-207)</td>
<td>11</td>
</tr>
<tr>
<td>pecks</td>
<td>13</td>
<td>(1-92)</td>
<td>8</td>
</tr>
<tr>
<td>bow-coos</td>
<td>9</td>
<td>(0-26)</td>
<td>32</td>
</tr>
<tr>
<td>o soliciting</td>
<td>455</td>
<td>(0-874)</td>
<td>776</td>
</tr>
<tr>
<td>f soliciting</td>
<td>176</td>
<td>(0-409)</td>
<td>143</td>
</tr>
</tbody>
</table>

* based on Mann-Whitney U-test between means, 1-tailed for long>short.
with a nest bowl and 50 pieces of string. The lights in the two rooms were switched to 12L:12D (8:00 - 16.00) so that both groups of males spent the same number of daylight hours with the females.

Recordings of the same behaviours as in experiment I were made using a check-sheet divided into 15 sec. intervals. Each row of 3 cages was observed for 2 minutes (i.e. a total of eight 15 sec. intervals) at 1, 3, 5, 7, 9, and 11 hours after the onset of light. An activity was scored as having either occurred or not during each interval. At the end of 3 days the females were removed and the lights returned to the original cycles.

3. Results and Discussion

Male nest-soliciting was displayed more frequently by L birds throughout the 3-day period (Table III). Soliciting shows a marked diurnal variation under both light regimes (see also Martinez-Vargas & Erickson, 1973), peak periods occurring early in the morning (fig. 2), but was higher in L birds than in S birds throughout the day. More L males were observed bow-cooing and pecking, although the total number of occurrences recorded was very small. Significantly more L males exhibited nest-soliciting on days 2 and 3 (Table IV). No other behaviours were recorded at levels high enough to analyse.

It thus appears that photoperiod not only affects courtship behaviour seen at the beginning of an encounter but also influences reproductive activities over an extended period, long days resulting in an increase in courtship displays.
TABLE III  Nest-soliciting displayed over a 3-day period by intact males held on short or long photoperiods prior to pairing. Values are based on the total number of 15 sec. intervals/day during which soliciting was observed (max. possible = 48).

<table>
<thead>
<tr>
<th></th>
<th>SHORT</th>
<th>LONG</th>
<th>p*</th>
</tr>
</thead>
<tbody>
<tr>
<td>n=12</td>
<td></td>
<td>n=12</td>
<td></td>
</tr>
<tr>
<td>Day 1</td>
<td>9a</td>
<td>28</td>
<td>&lt;.01</td>
</tr>
<tr>
<td></td>
<td>(0-24)b</td>
<td>(17-46)</td>
<td></td>
</tr>
<tr>
<td>Day 2</td>
<td>4</td>
<td>16</td>
<td>&lt;.01</td>
</tr>
<tr>
<td></td>
<td>(0-14)</td>
<td>(3.27)</td>
<td></td>
</tr>
<tr>
<td>Day 3</td>
<td>5</td>
<td>16</td>
<td>&lt;.01</td>
</tr>
<tr>
<td></td>
<td>(0-13)</td>
<td>(6-27)</td>
<td></td>
</tr>
</tbody>
</table>

* based on Mann-Whitney U-test between means, 1-tailed for long > short

a mean
b range
Fig. 2: Changes in the nest-soliciting behaviour of long and short day males over the 3-day test period, as measured by the number of intervals during which soliciting was observed. Open bars represent long day males, solid bars represent short day males.
NEST-COLICITING INTERVALS/2 MIN TEST

Day 1

Day 2

Day 3
TABLE IV  The number of males observed performing courtship activities during the 3-day test period. Birds were held on short and long photoperiods prior to testing.

<table>
<thead>
<tr>
<th>Activity</th>
<th>SHORT</th>
<th>LONG</th>
<th>p*</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n=12</td>
<td>n=12</td>
<td></td>
</tr>
<tr>
<td>chasing</td>
<td>3</td>
<td>1</td>
<td>ns</td>
</tr>
<tr>
<td>pecking</td>
<td>2</td>
<td>7</td>
<td>.05</td>
</tr>
<tr>
<td>bow-cooing</td>
<td>1</td>
<td>6</td>
<td>.05</td>
</tr>
<tr>
<td>nest-soliciting: day 1</td>
<td>9</td>
<td>12</td>
<td>ns</td>
</tr>
<tr>
<td>day 2</td>
<td>6</td>
<td>12</td>
<td>.05</td>
</tr>
<tr>
<td>day 3</td>
<td>6</td>
<td>12</td>
<td>.05</td>
</tr>
</tbody>
</table>

* based on Fisher Exact Probability Test, 1-tailed for long > short (Siegel, 1956).
CHAPTER III

EXPERIMENT II - THE INTERACTION OF PHOTOPERIOD AND ANDROGEN TREATMENT IN INTACT MALES

A. INTRODUCTION

In order to determine whether the differences seen in experiment I were due to changes in hormone levels or to some other mechanism, intact birds held on long and short days were treated with testosterone propionate. The levels of exogenous hormone administered were high, and it was assumed that gonadotropin secretion would be inhibited, reducing gonadal steroid production to a minimum and thereby eliminating any effect of endogenous androgen. If the effect of photoperiod on male courtship is due to changes in testosterone levels, then no differences would be expected between the two hormone-treated groups, both of which would presumably experience similar high androgen concentrations. If, on the other hand, photoperiod serves to alter responsiveness to testosterone, then hormone-treated males held on long daylengths would be expected to court more actively than those held on short daylengths.

B. METHODS

1. Subjects

The 24 males from the previous experiment were used again. The 24 stimulus females, which had been treated as described in section IB, had no prior experimental experience.
2. Experimental Procedure

Light cycles and housing were the same as those described for experiment I. The 12 males in each room were randomly divided into 3 groups of 4 each. In each of these groups 2 birds were injected daily with .2 mg testosterone propionate in .1 ml peanut oil (ST and LT birds). The remainder were controls, receiving .1 ml of the vehicle each day (SC and LC birds). Injections were administered intramuscularly, alternating between the right and left pectoral muscles. Treatment began 2 weeks before testing commenced and continued through the 2 weeks of the tests. Treatment and testing of the 3 sets of birds in each room was staggered, the first beginning on October 20, 1975 and the next two sets following at 2 week intervals (see Table V).

Following 2 weeks of hormone treatment each male was paired with a female. Prior to testing the females were kept visually isolated in holding cages on a light cycle of 14L:10D (8:00 - 22:00) for two weeks in an attempt to insure that they were in a similar reproductive condition. At the beginning of the test period each female was moved into the side of a partitioned experimental cage containing the nest bowl. Males were moved into the opposite side of the cages and 50 pieces of string, 12 cm long, were scattered on the floor on the male's side. If during the day most of the string was removed from the floor of the cage more was added. The eight test cages were suspended along the wall of the experimental room in two rows of 4 cages, and were visually isolated from each other. There was no transfer of sound between this room and either of the holding rooms.

Males were moved into the test room at 8:30 each day. On day 1
**TABLE V**  Schedule for treatment of experimental males in experiment II.

Birds were held under short (S) or long (L) photoperiods. Controls (C) were administered .1 ml peanut oil daily (O), while experimentals (T) received daily injections of .2 mg TP in .1 ml peanut oil.

<table>
<thead>
<tr>
<th>Oct 20-Nov 2</th>
<th>Nov 2-Nov 17</th>
<th>Nov 17-Nov 30</th>
<th>Dec 1-Dec 14</th>
</tr>
</thead>
<tbody>
<tr>
<td>SC (2)</td>
<td>O I</td>
<td>O P</td>
<td></td>
</tr>
<tr>
<td>ST (2)</td>
<td>A I</td>
<td>A P</td>
<td></td>
</tr>
<tr>
<td>LC (2)</td>
<td>O I</td>
<td>O P</td>
<td></td>
</tr>
<tr>
<td>LT (2)</td>
<td>A I</td>
<td>A P</td>
<td></td>
</tr>
<tr>
<td>SC (2)</td>
<td>O I</td>
<td>O P</td>
<td></td>
</tr>
<tr>
<td>ST (2)</td>
<td>A I</td>
<td>A P</td>
<td></td>
</tr>
<tr>
<td>LC (2)</td>
<td>O I</td>
<td>O P</td>
<td></td>
</tr>
<tr>
<td>LT (2)</td>
<td>A I</td>
<td>A P</td>
<td></td>
</tr>
<tr>
<td>SC (2)</td>
<td>O I</td>
<td>O P</td>
<td></td>
</tr>
<tr>
<td>ST (2)</td>
<td>A I</td>
<td>A P</td>
<td></td>
</tr>
<tr>
<td>LC (2)</td>
<td>O I</td>
<td>O P</td>
<td></td>
</tr>
<tr>
<td>LT (2)</td>
<td>A I</td>
<td>A P</td>
<td></td>
</tr>
</tbody>
</table>

I  isolated

P  paired for 6½ hrs/day during test period

(n)  number of birds
the partitions in each cage were removed for 20 minutes, one at a time, between 9:00 and 11:40, and then replaced. At 11:45 all partitions were removed. They were replaced at 3:30 and the males injected and returned to their holding cages in the short and long day rooms. The females remained in the nest-bowl side of the experimental cages. The light schedule in their room was 14L:10D (7:30 - 17:30). From days 2-14 the same procedure was followed except that all the partitions were removed at 9:00 or 9:15 and not replaced until 3:30.

