REPRODUCTIVE DEVELOPMENT AND FACTORS AFFECTING REPRODUCTION IN SEMI-DOMESTICATED CANADA GEESE

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ABSTRACT

REPRODUCTIVE DEVELOPMENT AND FACTORS AFFECTING REPRODUCTION IN SEMI-DOMESTICATED CANADA GEESE

by Jack Sheehan Wood

The Canada goose, Branta canadensis (Linnaeus) is one of the most important North American wildlife species. The subject of its management, from the viewpoint of habitat requirements, behavior, and rearing problems has been much discussed, but little is known of normal reproductive development, the association of behaviorisms to physiological changes, or of the physiology involved in these management problems. This study is an effort to advance the knowledge in these areas. Chief topics of research were the reproductive behavior in two established goose flocks, reproductive development under semi-domesticated conditions, and the possible use of hormonal treatments in altering these patterns.

Pairing occurred among individuals at all stages of normal reproductive development and during all periods of the year. Since pairing occurred in immature individuals it cannot be used as an index of reproducing pairs.

Libido is a function of the gonadal hormones, but there is reason to believe that it is in part controlled by the nervous system and independent of sex hormones in geese. The onset of breeding behavior does not necessarily indicate nesting probability. Territorial defense also occurs in immature geese, but apparently not in unmated birds.

Reproductive maturity is normally attained in the third year of life with a small percentage (about 5 percent) maturing in the second year. Most males appear to be physically mature in the second year but do not become active breeders until the following year. Both male and female first-year birds are immature and incapable of reproduction.

Gonadotrophic stimulation by subcutaneous injections of several hormonal compounds resulted in a variety of responses. The reproductive organs of two-year females were quite readily stimulated by these treatments. Although complete reproductive maturation was not known to have occurred, it is believed that with additional study it could be accomplished. Second-year males and both males and females in the third year were not noticeably stimulated. At no time during this study could any increase in libido be shown to have resulted from these treatments.

Follicular atresia occurred in individuals during nearly all stages of normal development. Its occurrence, therefore, is not believed to be an indication of reproductive inhibition. However, the presence of large numbers of well-developed follicles undergoing atresia during the early part of the breeding season may indicate predisposition to reproductive failure.

Canada geese, when adverse conditions existed, appeared to maintain their reproductive systems in a developed stage for extended periods of time without ovulating. Release from these conditions instigated a rapid response resulting in reproduction after a short time. The data indicate that these delays do not result in reduced clutch size except possibly very late in the breeding season.

The significance of the size of the available territory seemed to be related to the relative aggressiveness of the pairs involved. When pairs of nearly equal aggressiveness were penned together they nested on comparatively smaller areas. The importance of crowding as a deterrent to normal breeding activity seems to be an individual problem. The data in this study do not indicate any significant changes in clutch size due to variation in the extent of available area.

The endocrine cause of reproductive failure appeared to have been a lack of "ovulatory peaks" in the rate of secretion of the LH. The observed syndrome very closely resembled that described by Nalbandov (1958) and others in chickens which they attributed to a lack of LH peaks. A single attempt to force ovulation by progesterone treatment did not succeed. However, it is believed that additional tests should be made.

REPRODUCTIVE DEVELOPMENT AND FACTORS AFFECTING REPRODUCTION IN SEMI-DOMESTICATED CANADA GEESE

By

Jack Sheehan Wood

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INTRODUCTION

The Canada goose, *Branta canadensis* (Linnaeus), is often called the "big game" species of the birds. In this capacity it has attained a position of primary importance in wildlife management. Attempts to rear semi-domesticated flocks by federal and state agencies and by private individuals have demonstrated the adaptability and manageability of this species. However, even with this emphasis, little is known about the "internal mechanisms" of this bird. There is abundant literature on habitat requirements, behavior, and problems in rearing, but virtually none is available on normal reproductive development, the association of behaviorisms to physiological changes, and the physiological manifestation of management problems.

The Canada goose is an extremely adaptable bird. Both under semi-domesticated conditions and in the wild, they are found reproducing under a great variety of conditions. As an example of the extent of variation found, consider nesting density. C. S. Johnson (1947) reported that nesting geese, when confined, could not be crowded. At the Seney National Wildlife Refuge not more than one nesting pair to each half acre or acre of nesting territory was advisable. According to Johnson (*Ibid.*) nesting density was a problem and if sufficient space was not available, a reduced reproductive rate and clutch size would result. However, a brief survey of the literature reveals many populations nesting in far greater density with no significant decrease in clutch size (Table I).

While islands, particularly small islands, are universally felt to be the preferred habitat type, acceptable habitat covers a wide range of conditions. Table 2 is a partial list of habitat types used for nesting purposes as published by the various authors. If one is to consider the variety of conditions under which game breeders raise Canada geese, the list becomes unmanageable. Acceptable habitat appears to be a matter of individual response. Acceptance of any given habitat type may be a learned trait, but certainly is not species-wide.

Visibility advantage is usually considered to be the primary factor in selection of a nest site. Balham (1950) lists visibility of surrounding terrain, protection afforded, proximity of other nesting geese, and distance to water as the principle factors in nest site selection. Miller and Collins (1953) list identically the same four factors. Williams and Sooter (1940) report, in addition to these four factors, the presence of substantial nest bases. Although these are probably valid considerations when establishing an area for nesting purposes, the minimum requirements are extremely variable. As an example of an unusual situation which has been observed, Geis (1956) reports that 25 per cent of nesting pairs in the Flathead Valley were found in dense woods and heavy brush cover where visibility was limited to short distances. These nests were 100 to 300 feet from water.

The proximity of other nesting geese is of questionable importance as a consideration in nest site selection since the importance of the distance between nests is probably dependent upon the other factors and the relative aggressiveness of the pairs in question. This point will be discussed later. Klopman (1958) reported that nine yards was the minimum distance between nests observed by him.

It is apparent from these observations that Canada geese will tolerate a wide range of ecological conditions. Reproductive inhibition appears to result from exceeding levels of tolerance to the ranges of conditions, such as described above, within flocks or perhaps even individuals. The question then arises as to how these habitat variations affect normal reproductive development and how they inhibit reproduction when tolerance levels are exceeded.

This thesis considers the results of studies on: (1) the reproductive behavior in two established goose flocks, (2) reproductive development under semi-domesticated conditions, and (3) the ability of hormonal treatments to alter these patterns. This study was aimed at learning more about normal development, the endocrine cause of reproductive failure, and the relationships between behavior patterns and physiological reproductive development.

Table 1

Comparative Nesting Density and Clutch Size

Reference	Nesting Density	Average Clutch
	Lake Nesting	
Hanson & Browning (1959)	.003 to 4.0 per acre	5.3 in 1953 & 1955 5.5 in 1954 & 1956
Klopman (1958)	90 per acre (maximum)	5.0 in 1954 5.5 in 1955
Kossack (1950)	12 per acre	5.3 in 1946
Weigand (1960)	3 per acre (average)	5.44 in 1959
	Stream Nesting	
Craighead (1949)	8 per linear mile	5.0
Naylor & Hunt (1954)	3.6 per linear mile	5.3

Table 2

A List of Habitat Types Used for Nesting

Reference	Location	Type
Balham (1950)	Manitoba	Island, muskrat houses, beaver houses
Naylor (1953)	Lassen County, California	Island, bullrush over water, ditch banks, bullrush over land
Yocom (1952)	Washington	Osprey nests
Nelson (1953)	Alaska	Cliffs along a river
Miller & Collins (1953)	Siskiyou County, California	Muskrat houses, islands
Dow (1943)	Honey Lake Valley, California	Tule marshes, islands, hay stacks, irrigated meadow, muskrat houses, canal bank, willow clumps
Williams & Sooter (1940)	Utah and Oregon	Meadows, marsh, salt flats, knolls
Steel *et al*. (1957)	Grays Lake, Idaho	Island, fields, hay stacks, cattail islands, muskrat houses
Geis (1956)	Flathead Valley, Montana	Small islands, large islands, isolated peninsulas, osprey and heron nests, cliffs along river, muskrat houses, heavy brush cover, woods

MATERIALS AND METHODS

The study was carried on for a period of four years from 1959 to 1962. The experimental flocks, totaling 148 geese were used for hormonal treatments, as a source of reproductive organs for examination and for tests involving manipulation of habitat conditions. In addition, observations were made on the captive flocks at the Kellogg Bird Sanctuary near Hickory Corners, Michigan and at the Michigan State Game Farm near Mason, Michigan.