Thus all of the males interacted with the females for the same length of time each day, and still experienced the two experimental light cycles. At the same time all females exposed to the males were maintained on the same 14L:10D schedule.

The males were killed or castrated on day 15 and their testes weighed.

3. Recording Methods

Because of indications in experiment 1a that the effects of photoperiod are not restricted to initial courtship behaviour, it was decided that recordings should be made measuring reproductive activity over a 2 week period. Due to diurnal variations in behaviour short records were made throughout the day.

The initial 20 minute encounter on day 1 of each pair was recorded on an Esterline Angus 20 channel event recorder at a chart speed of 3 in/min. At 13:00 and 15:00 on day 1, and at 9:00, 11:00, 13:00, and 15:00 on days 2-14 15 minute check sheets divided into 15 second intervals were used. Four pairs of birds were observed at a time
from behind a blind. The order in which the two sets of 4 pairs were observed was alternated (i.e. set A was checked at 9:00, 11:00, etc. on day 2; 9:15, 11:15, etc. on day 3). Each set of birds contained one individual from each treatment group (ST; LT; SC; LC).

Any eggs laid were removed as soon as they were noticed, and the date recorded. In order to minimize differences in the stimuli produced by the nest, the string was taken from the nests at the end of each day, counted, and scattered on the floor on the opposite side of the cage. Any pieces lying directly beneath the nest had presumably been carried over the 1" high partition holder which lay across the centre of the cage, and were therefore also counted.

4. Behaviours Recorded

The behaviours recorded on the event recorder were the same as in experiment I. When using the check sheet most behaviours were scored if they were observed within a 15 sec. interval, although some activities, such as carrying, were noted every time they occurred. The activities recorded were as follows:

a) chase/peck (no. intervals) - Because chasing and pecking occur in close temporal association, bouts of one rapidly giving way to the other; and because the underlying motivation of both appears to be primarily aggressive, these two behaviours have been grouped together.

b) bow-coos (no. intervals)

c) male-nest soliciting (no. intervals)

d) male at-nest (no. intervals) - This is a measure of the total amount of time spent by the male at the nest site,
and includes sitting, allopreening, and soliciting at the nest.

e) male carrying (no. events)

f) male nest-building (no. intervals) - This is a measure of the total amount of time spent nest-building. It includes time spent handling or carrying string. In order to account for short breaks between these two behaviours during which the male returned from the nest to the floor, or appeared to search among the pieces of string before actually handling them, any intervals of less than 30 seconds occurring between handling and/or carrying are also included.

g) female nest-soliciting (no. intervals)

h) female at-nest (no. intervals) - This was recorded in the same manner as male at-nest.

i) female carrying (no. events)

j) active female nest-building (no. intervals) - This is a measure of the amount of time which the female spent performing 'male-type' building, and was measured in the same way as male nest-building. It does not include sitting at the nest and tucking material bought by the male into the nest.

k) begging (no. events)

l) billing (no. events)

m) sexual crouch (no. events) - This category includes only those crouches preceded by begging and billing.

n) Mount/copulation (no. events)

o) submissive crouch (no. events) - This includes crouches occurring within the first 2 minutes after the partition was removed and preceded by chasing and/or bowing.
5. Statistical Treatment of Data

All of the behavioural recordings, as well as the amount of string gathered were analysed using a Kruskal-Wallis one-way analysis of variance (Siegel, 1956). If the over-all differences were significant then selected pairs were compared (Kolstoe, 1973) using the Mann-Whitney U-test (Siegel, 1956). Testis weight was analysed with a two-way ANOVA followed by a Newman-keul test (Armitage, 1971).

C. RESULTS AND DISCUSSION

1. Initial 20 minute Interaction

Only male nest-soliciting, bowing, chasing, and pecking were seen in substantial numbers during the first 20 minutes of courtship (Table VI). No significant differences were observed for any of these activities. Testosterone appeared to diminish aggressive behaviour and increase courtship. The frequencies of male soliciting and bowing were slightly higher in LT than in ST birds. Bowing also appeared to be greater in LC than in SC males.

2. Check Sheets

a) Aggressive behaviour

Chasing and pecking occurred primarily and in the early morning, when the pair were placed together (Table VII). Although the differences among the groups were not significant, TP appeared to diminish aggressive behaviour. Longer daylengths were associated with a higher frequency of attacks (Table VIII).
TABLE VI  Summary of the courtship activity of hormone-treated and control males during the initial 20 minute interaction in experiment II. Chasing and soliciting are based on the number of seconds spent performing the activity per 20 minute test; pecking and bow-cooing are based on the number of events per 20 minute test.

<table>
<thead>
<tr>
<th></th>
<th>SHORT PHOTOPERIOD</th>
<th>LONG PHOTOPERIOD</th>
<th>_p*</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Control n=6</td>
<td>TP n=6</td>
<td></td>
</tr>
<tr>
<td>chasing</td>
<td>50 (0-137)</td>
<td>45 (17-157)</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td>21^a (0-60)^b</td>
<td>35 (4-109)</td>
<td></td>
</tr>
<tr>
<td>pecks</td>
<td>11.5 (1-22)</td>
<td>9.5 (1-23)</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td>4.5 (0-18)</td>
<td>12.5 (0-34)</td>
<td></td>
</tr>
<tr>
<td>bow-coos</td>
<td>17.5 (6-26)</td>
<td>23.5 (8-55)</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td>36.5 (11-105)</td>
<td>39.5 (0-73)</td>
<td></td>
</tr>
<tr>
<td>soliciting</td>
<td>410 (223-661)</td>
<td>403 (60-667)</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td>338 (132-732)</td>
<td>519 (120-805)</td>
<td></td>
</tr>
</tbody>
</table>

* based on Kruskal-Wallis ANOVA (Siefel, 1956)

a mean
b range
TABLE VII  The total number of 15 second intervals in which either chasing or pecking were observed in relation to the time of day. Males were treated with TP or oil while being held on long or short photoperiods.

<table>
<thead>
<tr>
<th>Time</th>
<th>SHORT PHOTOPERIOD</th>
<th></th>
<th>TOTAL</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Control</td>
<td>TP</td>
<td>LONG</td>
</tr>
<tr>
<td>9:00</td>
<td>75</td>
<td>39</td>
<td>249</td>
</tr>
<tr>
<td>11:00</td>
<td>6</td>
<td>0</td>
<td>15</td>
</tr>
<tr>
<td>13:00</td>
<td>3</td>
<td>1</td>
<td>30</td>
</tr>
<tr>
<td>15:00</td>
<td>2</td>
<td>0</td>
<td>11</td>
</tr>
</tbody>
</table>
TABLE VIII  The frequency of aggressive and courtship activities in TP-treated and control males held on long or short photoperiods. The results are based on the total number of intervals during which the activities were observed over the 14 day test period.

<table>
<thead>
<tr>
<th></th>
<th>SHORT PHOTOPERIOD</th>
<th>LONG PHOTOPERIOD</th>
<th>ANOVA*</th>
<th>U-TEST</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Control</td>
<td>TP</td>
<td>Control</td>
<td>TP</td>
</tr>
<tr>
<td></td>
<td>n=6</td>
<td>n=6</td>
<td>n=6</td>
<td>n=6</td>
</tr>
<tr>
<td>chase/peck</td>
<td>14&lt;sup&gt;a&lt;/sup&gt;</td>
<td>7</td>
<td>16</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td>(4-30)&lt;sup&gt;b&lt;/sup&gt;</td>
<td>(1-16)</td>
<td>(2-47)</td>
<td>(2-35)</td>
</tr>
<tr>
<td>bow-coo</td>
<td>12</td>
<td>7</td>
<td>16</td>
<td>32</td>
</tr>
<tr>
<td></td>
<td>(5-18)</td>
<td>(2-19)</td>
<td>(6-36)</td>
<td>(6-54)</td>
</tr>
<tr>
<td>soliciting</td>
<td>630</td>
<td>798</td>
<td>980</td>
<td>924</td>
</tr>
<tr>
<td></td>
<td>(448-840)</td>
<td>(462-1162)</td>
<td>(476-1232)</td>
<td>(560-1092)</td>
</tr>
<tr>
<td>time-at-nest</td>
<td>756</td>
<td>882</td>
<td>1316</td>
<td>1302</td>
</tr>
<tr>
<td></td>
<td>(322-1204)</td>
<td>(434-1176)</td>
<td>(588-1806)</td>
<td>(938-1862)</td>
</tr>
</tbody>
</table>

* based on Kruskal-Wallis ANOVA (Siegel, 1956)

<sup>a</sup> mean
<sup>b</sup> range
b) Courtship

Bow-cooing was more frequent in LT and LC birds than in the short day groups, although the differences were not significant (Table VIII).