<u>1959 Tests (Group I)</u>--On April 5, 1959, 40 two-year* Canada geese were divided into five groups with four males and four females per group and treated as follows: (1) control, (2) extension of photoperiod from 7 p.m. to 10 p.m. for seven days (light intensity was not measured), (3) 1.5 pituitaries in .2 cc saline solution per bird in a single injection, (4) 500 I.U. of Pregnant Mares Serum Gonadotrophin per bird after 7 days of 15 hours of light per day, and (5) 1.5 chicken pituitaries after extension of the photo period as above (Table 3). These geese were then released as a unit and no attempt was made to keep the groups segregated.

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*In this article the use of age expressed in years is meant to imply the year of its life in which it was living, thus a two-year goose would be in its second year, and over one year but less than two.

Numbered collar bands were used for identification of individuals. In all cases the birds were also banded with U. S. Fish and Wildlife Service bands thus insuring accurate identification if the collars were lost.

With the exception of the chicken pituitaries, the hormones used in this and all subsequent studies were commercially prepared compounds. The pituitaries were collected from freshly killed, reproductively mature chickens, and quick-frozen in dry ice. In 1961 these pituitaries were lyophilized for more convenient storage and more accurate determination of the dosage levels used. Final preparation consisted of homogenizing the pituitaries in .5 percent saline solution and inoculating the birds with the resulting crude solution. All of the solution to be used during a given study was made at one time and individual dosages were calculated on the basis of the percent of the total volume. In using this method, care was taken to homogenize the solution sufficiently to remove all particles large enough to obstruct the hypodermic needle.

Thirteen days after release, nine of the geese in Group I and two additional pairs of geese were sacrificed and their reproductive organs collected. The groups represented in this collection were as follows: (1) a pair of one-year geese, (2) a pair of two-year untreated geese, (3) a pair of three-year geese, (4) four pituitary-treated two-year geese (two with light and two without), (5) one female treated with light only, and (6) two light and P.M.S.-treated geese.

In August of 1959, five males from Group I and eight one-year females were released on an area to be used the following spring. They were kept there for nearly a month in the late summer and again two weeks prior to treatment in April of 1960. For this experiment and all subsequent work, bonded-plastic leg bands of the type designed by Mr. R. D. VanDeusen with engraved letters and numbers were used for identification of individuals.

<u>1960 Tests (Group II)</u>--On April 16, 1960, 31 two-year Canada geese in addition to the 13 already being used were treated and released on two separate areas. On one of these areas, designated Area I (Trial I), 20 two-year geese were divided into three units as follows: (1) three females treated with diethylstilbestrol (12 mg. implant pellet) followed in one week by 2.5 chicken pituitaries per bird, (2) eight males and three females treated with 2.5 chicken pituitaries per bird, and (3) two males and four females untreated controls (Table 4).

On Area II (Trial II), 24 geese were divided into four groups and treated as follows: (1) eight three-year males and four two-year females (exposed to the nesting area in August, 1959) receiving no hormone treatment, (2) four two-year females (exposed to the area in August, 1959) treated with 2.5 chicken pituitaries per bird, (3) four two-year females and three two-year males treated with 2.5 chicken pituitaries per bird and released on the test area after treatment, and (4) four two-year males untreated and then released on the test area (Table 5).

<u>1961 Tests (Group III)</u>--In the spring of 1961, weather permitted initiating the test program in March, nearly a month earlier than the previous two attempts. It was decided that treatment should be confined to ten pairs that seemed mated during the previous summer. In addition, six mated pairs from the Michigan State Game Farm, which had previously nested, were incorporated into the flock to test the effect of handling and confinement on the results of the other treatments. Three of these six pairs were transported and handled with the test birds and then returned to their previous nesting area. The other three pairs were handled, transported, and penned not far from the other test geese. Of the geese to be treated, two pairs were released at the Mason Game Farm on the sites vacated by the three "proved breeder" pairs which were incorporated into the test flock. The remaining of the original ten pairs were penned on three separate areas. Two of these enclosed areas contained three pairs each and the other, two pairs. Three females and three males which were not paired were treated and sacrificed, and their reproductive organs examined. The treatments used on these ten pairs consisted of four types: (1) control, (2) 3.5 chicken pituitaries per bird, (3) 5 chicken pituitaries per bird, and (4) 2.5 chicken pituitaries per bird and then five pituitaries per bird two weeks later. A similar combination of treatments was used on the unpaired

geese which were later sacrificed (Tables 6 and 7).

1962 Tests (Group IV)--For the experimental work during the spring of 1962 emphasis was placed on attempting to inhibit reproduction in mated pairs (which had previously nested) by crowding them, and then to induce ovulation in non-producing females by hormonal treatment. Thirteen pairs were placed in three pens, with five pairs on the area designated as the Buttonbush Pond (3 acres), four pairs on the Farmlane Pond (1 acre) and four pairs on the Experimental Pond (1/2 acre) (Figure 1). Of these 13 pairs, seven appeared to be suppressed because they did not apparently establish and defend territories, and it was these which were used for the hormonal treatment (Table 8). The females of four of these pairs were given subcutaneous injections of one milligram of progesterone in sesame oil and the remaining females and all males were left untreated. Following treatment, these seven pairs were then confined for 60 hours in small cages (approximately 18 square feet) within the pens which they had previously occupied. These cages were visited periodically during the following 60 hours to determine if oviposition resulted.

A mortality during the winter prohibited the re-use of some Group III pairs and reproducing pairs from the Michigan State Game Farm were substituted. This may have played a significant part in the failure of this experiment since their tolerances to crowded conditions were not known and the amount necessary to suppress them could not be predetermined.

During the entire four-year period, observations were made on the experimental flock concerning behavior, nesting success, and of the manner of utilization of the available areas. Similar observations were made of the Kellogg Bird Sanctuary and Michigan State Game Farm flocks.

The observations and conclusions presented here are a composite of the results of these past four tests with the experimental flock, the data from the two observed captive flocks, and a general survey of the literature available on the Canada goose.

Table 3

Table of Treatment and Disposition of Canada Geese (Group I) for Hormone Experiment on April 5, 1959

Collar band	Sex	Treatment	Breeding activity	Time Post-treatment of sacrifice
1	m	Pituitary*	Paired 28	13 days
2	f	Light & pituitary		
3	m	Pituitary		
4	f	Light**		13 days
5	f	Control		18 days
6	f	Pituitary	Paired 34	13 days
7	m	Control		13 days
8	m	Pituitary	Paired female unknown	
9	m	Light		
10	m	Control		
11	f	Pituitary		
12	m	Light		
13	f	Light & P.M.S.***		13 days
14	f	Control		
15	f	Light & P.M.S.	Paired ?	
16	m	Light	Paired 24	
17	m	Light & pituitary	Paired 44	
18	m	Control	Paired 36	
19	m	Pituitary		
20	m	Light & P.M.S.	Paired female wild	

Table 3 (continued)

Collar band	Sex	Treatment	Breeding activity	Time Post-treatment of sacrifice
21	f	Light	Paired ?	
22	m	Control		
23	m	Control		
24	f	Light & pituitary	Paired 16	
25	f	Pituitary		
28	f	Pituitary	Paired 1	13 days
29	m	Light & P.M.S.		13 days
30	m	Light		
31	f	Control		
33	f	Light		
34	m	Light & pituitary	Paired 6	13 days
35	f	Light & P.M.S.		
36	f	Light & P.M.S.	Paired 18	
39	m	Light & P.M.S.		
40	f	Light		
41	m	Light & pituitary		
42	m	Light & pituitary		
43	f	Light & pituitary		
44	f	Light & pituitary	Paired 17	
45	f	Light & P.M.S.		

*Light--15 hours per day, for 7 days.