Control birds performed significantly more nest-soliciting when held on long days, but there was no difference between the two photoperiods in the androgen-treated males. Testosterone increased soliciting under short daylengths but was ineffective under long ones. This pattern suggests that daylength may influence nest-soliciting via changes in steroid levels. If it is assumed that LC males are producing endogenous testosterone at concentrations capable of inducing maximum levels of soliciting while SC birds are producing much lower amounts, and that the TP injections are capable of supplementing submaximal levels of endogenous testosterone, then no differences would be expected among LC, LT, and ST birds, all of which experienced maximal androgen stimulation, while SC birds would be less active than the rest. Alternatively long daylengths may increase responsiveness to testosterone, resulting in higher levels of soliciting in LC than SC birds. If those males receiving exogenous androgen are already exhibiting maximum levels of soliciting, then the sensitizing effect of long photoperiods would not be observed between LT and ST males.

Overall variations in the amount of time spent by the male at the nest site were significant, although the differences between pairs of treatments were not. This behaviour appears to vary in a manner similar to soliciting, but with a greater difference between LT and ST males.

There were no significant differences in any of the copulatory behaviours or in female courtship (Table IX).
TABLE IX  Frequency of copulatory and female courtship activities performed by pairs in which the males had been treated with TP or oil while being held on long or short photoperiods. Based on the total number of events or 15 sec. intervals over the 14 day test period.

<table>
<thead>
<tr>
<th>Activity</th>
<th>SHORT PHOTOPERIOD</th>
<th>LONG PHOTOPERIOD</th>
<th>ANOVA*</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Control/TP</td>
<td>Control/TP</td>
<td></td>
</tr>
<tr>
<td></td>
<td>n=6</td>
<td>n=6</td>
<td></td>
</tr>
<tr>
<td>Begging events</td>
<td>24(^a)</td>
<td>23</td>
<td>36</td>
</tr>
<tr>
<td></td>
<td>(17-30)(^b)</td>
<td>(4-41)</td>
<td>(21-66)</td>
</tr>
<tr>
<td>billing events</td>
<td>11</td>
<td>14</td>
<td>17</td>
</tr>
<tr>
<td></td>
<td>(0-24)</td>
<td>(2-22)</td>
<td>(10-27)</td>
</tr>
<tr>
<td>sexual crouch events</td>
<td>11</td>
<td>7</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>(8-17)</td>
<td>(0-17)</td>
<td>(3-18)</td>
</tr>
<tr>
<td>mounts/copulations events</td>
<td>2.5</td>
<td>3.0</td>
<td>3.2</td>
</tr>
<tr>
<td></td>
<td>(0-5)</td>
<td>(0-8)</td>
<td>(1-4)</td>
</tr>
<tr>
<td>submissive crouch events</td>
<td>1.0</td>
<td>2.2</td>
<td>1.7</td>
</tr>
<tr>
<td></td>
<td>(0-5)</td>
<td>(0-8)</td>
<td>(0-4)</td>
</tr>
<tr>
<td>female soliciting intervals</td>
<td>588</td>
<td>588</td>
<td>679</td>
</tr>
<tr>
<td></td>
<td>(28-784)</td>
<td>(28-1330)</td>
<td>(406-952)</td>
</tr>
<tr>
<td>female-at-nest intervals</td>
<td>1218</td>
<td>1554</td>
<td>2016</td>
</tr>
<tr>
<td></td>
<td>(14-2688)</td>
<td>(28-2618)</td>
<td>(1400-2590)</td>
</tr>
<tr>
<td>female carrying events</td>
<td>4</td>
<td>3</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>(0-13)</td>
<td>(0-12)</td>
<td>(0-45)</td>
</tr>
<tr>
<td>female building intervals</td>
<td>12</td>
<td>6</td>
<td>29</td>
</tr>
<tr>
<td></td>
<td>(0-32)</td>
<td>(0-18)</td>
<td>(0-126)</td>
</tr>
</tbody>
</table>

* based on Kruskal-Wallis ANOVA (Siegel, 1956)

\(^a\) mean

\(^b\) range
c) Nest-building

Of the three measures of male nest-building recorded—time spent building, number of carrying events, and amount of string found in the nest—all indicated that LT and LC birds build at higher rates than ST and SC birds respectively, and that TP increases building in short but not long day males (Table X). Figs. 3 and 4 show that these differences persisted over most of the 14 day test period. It is thus apparent that testosterone increases nest-building, on short days at least. But large differences were seen between LT and ST birds, both of which presumably had very high plasma testosterone concentrations, suggesting that day-length alters male building through some means other than steroid levels.

Although measures of male building were positively correlated with female carrying and building, it is unlikely that active building by the female was responsible for differences in the amount of string collected, as neither activity varied significantly among the groups; and in any event both were infrequent in all pairs.

The female may influence nest-building through her effect on male behaviour. Attachment of the female to the nest site is necessary for successful nest-building. Several authors have suggested that female activities such as nest-soliciting or time spent at the nest site determine the degree of building exhibited by the male (Martinez-Vargas & Erickson, 1973; Martinez-Vargas, 1971; White, 1975a; Cheng & Silver, 1975; Liley, 1976).

In this study all of the females were isolated prior to pairing and were held on identical photoperiods. Thus they were all presumably
TABLE X  Nest-building activity of TP-treated and control males held on long or short photoperiods. Based on totals for the 14-day test period.

<table>
<thead>
<tr>
<th></th>
<th>SHORT PHOTOPERIOD</th>
<th></th>
<th>LONG PHOTOPERIOD</th>
<th></th>
<th>ANOVA*</th>
<th>U-TEST**</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Control n=6</td>
<td>TP n=6</td>
<td>Control n=6</td>
<td>TP n=6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>nest-building</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>intervals</td>
<td>42^a (0-140)</td>
<td>126 (0-224)</td>
<td>280 (154-518)</td>
<td>350 (210-532)</td>
<td>.01</td>
<td>LT&gt;ST .002</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>LC&gt;SC .002</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>LT&gt;LC ns</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>ST&gt;SC  ns</td>
<td></td>
</tr>
<tr>
<td>carrying</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>events</td>
<td>10 (0-30)</td>
<td>35 (0-63)</td>
<td>72 (12-81)</td>
<td>91 (41-139)</td>
<td>.01</td>
<td>LT&gt;ST .021</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>LC&gt;SC .008</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>LT&gt;LC ns</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>ST&gt;SC  .047</td>
<td></td>
</tr>
<tr>
<td>string</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>pieces</td>
<td>112 (0-238)</td>
<td>266 (0-406)</td>
<td>700 (98-1890)</td>
<td>826 (448-1470)</td>
<td>.01</td>
<td>LT&gt;ST .001</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>LC&gt;SC .008</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>LT&gt;LC ns</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>ST&gt;SC  .021</td>
<td></td>
</tr>
<tr>
<td>string relative&lt;sup&gt;c&lt;/sup&gt; to ° at nest</td>
<td>10 (0-21)</td>
<td>17 (14-22)</td>
<td>33 (6-84)</td>
<td>42 (21-63)</td>
<td>.001</td>
<td>LT&gt;ST .002</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>LC&gt;SC .032</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>LT&gt;LC ms</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>ST&gt;SC  .047</td>
<td></td>
</tr>
</tbody>
</table>

* based on Kruskal-Wallis ANOVA (Siefel, 1956) between means
** based on Mann-Whitney U-test (Siegel, 1956) between means, 1-tailed
a mean
b range
c based on \[\frac{\text{total string}}{\text{total intervals}} \times 100\]
Fig. 3. The amount of string collected in relation to the number of days since pairing. \( n = 6 \) for all groups.
Fig. 4 Frequency of male nest-building in relation to the number of days since pairing. \( n = 6 \) for all groups.
in similar reproductive condition at the beginning of the tests, and any differences in their behaviour were probably a reflection of differences in the behaviour of the males. Although male courtship did vary among the groups, no significant differences were observed for either female nest-soliciting or time-at-nest (Table IX). In addition, figs. 5 and 6 indicate that the nest-related behaviour of the four groups of females was very similar. The total amount of building performed by the males therefore appears unrelated to the female. However, evidence does exist suggesting that the female may have a more subtle effect. Examination of Table XI shows that measures of male building were positively correlated with both female soliciting and time-at-nest. This correlation may be the result of small variations in female behaviour which were not obvious enough to show up in comparisons between groups. It could be argued that these might account for the differences between groups in male nest-building, but by taking the average amount of string collected by the pair as a proportion of the number of intervals spent by the female at the nest, it can be seen that group differences in nest-building occur independently of the female's attachment to the nest site (Table X). Moreover, it is equally possible that the degree of nesting behaviour displayed by the male influences female nesting behaviour (see also Martinez-Vargas, 1974).