**Pituitary--30 chicken pituitaries in .5 percent saline solution, total 4 cc. Dosage--.2 cc. solution per bird.

***P.M.S.--500 International Units per bird.

Table 4

Table of Treatment and Disposition of Canada Geese (Group II, Trial I) for Hormone Experiment on April 16, 1960

Plastic band no.	Sex	Age	Treatment	Breeding activity	Comments
A	f	2	Stil.* & Pit.	Paired PP	
B	f	2	Stil. & Pit.	Paired MM	
C	f	2	Control	Paired VV	
D	m	2	Pit.**		
E	m	2	Pit.		
F	m	2	Control	Paired QQ	
MM	m	2	Pit.	Paired B	
NN	f	2	Control	Paired XX	
OO	f	2	Control		
PP	m	2	Pit.	Paired A	
QQ	f	2	Pit.	Paired F	
RR	m	2	Pit.	Paired UU	Dosage questionable, needle came out
SS	m	2	Pit.		
TT	f	2	Control		
UU	f	2	Pit.	Paired RR	
VV	m	2	Control	Paired C	
WW	f	2	Pit.		
XX	m	2	Pit.	Paired NN	
YY	m	2	Pit.		
ZZ	f	2	Stil. & Pit.		

*Stil.--Diethylstilbestrol implant pellet (12 mg.) in the neck (4-9-60).
**Pit. --Chicken pituitaries, dosage 2.5 (.0640 grms.) per bird in .3 cc. of .5 percent saline solution (4-16-60).

Table 5

Table of Treatment and Disposition of Canada Geese (Group II, Trial II) for Hormone Experiment on April 16, 1960

Plastic band no.	Sex	Age	Treatment	Breeding activity	Comments
AA	f	2	Cont.* & Exp. **	Paired EE	
BB	m	3	Cont. & Exp.		
CC	f	2	Cont. & Exp.		
DD	f	2	Pit. & Exp.		
EE	m	3	Cont. & Exp.	Paired AA	
FF	f	2	Pit.*** & Exp.		
GG	f	2	Pit. & Exp.		
HH	f	2	Cont. & Exp.		
II	m	3	Cont. & Exp.		
JJ	m	3	Cont. & Exp.		Found dead 5-7-60, cause unknown (lead poisoning?)
KK	f	2	Cont. & Exp.		
LL	f	2	Pit. & Exp.		
B1.12	m	3	Cont. & Exp.		Found dead week of 4-30-60, cause unknown

Table 5 (continued)

Plastic band no.	Sex	Age	Treatment	Breeding activity	Comments
M	m	2	Cont.		
N	f	2	Pit.	Paired S	
O	m	2	Pit.		
P	m	2	Cont.		Found dead 5-21-60, cause unknown
Q	m	2	Pit.	Paired K	
R	f	2	Pit.		
S	m	2	Pit.	Paired N	
H	m	2	Cont.		Found dead 5-21-60, cause unknown
J	m	2	Cont.		Found dead 5-21-60, cause unknown
K	f	2	Pit.	Paired Q	
L	f	2	Pit.		

*Cont.--Control.
**Exp. --Exposed to area August 7, 1959, to September 4, 1959, and April 2, 1960, to April 16, 1960.
***Pit. --Chicken pituitaries, dosage 2.5 (.0640 grms.) per bird in .3 cc. of .5 percent saline solution April 16, 1960.

Table 6

Table of Treatment and Disposition of Canada Geese (Group III) for Hormone Experiment on March 11, 1961

Plastic band no.	Pair no.	Sex	Age	Treatment	Pen Area (Figure 1)	Comments
EE	1	m	4	Control	Experimental Pond	Paired
R		f	3			
MM	2	m	3	3.5 Pit.**	Experimental Pond	Paired
B		f	3	3.5 Pit.		
UU	3	f	3	3.5 Pit.	Experimental Pond	Paired
E		m	3	3.5 Pit.		
YY	4	m	3	Control	Farm Lane Pond	Paired
WW		f	3	Control		
PP	5	m	3	2.5 +5 Pit.*	Farm Lane Pond	Paired
A		f	3	2.5 +5 Pit.*		
Q	6	m	3	Control	Long Woods Pond	Paired
K		f	3	Control		
VV	7	m	3	5 Pit.	Long Woods Pond	Paired
C		f	3	5 Pit.		
F	8	m	3	5 Pit.	Long Woods Pond	Paired
QQ		f	3	5 Pit.		
NN	9	f	3	Untreated	Mason Game Farm	Paired
XX		m	3	Untreated		

Table 6 (continued)

Plastic band no.	Pair no.	Sex	Age	Treatment	Pen Area (Figure 1)	Comments
D	10	m	3	Untreated	Mason Game Farm	Paired
CC		f	3	Untreated		
351	11	m	7	Untreated	Buttonbush Pond	Reproducing pair from
326		f	7	Untreated		Mason Game Farm
316	12	m	7	Untreated	Buttonbush Pond	Reproducing pair from
375		f	7	Untreated		Mason Game Farm
--	13	m	4	Untreated	Buttonbush Pond	Reproducing pair from
--		f	4	Untreated		Mason Game Farm
325	14	m	7	Untreated	Mason Game Farm	Transported & returned
332		f	7	Untreated		to Mason Game Farm
333	15	m	6	Untreated	Mason Game Farm	Transported & returned
335		f	7	Untreated		to Mason Game Farm
--	16	m	6	Untreated	Mason Game Farm	Transported & returned
5		f	10	Untreated	Mason Game Farm	to Mason Game Farm

*Two doses given the first on March 11, 1961, and the second on March 25, 1961.
**Pit.--Crude solution of chicken pituitaries homogenized in .5 percent saline solution.

Table 7

Table of Treatment and Disposition of Canada Geese (Group III) Sacrificed for Hormone Experiment on March 11, 1961

Plastic band no.	Sex	Age	Treatment	Pen area (Figure 1)	Comments
CC	f	3	5 Pit.**	Long Woods Pond	Unpaired (sac. 3-21-61)
SS	m	3	5 Pit.	Long Woods Pond	Unpaired (sac. 3-21-61)
0	m	3	3.5 + 5 Pit.*	Long Woods Pond	Unpaired (sac. 4-3-61)
--	f	4	3.5 + 5 Pit.*	Long Woods Pond	Unpaired (sac. 4-3-61)
RR	m	3	Control	Long Woods Pond	Unpaired (sac. 3-21-61)
--	f	3	Control	Long Woods Pond	Unpaired (sac. 3-21-61)

*Two doses given the first on March 11, 1961, and the second on March 25, 1961.
**Pit.--Crude solution of chicken pituitaries homogenized in .5 percent saline solution.

Figure 1. Map of the Kellogg Bird Sanctuary showing confinement areas.

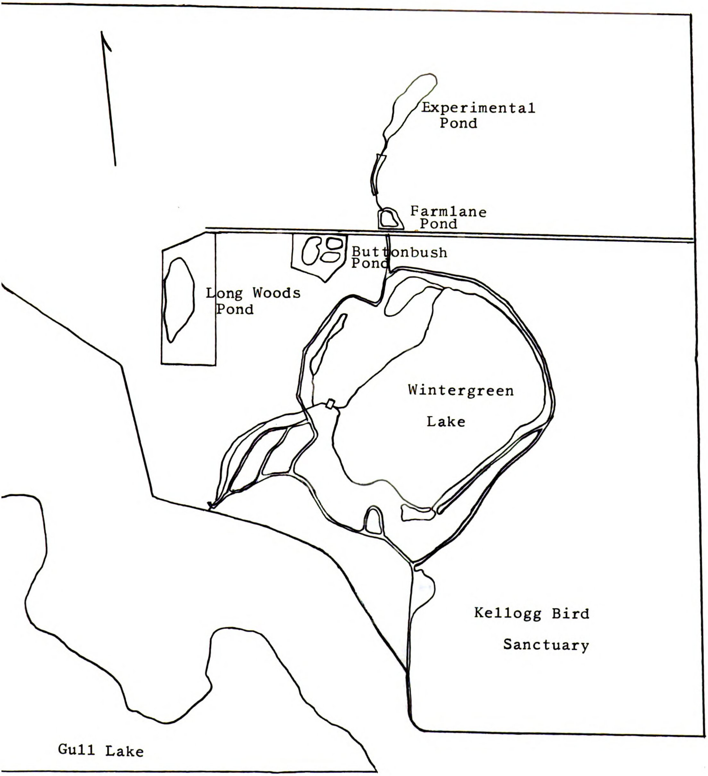

Experimental
Pond
Farmlane
Pond
Buttonbush
Pond
Long Woods
Pond
Wintergreen
Lake
Kellogg Bird
Sanctuary
Gull Lake