Even though the absolute levels of building cannot be accounted for by differences in the female's behaviour, she does appear to play a role in determining its occurrence. Figs. 7 and 8 show that the measures of male building are related to the laying of the eggs, peaking either the day before or the day of the first egg (see also Liley, 1976). In order
Fig. 5. Female nest-soliciting in relation to the laying of the 1st egg (day 0).
Fig. 6. The amount of time spent by the female at the nest site in relation to the laying of the 1st egg (day 0).
TABLE XI Spearman rank correlation coefficients (Siegel, 1956) among male and female activities, latency to egg-laying, and testis weight. Based on combined values for all groups (n=24) except those involving testis weight which are based on combined values for SC and LC (n=12).

|       | female at nest | male at nest | female Cy | male Cy | male NB | female NB | female NS | male NS | female Cy NS | male Cy NS |
|-------|----------------|--------------|-----------|---------|---------|-----------|-----------|---------|---------------|------------|--------|
| BC    | 0.221          | 0.528**      | 0.499**   | 0.536** | 0.467** | 0.514**   | 0.433**   | 0.288   | 0.233         | 0.233      | 0.288  |
| Chase | 0.210          | 0.033        | 0.317**   | 0.233   | 0.233   | 0.317**   | 0.233     | 0.317   | -0.097        | 0.097      | 0.317  |
| string| 0.003          | 0.017        | 0.017     | 0.017   | 0.017   | 0.017     | 0.017     | 0.017   | 0.017         | 0.017      | 0.017  |
| beg   | 0.092          | 0.072        | 0.187     | 0.136   | 0.311   | 0.311     | 0.523**   | 0.523   | 0.523         | 0.523      | 0.523  |
| bill  | 0.092          | 0.072        | 0.187     | 0.136   | 0.311   | 0.311     | 0.523**   | 0.523   | 0.523         | 0.523      | 0.523  |
| crouch| -0.202         | 0.143        | -0.202    | 0.143   | -0.202  | 0.143     | -0.202    | -0.202  | -0.202        | -0.202     | -0.202 |
| Mt/cop| -0.509         | 0.509        | -0.509    | 0.509   | -0.509  | 0.509     | -0.509    | -0.509  | -0.509        | -0.509     | -0.509 |
| eggs  | -0.275         | -0.275       | -0.275    | -0.275  | -0.275  | -0.275    | -0.275    | -0.275  | -0.275        | -0.275     | -0.275 |

*p = .05
**p = .01
***p = .001
Fig. 7. Male nest-building in relation to the laying of the 1st egg (day 0).
Fig. 8. The amount of string collected in relation to the laying of the 1st egg (day = 0).
for building to be synchronized with egg-laying, the female must necessarily be involved in controlling, or at least stimulating, building by the male. Thus it is likely that the female regulates the timing of nest-building behaviour in the male, but that other factors, such as photoperiod, control his responsiveness to the stimuli presented by the female, resulting in variations in the absolute amount of building.

3. Latency to Egg-laying

Eggs were laid by all LT and LC, 5 of 6 ST, and 3 of 6 SC females. Table XII shows that there was little difference in the latency to laying of the four groups. It thus appears that the level of courtship displayed by all of the males was great enough to stimulate ovulation, although there is some indication that SC males, which exhibited the lowest levels of nest-soliciting were somewhat less effective.

4. Testis Weight

Because some males were castrated rather than killed at the end of the experiment, the right testis being removed one week after the left, only the weights of the left testes were considered.

Long daylengths resulted in higher testis weights in control birds (Table XIII). This is in keeping with preliminary results reported by Hutchison (1976); but whereas the increase in testis weight in the present study was slight (.08 gm), Hutchison observed a ten-fold difference (LD, 0.45 gm; SD, 0.04 gm). One possible explanation is that the birds may have been tested at different times of year. Liley found that female ring doves held on long and short photoregimes in December exhibited a much greater degree of oviduct and follicular development on long days (Liley, 1976),
TABLE XII  Latency to first egg, based on the number of days since pairing. The mean was calculated by assigning a value of 15 to all birds which did not lay within the test period.

<table>
<thead>
<tr>
<th>Day</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
<th>11</th>
<th>12</th>
<th>13</th>
<th>14</th>
<th>14+</th>
<th>(\bar{x})</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>LT</td>
<td></td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>9.8</td>
</tr>
<tr>
<td>ST</td>
<td></td>
<td></td>
<td>1</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>9.5</td>
</tr>
<tr>
<td>LC</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>10.5</td>
</tr>
<tr>
<td>SC</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td>1</td>
<td>1</td>
<td></td>
<td>3</td>
<td>11.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
TABLE XIII  Testis weight in grams, based on left testis.  n=6 in all four groups.  Values = mean ± standard error.

<table>
<thead>
<tr>
<th></th>
<th>SHORT DAY</th>
<th>LONG DAY</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>.41 ± .05</td>
<td>.49 ± .04</td>
</tr>
<tr>
<td>TP</td>
<td>.18 ± .06</td>
<td>.32 ± .04</td>
</tr>
</tbody>
</table>

Two-way ANOVA (Armitage, 1971):

<table>
<thead>
<tr>
<th></th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Effect of photoperiod</td>
<td>4.93</td>
<td>&lt;.05</td>
</tr>
<tr>
<td>Effect of hormone treatment</td>
<td>16.53</td>
<td>&lt;.005</td>
</tr>
<tr>
<td>Interaction</td>
<td>.48</td>
<td>ns</td>
</tr>
</tbody>
</table>

Newman-keul test (Armitage, 1971)

<table>
<thead>
<tr>
<th></th>
<th>Q</th>
<th>df</th>
<th>Q₀.₀₅</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>LT ≠ ST</td>
<td>2.87</td>
<td>2,20</td>
<td>2.95</td>
<td>ns</td>
</tr>
<tr>
<td>LC ≠ SC</td>
<td>1.64</td>
<td>2,20</td>
<td>2.95</td>
<td>ns</td>
</tr>
<tr>
<td>LT ≠ LC</td>
<td>3.49</td>
<td>3,20</td>
<td>3.58</td>
<td>ns</td>
</tr>
<tr>
<td>ST ≠ SC</td>
<td>4.72</td>
<td>3,20</td>
<td>3.58</td>
<td>&lt;.05</td>
</tr>
</tbody>
</table>
while no differences were observed in birds tested during the spring (Liley, in press). In addition, the photoperiods used by Hutchinson (LD 13L:11D; SD 6L:18D) were not the same as those employed here (LD 16L:8D; SD 8L:16D).

Conflicting effects of exogenous androgen treatment on testis function in birds have been cited in the literature. In pigeons and doves exogenous testosterone has been reported to stimulate testis functions (Chu & You, 1946; Lofts & Murton, 1973), cause testicular degeneration (Chu, 1940) or have little effect (Lahr & Riddle, 1944). In the current study TP reduced testicular weight in both L and S birds. Testicular atrophy would be expected in response to androgen treatment, as testosterone is known to decrease endogenous LRF in mammals, resulting in lowered LH, and possibly FSH, release (Franchimont, 1975). Steroids have also been shown to act at the pituitary level, reducing responsiveness to LRF (McCann, 1974).

Contrary to expectations the collapse of the testes was not complete, and those of LT males remained nearly twice as large as those of ST males, although the difference was not significant. This might be attributed to several possible causes. Because the birds had been held on the two light schedules prior to hormone administration, it is quite likely that the initial size of the testes in the two groups varied. Collapse of the (presumably) larger testes of the L birds might have required higher levels of TP or a longer period of administration. It is also conceivable that photoperiod affects some aspect of the endocrine system such as hypothalamic/pituitary responsiveness to testosterone
inhibition, LRF or LH production, testicular responses to LH, etc. At the moment, however, such suggestions remain purely speculative.

The finding that the testes of LT birds were larger than those of ST birds casts doubt upon the earlier interpretation of the influence of photoperiod on nest-building. While it can be argued that natural plasma testosterone levels are low (1.60 ng/ml - Hutchison & Katongole, 1975) and that daily injections of .2 mg TP are probably high enough to mask any endogenous differences, no studies have yet been done examining plasma levels resulting from such injections and the possibility remains that LT males experienced greater androgenic stimulation, due to summation of endogenous and exogenous testosterone, than did ST males. It is therefore possible that the observed differences in nest-building are, after all, the result of differences in androgen levels and that it is not necessary to hypothesize the existence of an alternate mechanism.

D. SUMMARY

1. Neither aggressive behaviour nor bow-cooing varied significantly among the four treatment groups, although bowing was more frequent on long days than short (fig. 9).

2. Nest-soliciting was less intense in SC birds than in the remaining three groups. It is suggested that long daylengths cause an increase in either androgen levels or responsiveness to androgens.

3. Nest-building was greater in LD birds in both TP and control groups, suggesting that it is influenced by photoperiod via some nongonadal mechanism.

4. TP causes testicular regression, while long daylengths stimulate growth.
5. No differences were observed in copulatory behaviours, female activities, or latency to egg laying.
Fig. 9. Summary of the differences between the various groups of males in experiment II. CH/PK = chase/peck; BC = bow-coo; NS = male nest-soliciting; NB = male nest-building; CY = male carrying; STRING = amount of string collected.

The scales vary. One unit = 10 intervals for CH/PK, BC, NS, and NB; 20 intervals for Cy; 10 pieces for string; .10 gm for testes. CH/PK, BC, and Cy are based on totals over the 14 day test period; NS, NB, and string are based on average values/day.

A= LT; B= LC; C= ST; D= SC males
EXPERIMENT III - THE EFFECT OF PHOTOPERIOD ON THE HORMONAL INDUCTION OF REPRODUCTIVE BEHAVIOUR IN CASTRATE MALES

A. INTRODUCTION

Because testis weight varied between LT and ST birds in experiment II no definite conclusions could be drawn concerning the effect of photoperiod on hormone action. In order to eliminate any possible differences arising from unequal endogenous androgen contributions the experiment was repeated using castrates.

B. METHODS

1. Subjects

Thirty experimentally naive males were used as subjects, and twenty-four experimentally naive females as stimulus animals.