Table 8

Table of Treatment and Disposition of Canada Geese (Group IV) for Hormone Experiment on March 31, 1962

Plastic band no.	Pair no.	Sex	Age	Treatment	Pen area (Figure 1)
EE	1	m	5	None	Experimental Pond
R		f	4		
MM	2	m	4	None	Experimental Pond
B		f	4		
UU*	3	f	4	Control	Experimental Pond
E		m	4		
376(QQQ)	17	f		None	Experimental Pond
417		m			
YY	4	m	4	None	Farmlane Pond
WW		f	4		
Q	6	m	4	Control	Farmlane Pond
K		f	4		
PP	5	m	4	None	Farmlane Pond
A		f	4		
NN	9	f	4	1 mg.	Farmlane Pond
XX		m	4	Progesterone	
-(EE)	16	m	7	1 mg.	Farmlane Pond
5		f	11	Progesterone	
-(JJ)	13	m	5	None	Buttonbush Pond
-		f	5		
353(01)	18	f		1 mg.	Buttonbush Pond
343		m		Progesterone	
335(SSS)	15	f	8	Control	Buttonbush Pond
333		m	7		
381	19	m		1 mg.	Buttonbush Pond
319		f		Progesterone	

*The male was driven off by number 22 of the Kellogg Bird Sanctuary flock during the first week in the area.

RESULTS AND DISCUSSION

Geese used during this study were semi-domesticated and therefore the statements made here do not necessarily apply to wild Canada geese. It is reasonable to expect that the reproductive physiology is essentially the same and that the association of behaviorisms and physiology are similar, but they may respond quite differently to the manipulation of existing conditions.

Reproductive Behavior and Its Association to Maturity and the Gonadal Hormones

Discussion of the various calls and mannerisms associated with reproduction have been covered in several previous studies, notably by Kossack (1950), Balham (1950), and Collias (1959). This study recounts the various behavior characteristics only as they are related to reproductive development and physiological changes.

The onset of behavior characteristics similar to those of mature mated geese is not necessarily proof of physical maturity. It is a common sight to see geese of less than one-year imitating parts of the courtship behavior. However, at no time during this study was a known immature or an unpaired mature goose seen to perform the complete courtship ritual as described by Kossack (1950). This study showed that the onset of displaying is not indicative of sexual maturity, since behaviorisms commonly associated with reproduction were frequently observed to be performed by immature geese.

It has been observed that libido is a function of the gonadal hormones (Nalbandov, 1958), but there is reason to believe that it is in part controlled by the nervous system and independent of sex hormones, at least in geese. This may partly account for the occurrence of these reproductive behaviorisms in immature individuals. Nalbandov (*ibid.*) says about humans that:

> Because of the well-known relation between libido and androgen, it was expected that the hormone would correct low sex drive or impotence in males. In general, however, androgen is able to correct low sex drive only if this condition is due to testicular hypofunction and deficiency of the hormone. Many cases of male impotence seem to be due to phychological involvement and cannot be corrected by androgen medication.

In a preliminary study at the Kellogg Bird Sanctuary, Smith and VanDuesen (1958) reported that testrosterone proprionate and diethylstilbestrol treatment would produce only part of the behavior characteristics of mature geese. They also reported that no increase in aggressiveness or change in social status resulted from these treatments.

The results of this study are not conclusive. In a few instances there was an indication that treatment with chicken pituitaries may have increased libido in two-year geese. There was no apparent response to treatment in either paired or unpaired three-year birds. In addition, at no time during this study was there any apparent change in social status resulting from treatment, but paired geese were usually dominant to unpaired, and nesting geese usually dominant to either paired or unpaired geese not actively nesting. One notable exception to this was the defeat of a mature pair which were incubating, by a two-year pair, VV and C in Table 4. This two-year pair did not attempt to nest after driving off the adults.