2. Surgery

The males were bilaterally castrated under sodium pentabarbital (*Nembutal) anaesthesia (3.0 - 3.5 mg pentabarbital/bird) in a two-stage operation, the second testis being removed one week after the first.

3. Housing

The birds were housed in exactly the same manner as that described in experiment II.

4. Experimental Procedure and Recordings

The males were divided into three groups, ten animals apiece,
and the entire procedure was staggered to allow for two weeks difference between consecutive groups (see Table XIV).

The males were brought in from the aviary in April 1976, and held in individual cages on a 14L:10D cycle for one week. They were then pre-tested by pairing each male with a responsive female for 10 minutes. Any male failing to display both bowing and nest-soliciting within that interval was discarded. The remaining birds were castrated, the left testis being removed on the day of the pre-test, the right testis a week later. After a recovery period of two weeks each male was again paired with a female for 10 minutes and any birds which either bowed or solicited were eliminated. Of the original 30 males three failed to exhibit both bow-cooing and nest-soliciting during the pre-test, three were eliminated due to breakage of the testes during castration, and two displayed during the post-castration test.

Following the post-castration test the males were moved to the two experimental rooms and held on LD (16L:8D) or SD (8L:16D) cycles for five weeks. Of the 11 birds in each room 8 were chosen for hormone treatment (LT and ST birds) and 3 as controls (LC and SC birds). Because the ability of exogenous testosterone to induce sexual behaviour is known to decrease with time since castration in ring doves (Hutchison, 1969 & 1974a) as well as mammals (Davidson, 1972), the LT and ST birds were given maintenance doses of testosterone (.2 mg TP in 1. ml peanut oil twice a week) for the first five weeks. Controls received .1 ml of the vehicle only.

Testing began at the end of the five week period. During that
### TABLE XIV  Treatment Schedule for Experiment III

<table>
<thead>
<tr>
<th>weeks</th>
<th>ST (2)</th>
<th>LT (2)</th>
<th>SC (1)</th>
<th>LC (1)</th>
<th>ST (3)</th>
<th>LT (3)</th>
<th>SC (1)</th>
<th>LC (1)</th>
<th>ST (1)</th>
<th>LT (1)</th>
<th>SC (3)</th>
<th>LC (3)</th>
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<td>S, MT</td>
<td>S, MT</td>
<td>S, MT</td>
<td>S, MT</td>
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</tbody>
</table>

- **n**: number of birds
- **c**: castration, i.e., removal of 2nd testis
- **R**: post-castration recovery period
- **P**: post-castration test
- **S, L**: short or long daylengths
- **MT, MO**: maintenance treatment with TP or oil
- **T, O**: daily treatment with TP or oil
- **Test**: daily pairing and observations
period the hormone and control injections were administered daily. The procedure was identical to that used in experiment II with three exceptions: (1) during the test period injections were administered at 8:30; (2) on day 1 all partitions were removed at 0:00 and recordings made using a check sheet rather than the event recorder; and (3) in addition to those behaviours listed for experiment II, male and female allopreening were also recorded.

5. Elimination of Data.

At the end of the test period all of the males were killed and checked for testicular material. One ST and one LC bird were discarded, as their testes had partially regenerated. An LT bird which spent virtually all of its time sleeping was also eliminated. It is possible that for some reason testosterone, which is known to have an anaesthetic effect in high doses (Davis, 1964) acted as a sedative in this particular bird.

C. RESULTS AND DISCUSSION

1. Aggressive Behaviour

The frequency of chasing/pecking was twice as high in ST as LT birds, but the difference was not significant (Table XV). Controls on both photoregimes were much more aggressive than testosterone-treated males, and frequently engaged in wing-beating, a behaviour usually seen only in male-male interactions.

2. Courtship

The only courtship performed by the control castrates consisted of
TABLE XV Frequency of aggressive and courtship activities in castrates, based on the total number of intervals during which the activities were observed. The males were treated with TP or oil while being held on long or short photoperiods.

<table>
<thead>
<tr>
<th>Activity</th>
<th>SHORT PHOTOPERIOD</th>
<th>LONG PHOTOPERIOD</th>
<th>p*</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Control n=3</td>
<td>TP n=7</td>
<td>Control n=2</td>
</tr>
<tr>
<td>chasing/pecking</td>
<td>53(^{a}) (5-80)(^{b})</td>
<td>28 (0-75)</td>
<td>68 (43-93)</td>
</tr>
<tr>
<td>bow-cooing</td>
<td>-</td>
<td>13 (7-26)</td>
<td>-</td>
</tr>
<tr>
<td>nest-soliciting</td>
<td>-</td>
<td>604 (164-1180)</td>
<td>-</td>
</tr>
<tr>
<td>male-at-nest</td>
<td>6 (0-17)</td>
<td>748 (213-1117)</td>
<td>1.5 (0-3)</td>
</tr>
<tr>
<td>allopreening</td>
<td>5 (2-13)</td>
<td>93 (28-145)</td>
<td>30 (1-60)</td>
</tr>
</tbody>
</table>

* based on Mann-Whitney U-test (Siegel, 1956) of means, 1-tailed for LT>ST

a mean

b range
low levels of allopreening and sitting at the nest site. Testosterone-treated males, on the other hand, exhibited the various courtship activities at levels comparable to those seen in intact birds in experiment II (Table XV, figs. 10 & 11). There were no differences between LT and ST birds in terms of any of these behaviours. Similarly, copulatory behaviours were infrequent or absent in controls, while in both the LT and ST groups levels resembled those of intact pairs (Table XVI).

Females mated with oil-treated males continued to solicit, sit at the nest, and allopreen, but at lower levels than those of hormone-treated pairs; no doubt as a result of the lack of male courtship. There were no significant differences between the LT and ST females (Table XVI; figs. 12 and 13).

3. Nest-building

Control males did not participate in nest-building despite the fact that females paired with them exhibited considerable nest-soliciting and sitting at the nest (Table XVII).

LT males were more active than ST males in terms of all three measures of nest-building. The differences in the amount of time spent building and the number of pieces of string collected were significant. As in experiment II building peaked shortly before the first egg was laid (figs. 14, 15, and 16).

LT females also built significantly more than ST females, but the frequency was so low that it was not likely to have seriously influenced the total string counts.
Fig. 10. Nest-soliciting performed by castrates in relation to the laying of the 1st egg (day 0).
Fig. 11 Amount of time spent by castrates at the nest site in relation to the laying of the 1st egg (day 0).
TABLE XVI Frequency of copulatory and female courtship activities of pairs in which the males were treated with TP or oil while being held on long or short photoperiods. Values are based on totals for the 14 day test period.

<table>
<thead>
<tr>
<th></th>
<th>SHORT PHOTOPERIOD</th>
<th>LONG PHOTOPERIOD</th>
<th>p*</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Control n=3</td>
<td>TP n=7</td>
<td>Control n=2</td>
</tr>
<tr>
<td>begging events</td>
<td>2a (0-4)b</td>
<td>20 (10-31)</td>
<td>2 (0-4)</td>
</tr>
<tr>
<td>billing events</td>
<td>-</td>
<td>8 (1-12)</td>
<td>-</td>
</tr>
<tr>
<td>sexual crouch events</td>
<td>.3 (0-1)</td>
<td>6 (1-12)</td>
<td>-</td>
</tr>
<tr>
<td>mounts/copulations events</td>
<td>-</td>
<td>2.7 (0-7)</td>
<td>-</td>
</tr>
<tr>
<td>submissive crouch events</td>
<td>0.7 (0-2)</td>
<td>1.1 (1-4)</td>
<td>-</td>
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<tr>
<td>female soliciting intervals</td>
<td>441 (118-737)</td>
<td>425 (217-760)</td>
<td>296 (3-591)</td>
</tr>
<tr>
<td>female-at-nest intervals</td>
<td>800 (336-1242)</td>
<td>1279 (401-2078)</td>
<td>549 (0-1098)</td>
</tr>
<tr>
<td>female carrying events</td>
<td>1.7 (0-5)</td>
<td>1.7 (0-10)</td>
<td>1.0 (0-2)</td>
</tr>
<tr>
<td>female building intervals</td>
<td>7.7 (0-23)</td>
<td>4.7 (0-19)</td>
<td>1.5 (0-3)</td>
</tr>
<tr>
<td>female allopreening intervals</td>
<td>7 (0-14)</td>
<td>92 (64-145)</td>
<td>22 (0-44)</td>
</tr>
</tbody>
</table>

* based on Mann-Whitney U-test (Siegel, 1956) of means, 2-tailed for LT vs ST
a mean
b range
Fig. 12. Female nest-soliciting in relation to the laying of the 1st egg (day 0).
Fig. 13 Amount of time spent by females at the nest site in relation to the laying of the 1st egg (day 0).
TABLE XVII   Nest-building activity of TP-treated and control castrates held on long or short photoperiods. Based on totals for the 14-day test period.

<table>
<thead>
<tr>
<th></th>
<th>SHORT PHOTOPERIOD</th>
<th>LONG PHOTOPERIOD</th>
<th>p*</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Control n=3</td>
<td>TP n=7</td>
<td>Control n=2</td>
</tr>
<tr>
<td>nest building intervals</td>
<td>-</td>
<td>71&lt;sup&gt;a&lt;/sup&gt;</td>
<td>255</td>
</tr>
<tr>
<td></td>
<td>(15-179)&lt;sup&gt;b&lt;/sup&gt;</td>
<td></td>
<td>(22-631)</td>
</tr>
<tr>
<td>carrying events</td>
<td>-</td>
<td>19</td>
<td>69</td>
</tr>
<tr>
<td></td>
<td>(3-63)</td>
<td></td>
<td>(4-167)</td>
</tr>
<tr>
<td>string pieces</td>
<td>1</td>
<td>137</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>(0-4)</td>
<td>(46-395)</td>
<td>(0-6)</td>
</tr>
<tr>
<td>string relative&lt;sup&gt;c&lt;/sup&gt; to ♀ at nest</td>
<td>-</td>
<td>10.2</td>
<td>30.8</td>
</tr>
<tr>
<td></td>
<td>(4.9-19.0)</td>
<td></td>
<td>(11.7-63.1)</td>
</tr>
</tbody>
</table>

* based on Mann-Whitney U-test (Siegel, 1956) of means, 1-tailed for LT<ST

a mean
b range
c based on \[ \frac{\text{total string}}{\text{total intervals ♀ at nest}} \times 100 \]
Fig. 14 Nest-building by castrates in relation to the laying of the 1st egg (day 0).
Fig. 15 Amount of string collected by castrates in relation to the laying of the 1st egg (day 0).
Fig. 16. Carrying by castrates in relation to the laying of the 1st egg (day 0).
Table XVIII indicates a positive correlation between the females' behaviour and nest-building, but again the total amount of string collected by birds exposed to long daylengths was greater regardless of the amount of time spent by the females at the nest (Table XVII).

4. Latency to Egg-laying

The latency to the first egg was shorter for LT females than the other 3 groups (Table XIX). The significant difference between the two hormone-treated groups cannot be explained in terms of male courtship, since levels exhibited by the two groups were similar. There is a possibility, however, that male nest-building behaviour, which begins about 5 days prior to egg-laying, or stimuli emanating from the nest, may stimulate ovulation (see Lehrman et al., 1961). The females used in this study were obviously at advanced stages of ovarian growth when paired, as evidenced by the fact that 3 of 5 females paired with castrates laid eggs (see Cheng, 1974).

D. SUMMARY

1. Castrated males ceased to exhibit courtship and nest-building behaviour, but were highly aggressive.

2. No differences were seen between LT and ST pairs in terms of male or female courtship or copulatory behaviour.

3. LT males built significantly more than ST males as did females paired with LT birds.

4. Females paired with LT males laid sooner than those paired with ST or control males, suggesting that stimuli from male nest-building or the nest may be involved in the induction of ovulation.
TABLE XVIII Spearman rank correlation coefficients (Siegel, 1956) among male and female activities and the latency to egg-laying. Based on combined values for LT and ST castrates (n=14).

<table>
<thead>
<tr>
<th></th>
<th>Chase</th>
<th>NS at nest</th>
<th>CB</th>
<th>NS</th>
<th>NS at nest</th>
<th>Cy</th>
<th>string at nest</th>
<th>o+</th>
<th>o+</th>
<th>o+</th>
<th>o+</th>
<th>o+</th>
<th>beg</th>
<th>bill</th>
<th>crouch</th>
<th>MT/cop</th>
<th>o+</th>
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* p=.05
** p=.01
TABLE XIX  Latency to first egg, based on the number of days since pairing. The mean was calculated by assigning a value of 15 to all birds which did not lay within the test period.

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* based on Median Test (Siegel, 1956), 1-tailed for LT>ST
CHAPTER V

GENERAL DISCUSSION

A. AGGRESSIVE BEHAVIOUR

1. The Role of Photoperiod

Photoperiod does not have any clear effect on aggressive behaviour in doves. In all of the treatment groups—intacts and castrates, with or without testosterone treatment—levels of chasing/pecking were similar in birds held on both long and short days.

Hutchison (1976) reported that male doves implanted intracranially with TP 30 days after castration exhibit similar levels of chasing whether they are exposed to 14L/day or 6L/day. An earlier experiment (Hutchison, 1974) had indicated that castrates implanted 90 days after gonadectomy are more aggressive if held on 13L/day than if held on 8.5L/day. This difference may reflect an increase in sensitivity to photoperiod with time following castration, or may stem from the fact that the two groups in the earlier experiment were tested several years apart. The more recent results are in agreement with those reported here in relation to the effects of photoperiod on aggression in androgen-treated castrates. They differ, however, in that Hutchison recorded much higher levels of chasing in intact birds held on long than on short days, while no differences were seen in the present study.

2. The Effects of Castration and Androgen

In the majority of birds which have been studied aggression has been shown to depend upon the presence of testosterone (see van Tienhoven,
1968, for review). Evidence based on doves and pigeons is conflicting. In intact birds exogenous testosterone will increase social rank (Bennett, 1940) but will not alter the frequency of attacks (Murton et al., 1969; Vowels & Harwood, 1966). Results reported here also indicate little effect of TP in intact birds.

Gonadectomy has been reported to result in total (Hutchison, 1967 & 1970a; Pietras & Wenzel, 1976) or partial (Erickson, 1966; Hutchison, 1970b & 1971; Silver et al., 1973) elimination of chasing in both doves and pigeons. Brain implants or injections of TP restore chasing in castrates, but only to levels significantly lower than those seen prior to gonadectomy (Hutchison, 1971 & 1974a). Contrary to these results, Martinez-Vargas (1974) observed no differences between oil and TP treated castrated doves; both attacked females upon their introduction.

In the present study castration resulted in an increase in aggression which was reversed by androgen treatment. One possible reason for the disparity between this report and previous ones is that results reported here were based on observations extending over a two week period, while those listed above record responses occurring only during the initial interaction of a pair, in some cases using periods as short as 3 minutes (i.e. Hutchison's papers). If the percentage of males exhibiting chasing/pecking during the first 15 minutes of experiment III are compared, adding together birds from the two photoperiods, then only 40% (2/5) of the control males displayed aggressive behaviour, as compared to 86% (12/14) of the TP-treated castrates and 92% (11/12) of the oil-treated intact males in experiment II.
It appears that although castrates are slower to respond, once they do the frequency and duration of their attacks exceed those of the androgen-treated groups.

3. Evidence of Two Distinct Types of 'Chasing

Up to this point chasing of female doves by the males has been considered an 'aggressive' behaviour. The term 'aggressive' is commonly used for a number of activities which may occur in various different contexts, including behaviour directed towards conspecific males and females in flocking, territorial, sexual, and hierarchal situations. It should be recognized that several kinds of aggression exist, each probably associated with different casual mechanisms.

In ring doves chasing of the female appears to be indicative of a sexual as well as an aggressive tendency; it occurs in close temporal association with more overtly sexual activities such as bowing and soliciting, and certain postural features, such as the raising of the dorsal feathers, are similar to those seen prior to copulation. It is therefore likely that chasing, like driving in the pigeon, is an ambivalent behaviour involving sexual, aggressive, and possibly escape tendencies (Goodwin, 1952 & 1956b; Fabricius & Jansson, 1963).

Aggressive behaviour occurring during encounters between males differs from that described above. Chasing is rarely accompanied by dorsal feather raising (McFarland & Bahr, 1968), and commonly gives way to wing-beating, a behaviour which is absent from interactions between successfully paired males and females (Lovari & Hutchison, 1975).

In the present study both types of chasing were observed. The
behaviour of intact males and TP treated castrates was the same as that seen in normal male-female interactions. Chasing by the oil-treated castrates, however, more closely resembled that of male-male encounters—the rump feathers were rarely raised and bouts of wing-beating occurred frequently. Coupled with the fact that the sexual motivation of these birds was obviously very low, as would be expected in fights between males, these factors suggest that the oil-treated castrates responded to females as they would to consexual intruders. Fig. 17 shows that unlike TP-castrates, which exhibit a steady decline in chasing following pairing, controls continued to show a high response during initial morning encounters for the first five days. Perhaps increasing sexual tendencies in hormone-treated birds progressively inhibited aggression, while controls fought for five days before accepting the intruder?

Somewhat similar results have been reported in pigeons. Both gonadectomized (Carpenter, 1958) and hypophysectomized (Collias, 1944) pigeons have been observed to successfully defend their territories against intact male intruders. In the case of the hypophysectomized birds fighting was vigorous and included wing-beating but no bow-cooing. Females were also attacked, but when the males were treated with TP aggression towards the females ceased and pairing occurred (Collias, 1944).

If, as has been suggested, the behaviour of the castrates more closely resembled that displayed towards intruding males than responsive females, then the apparent independence of aggressive behaviour from testosterone is less puzzling. In numerous bird species males remain
Fig. 17 Chasing by control and TP-treated castrates in relation to the time since pairing. Values are given for all four daily tests (9:00, 11:00, 1:00, 3:00). Solid squares represent the combined scores for ST and LT males (n=14), open squares represent the combined scores for SC and LC males (n=5).
aggressive during the winter months when the testes are small, and androgen levels presumably low (Davis, 1964). In some species (i.e. the ring-necked pheasant) other males may be tolerated outside the breeding season and females attacked (Guhl, 1961). Often there is a shift throughout the year in the amount of space which is defended (Wilson, 1975). Thus it can be seen that the type of agnostic behaviour displayed varies in form, and in its relation to androgen concentrations.

Aggression in the absence of high testosterone levels has also been observed in mammals. Mice will continue to fight for several months following gonadectomy, even in the absence of the adrenals (Edwards & Rowe, 1975). Castration of infant or adult mongolian gerbils (*Meriones unguiculatus*) increases intermale aggression, while TP treatment decreases fighting in both gonadectomized males and females (Anisko et al., 1973).

4. The Possible Involvement of Gonadotropins

Because aggression occurs in the absence of testosterone and occasionally is even increased by castration, it has been suggested that LH may be responsible for controlling aggressive behaviour in some species (Davis, 1964).

Castration stimulates the synthesis and release of LRF in rats (Moguilevsky, 1975) and increased pituitary responsiveness to it (McCann, 1974). In the Japanese quail gonadectomy causes large increases in plasma LH and FSH (Follett, 1976).

Baggerman (1966) found that gonadectomy had little effect on the agnostic behaviour of male stickleback (*Gasterosteus aculeatus* L.) if performed before the onset of breeding. Castrates held on long (16L:8D) days remain
aggressive, but those held on short (8L:16D) days do not (Hoar, 1962). It has been proposed that LH is responsible for agonistic behaviour in sticklebacks prior to the breeding season. Exogenous LH will increase the level of aggression seen in methyl-testosterone treated castrates, but neither hormone alone will induce fighting in SD fish (Hoar, 1962).

Female *Quelea quelea* show an increase in agonistic behaviour if ovariectomized during the breeding season (Lazarus & Crook, 1973). Injections of TP do not alter the dominance status or agonistic behaviour of intact males; LH, on the other hand, will increase aggression in intact males or females and in ovariectomized females (Lazarus & Crook, 1973; Crook & Butterfield, 1968).

Gonadotropins may play a direct role in the control of aggression in starlings, as well. If male starlings are castrated they continue to sing, and in some cases their social rank may increase (Davis, 1964). In paired encounters between intacts and castrates, the castrates were found to be dominant in the majority of cases (Mathewson, 1961). Testosterone injections do not increase rank positions (Davis, 1957), but LH injections do (Davis, 1964; Mathewson, 1961). Vandenbergh (1964) paired intact males held on 15L/day with males held on 8L/day. In 58 of 85 pairs the long day bird was submissive. He suggests that these results support claims that LH causes increased aggression in starlings, since the testes of the SD birds appeared to be inactive. However, short photoperiods would also be expected to lower LH levels.

Van Tienhoven (1968) has cautioned against considering the starling work as conclusive evidence of direct gonadotropic involvement in aggressive behaviour, since all of the experiments cited above, with
the exception of Vanderbergh's, failed to give statistically significant results, or involved injection of hormones at levels far outside the physiological range.

LH control of intermale aggressiveness could account for the large increase in agonistic behaviour seen in castrated ring doves, if it is assumed that they reacted towards females as consexual intruders. If testosterone stimulates the normal chasing of females, which is related to sexual behaviour, and inhibits gonadotropin secretion, then lower levels of intermale-type chasing would be expected in TP-treated castrates, as was observed. This explanation, however, is purely hypothetical, and depends on several questionable assumptions. In addition, little is known of the normal levels of LH in doves, although Murton et al. (1969) report that it is very low in feral pigeons during the bowing and nest-soliciting stages of the cycle.

In summary, then, it is proposed that the aggressive behaviour displayed by castrated male doves is qualitatively distinct from that seen in normal male-female pairs. What is commonly termed chasing in doves is probably an ambivalent behaviour involving sexual as well as aggressive tendencies. Chasing by oil-treated castrates, however, is likely a pure agonistic behaviour related to normal intermale aggression and possibly to the male-female aggression observed outside the breeding season in many species.

In addition, it is suggested that hormonal control of these two types of behaviour differ; sexual chasing appears to depend upon the presence of high androgen levels (see Hutchison, 1974c), while intermale-type
chasing does not. It is tempting to suggest that this second type of aggression is related to high gonadotropin concentrations, but such a conclusion is, as yet, unjustified.

B. COURTSHIP AND COPULATORY BEHAVIOUR

1. The Role of Photoperiod

Intact male doves held on long days court more actively than those held on short days, exhibiting higher levels of bow-cooing, nest-soliciting, and time spent at the nest-site. Androgen treatment of intacts in experiment II abolished differences in nest-soliciting, but bow-cooing and time-at-nest remained higher in LT birds (differences in the mean levels of these last two behaviours were large but not significant in both oil and TP-treated birds). Because the testis weight was greater in LT than ST males the role played endogenous androgens was unclear. Repetition of the experiment using castrates injected with TP showed that all three measures of hormone-induced courtship were similar in birds held on the two photoregimes. Oil-treated castrates did not display, indicating that male courtship is dependent upon the presence of androgens.

It has been suggested that long daylengths affect courtship by means of either an increase in testosterone levels or an increase in sensitivity to androgens (see Chapter III, section C2). In experiment III exogenous TP was equally effective on long and short days. Since the levels of soliciting exhibited were similar to those of the SC birds in experiment II (cf. tables VIII and XV), it cannot be assumed that the LT and ST males were performing at a maximum level, thereby masking any differences
in sensitivity to testosterone. It therefore seems likely that photoperiod controls male courtship by stimulating the hypothalamo-pituitary-gonad axis, resulting in an increase in secretion of testicular androgen. Such an interpretation depends upon the assumption that all three activities vary directly with androgen concentration.

In experiment II there was no correlation between testis size and courtship in control birds, and only soliciting was significantly altered by TP injections. However, courtship in male doves has been observed to increase with higher hypothalamic concentrations of TP (Barfield, 1971; Hutchison, 1970b). In addition with daily injections of TP at levels of 100 µg or less there is a direct relationship between androgen concentration and the level of courtship activity (Erickson, 1970). Thus it is plausible that increasing endogenous testosterone levels are responsible for the higher courtship activity observed in intact male birds on long days, although the evidence presented thus far is inconclusive.

2. Control of Copulatory Behaviour.

The daylengths to which the males were exposed had no effect on any of the activities associated with copulation. The mean values of begging, billing, and crouching for the LT-castrate pairs in experiment III were double those of the ST-castrate pairs, but the variability in both groups was large, and none of the differences was significant.

Although oil-treated castrates were not involved in copulatory activities, indicating that androgen is necessary for their occurrence, TP injections had virtually no effect in intact birds.

Billing, sexual crouching and mounting may persist longer than
courtship behaviour in gonadectomized male and female doves (Cheng, 1973a). Liley observed no clear relationship between copulation in female doves and the endocrine state as assessed on the basis of ovary and oviduct development (Liley, 1976) and exogenous hormone treatment (Liley, in press). He concludes that nest-oriented and copulatory behaviours are under the control of different casual factors. It is of interest that androgen implanted into the preoptic region of capons will induce copulatory behaviour in the absence of any courtship or aggressive displays (Barfield, 1965 & 1969).

The present study also indicates that copulatory behaviour may not be influenced by the same factors as courtship and nest-building. Although the female initiates the sequence by begging, the levels of billing and mounting suggest that the males' responsiveness is independent of both photoregime and androgen concentration (provided some is present). In intact birds the four copulatory activities were not correlated with courtship or nest-building behaviours, or with testis size in control birds (Table XI). In TP-treated castrates there was a positive correlation between billing and time spent by the male at the nest, but otherwise both billing and mounting/copulation were again independent of courtship and building activities (Table XVIII).

3. The Relationship of the Male's Photoregime to Female Behaviour and the Latency to Egg-laying

The courtship behaviour of the females did not vary significantly with changes in the treatment of their mates. Even those females paired with oil-treated castrates exhibited quite high levels of soliciting and
sitting at the nest. There was no correlation between either of these behaviours and levels of chasing, bowing, or nest-building in the males. High levels of female courtship were, however, associated with shorter latencies to egg-laying, suggesting that the females' behaviour was dependent upon their endocrine state rather than upon the behaviour of the males (cf. Martinez-Vargas, 1974). The relationship of female soliciting and time spent at the nest to male nest-building has been discussed previously.

Females paired with long-day males displayed more active nest-building than those paired with short-day males (the only significant difference was between the LT-castrate and ST-castrate groups). Both active nest-building and carrying were strongly correlated with measures of male nest-building. Active building by females usually occurred after male building had declined, and was possibly influenced by stimuli emanating from the nest or from participation in building.

The latency to egg-laying did not vary between groups in experiment II, although male courtship is known to stimulate ovulation (Erickson & Lehrman, 1964; Erickson, 1970; Barfield, 1971). The effectiveness of male behaviour depends, however, on the reproductive state of the female. Castrated males are ineffective in inducing ovulation in birds with small follicles (1.5 - 5.5 mm), but are as effective as intacts for birds with large follicles (7 - 13 mm) (Cheng, 1974). Thus there appears to be a threshold of responsiveness in females which is related to their endocrine condition; above this threshold the mere presence of another bird is effective, while below it complete male
courtship activity is required. Lambe & Erickson (1973) noted a similar all-or-none phenomenon. In groups of females exposed to the shadow of a courting male or to castrates half laid eggs within 7 days while the remainder not only failed to ovulate, but also exhibited very little development of the reproductive tract. Since the stimulus females in the present study were held on 14L:10D for two weeks prior to testing it is likely that they were in advanced ovarian stages when the experiments began, and thus responded equally well to all males.

In experiment III the latencies of the ST, LC, and SC groups were similar, but the LT pairs laid significantly sooner than the ST pairs. The explanation outlined above could account for the similarity between the control castrates and ST groups, but not for the shorter latency in the LT group. Courtship activity of the LT males did not differ from that of the others. In fact, the only distinction was in nest-building: LT males built much more than ST males or controls. White (1975b) has reviewed the evidence of stimulation of ovulation by the nest and by participation in nest-building. She concludes that "some participation in nest-building is important in facilitating egg-laying." The reason why nest-building should have affected the latency to laying in the third experiment but not in the second is unclear. Liley (in press) noted that paired female doves held on long photoperiods came into breeding condition sooner than those held on short ones in December but not in March, and he suggests that courtship stimulation may be more effective in the spring. It is possible that the females used in this study exhibited a similar change in responsiveness to males;
and that those paired in late October/early November (experiment II) were not responsive to male building activity, while those paired in June (experiment III) were.

C. MALE NEST-BUILDING

1. The Influence of Daylength and Androgens

The occurrence of nest-building behaviour in male ring doves is dependent upon the presence of gonadal hormones. If males are castrated they will not participate in nest-construction, even if presented with adequate stimulation from the female. Injections of testosterone propionate and estradiol benzoate are both effective at reinstating building in castrated male doves (Martinez-Vargas, 1974).

The amount of building exhibited by any individual is determined by the interaction of both external and internal factors. Thus, testosterone propionate and estradiol benzoate will not induce building in intact male feral pigeons paired with females for only 30 minutes/day (Murton et al., 1969). In the dove the gathering behaviour of males is related to the firmness with which the female is attached to the nest site. Males whose mates perform high levels of soliciting and spend much of their time in the nest build more actively than those whose mates display little nest-oriented behaviour (Martinez-Vargas & Erickson, 1973). The state of the nest also influences building. Pairs given complete nests follow the same cycle of building as those without nest, with building beginning to increase about 4 days before the first egg is laid. The absolute amounts of building, however, are much greater in pairs with no nest (White, 1975b).
Photoperiod has a marked effect on building behaviour. Long-day birds are more active than short-day birds over much of the building cycle, but the pattern remains the same in both groups, with building increasing from day -5 or -4 to day -2 or -1, then dropping off. (This pattern is similar to that described by White ((1975b)), although she noted that the drop just prior to egg laying was not seen in those pairs whose nests were removed each day.) Since LT castrates build more than ST castrates, the photoperiodic effect does not appear to be mediated by changes in the levels of gonadal hormones.

2. The Relationship of Nest-Building to Other Reproductive Behaviours

It is of interest that although both courtship and building activities can be induced by testosterone treatment in male doves, only those behaviours directly associated with nest-construction are subject to the non-gonadal influence of photoperiod. Also, it is striking that it is nest-building behaviour which has been shown to be influenced by similar effects in both stickleback, (Hoar, 1962) and canaries (Hinde & Steel, 1975). In female doves both nest-soliciting and nest-building appear to be affected by daylength. Because the birds were intact, however, it is possible that one or both of these behaviours were affected by endogenous hormone production, as was courtship in experiment II of the present study.

The results cited above suggest that the control of nest-building behaviours may be separate from that governing courtship. In the normal reproductive cycle courtship and building activities
occur at different times of day. Soliciting and bowing are most frequent soon after the onset of light; building several hours later (Martinez-Vargas & Erickson, 1973; Martinez-Vargas, 1974). Moreover, courtship declines as the date of egg-laying approaches, while building increases until shortly before ovulation (fig. 18; see also Martinez-Vargas & Erickson, 1973; Gerlach et al., 1975; White, 1975b). Thus, even though both groups of activities are androgen-dependent, their occurrence is not determined by a unitary drive. The mechanisms controlling the appearance of courtship and nest-building are distinct and seem to be differentially affected by various external factors.

3. Possible Non-gonadal Mechanisms Involved in the Control of Male Nest-building by Photoperiod

There are several possible mechanisms which might be responsible for the observed differences in nest-building seen between the two photoperiods; daylength may function via a non-gonadal endocrine system; it may alter hypothalamic responsiveness to steroids as a result of changes in endogenous hormone levels, or it may affect hypothalamic sensitivity directly.

Hormones other than gonadal steroids are known to alter various aspects of behaviour. For instance, migratory restlessness and hyperphagia associated with pre-migratory fat deposition can be induced by long photoperiods in both intact and castrated birds (Lofts & Lam, 1973). These behaviours appear to be dependent upon prolactin, which may act synergistically with adrenocortical and gonadotropic hormones (Meier, 1972, van Tienhoven, 1968). Little is known of any possible synergistic
Fig. 18 The frequency of various reproductive activities in relation to the laying of the 1st egg (day 0).

CH/PK = chase/peck  BC = bow-coo; NS = male nest-soliciting; NB = male nest-building.

Values represent the combined scores of all males in experiment II.
CH/PK

n = 7 10 14 16 17 19 20 20 20 20 19 17 16 13 10

DAYS IN RELATION TO FIRST EGG

BC

NS

NB

DAYS IN RELATION TO FIRST EGG
effects between these hormones and androgens in male doves. Prolactin will
not augment nest-building in short day estrogen-treated ovariectomized
canaries (Hinde & Steel, 1975) but does induce later stages of nesting
behaviour in estrogen-treated ovariectomized budgerigars (Hutchison, 1975).
Furthermore, prolactin levels in male doves are low prior to incubation
(Lehrman, 1964).

Evidence of gonadotropic involvement in aggressive behaviour has
been mentioned. Involvement in nest-building is unlikely, however, as LH
has been found to have no effect on building in gonadectomized female
canaries (Hinde & Steel, 1975) or in Quelea quelea (Crook & Butterfield,
1968). In addition, LH levels appear to be very low in courting pigeons
(Murton et al., 1969).

More recently hypothalmic releasing factors have been implicated
in the control of mammalian sexual behaviour. LRF injections potentiate
the lordosis-inducing effect of low doses of estrogen in ovariectomized
rats (Moss & McCann, 1973 & 1975). The effect of LRF is independent of
changes at the pituitary level, since neither LH nor FSH will increase the
response to estrogen (Moss, 1974), and releasing factor is still effective
in hypophysectomized rats (Pfaff, 1973). It would be interesting to see
whether hypothalamic hormones affect behaviour in birds as well.

The pineal gland has been examined as a possible mediator of
photoperiodic effects in vertebrates (see reviews by Wurtman et al., 1968;
Ralph, 1970; Menaker & Oksche, 1974) and Steel & Hinde (1972) have suggested
that it may play a role in the photoperiodic control of nest-building in
canaries.
A second possible mechanism of photoperiodic influence involves changes in endogenous steroid production (Liley, 1976). Responsiveness to steroid hormones is known to decrease with time after gonadectomy in male (Davidson, 1972) and female (Damaso & Davidson, 1973) rats and in male ring doves (Hutchison, 1969 & 1974a). Thus, male doves exhibit significantly less courtship in response to intramuscular injections and intrahypothalamic implants of testosterone propionate if treated 90 days after castration than if treated 15 days after (Hutchison, 1974b). This decline in responsiveness appears to be reversed following exposure to testosterone (Hutchison, 1975 & 1976).

Liley (in press) has suggested that differences in the ability of exogenous hormones to elicit nest-oriented behaviour in female doves held on long and short photoregimes may be due to differences in endogenous hormone levels prior to treatment. Thus low production of endogenous estrogen by short day females, whose reproductive tracts were poorly developed, could have resulted in a decline in hypothalamic sensitivity such that lower levels of behaviour were displayed in response to exogenous hormones.

Similar consequences of variations in endogenous steroids could account for the differences observed in the building behaviour of the males in experiment II. This is supported by Hutchison's (1976) observation that male doves display less aggression and courtship if implanted with TP in winter, when testosterone production is presumably low, than if implanted in the summer.

In experiment III of the current study, however, endogenous
hormone levels did not differ between the long and short day groups, as all experimental males had experienced the same photoperiod prior to castration. Moreover, both groups were given similar maintenance levels of TP before being tested. In spite of this, levels of nest-building were greater on long days. It must be concluded, therefore, that if the responsiveness of the hypothalamus to androgens was altered by photoperiod the effect must have been direct or else mediated by some factor other than gonadal hormones.

In conclusion, daylength appears to influence both the production of and responsiveness to gonadal steroids. Long days result in greater gonad weights and an increase in courtship which appears to be due to higher testosterone levels. Long daylengths also potentiate the ability of testosterone to induce nest-building behaviour. Thus it is clear that the hormonal induction of behaviour is not a stable stimulus-response type of mechanism, but rather part of a dynamic relationship between the external and internal environments.


Liley, N.R. in press. The role of estrogen and progesterone in the regulation of reproductive behaviour in female ring doves (Streptopelia risoria).