A part of the lack of response to chicken pituitary treatment with reference to libido may have been due to these pituitaries being deficient in Leutenizing Hormone (LH) as will be discussed. If reproductive behavior is dependent upon androgen stimulation and androgen secretion dependent upoh LH (Nalbandov, 1958), an increase in libido would not result when using LH deficient pituitaries regardless of the amount of Follicle Stimulating Hormone present (FSH).

In addition to the inability to demonstrate a direct relationship between libido and stimulation by these gonadotrophic treatments, it was noted that even during periods of reproductive quiescense, fright would induce a behavioral response similar to the precopulatory display. Since these behaviorisms were not limited to periods of gonadotrophic stimulation and usually followed a period of obvious excitation, it appeared to be a neural response. The theory that it is in part neural and independent of gonadal hormones could also help to explain the occurrence of precopulatory behavior in very young birds as previously stated, since all observations of such displays during this study occurred during periods of excitation. This excitation usually occurred during periods of social strife within the flock. However, a similar response could be obtained by frightening them. In this case, the response was somewhat delayed and did not occur until after the initial "flight" reaction had subsided.

Territorialism in geese appears to be closely related to pairing. Unlike most other species which exhibit this phenomenon, it is not a characteristic of unmated birds. In a survey of the literature and in observations of the Kellogg Bird Santuary flock, the Mason Game Farm flock, and the experimental flock used in this study, there were no known instances of territory establishment by unmated geese.

There is uncertainty as to what constitutes territorial defense. Based on observations of the mature pairs available for this study, territorial defense occurs in three phases. Initially it is not truly a defense of a territory at all, but rather a defense of the female and possibly an ill-defined area about her. During this phase the location and boundaries of this area vary considerably. The second phase appears when the pair has selected a nest area, but before the time of oviposition is near. The exact preovulatory length of time is not known, but seems to vary. The territory is then limited to a definite area and the male defends against the intrusion of other geese. The boundaries of the territory at this time vary with the ability of the male to defend them. In neither of the first two phases would the males defend if threatened by either a dog or man.

The third phase includes a fixed area of fairly well defined boundaries and defense attempted against the intrusion of a dog or person as well as against other geese. This phase of territorial defense was observed to begin seven days or less before the first egg. It is interesting to note here that though both of the first two steps were observed to have occurred with both immature pairs and "unfruitful" adult pairs, the third phase, when it occurred, always preceeded at least an attempt to nest. However, not all mature reproducing pairs displayed this aggressiveness and a lack of it did not appear to indicate a predisposition to reproductive failure.

The role of pairing in the reproductive scheme of the Canada goose has been discussed many times (Balham, 1950, and Kossack, 1950). This interest stems from the fable that geese mate for life. In spite of this interest in pairing, the role of pairing is very poorly understood and observational data are often misinterpreted.

Pairing is the social union of a male and a female. With geese, pairing involves mutual selection and defense against other members of the same species. Although libido is probably the underlying cause, pairing is not necessarily related to sexual maturity, nor periods of sexual stimulation.

In addition to immature geese which display behavior patterns similar to those of breeding pairs, some successful nesting pairs fail to show the aggressiveness normally associated with mating and nesting. An example of this last point is Pair 3 (Table 6). This pair was formed by a female in the experimental flock and a male from the Kellogg Bird Sanctuary flock. It was not known that they were actively nesting until the female was sacrificed and the reproductive organs examined (Figure 9). At no time were they known to have defended a territory even against other geese.

Observational data on the Mason Game Farm and Kellogg Bird Sanctuary flocks indicate that it is not uncommon for geese to pair in their first year. In the second year pairing is common and these pairs often imitate the actions of mature geese even to the point of copulation and nest building. Most certainly some of these are mature (about 5 percent do succeed), but many two-year geese and probably all one-year geese are physically immature.

Examination of the reproductive organs of both paired and unpaired two- and three-year geese showed no relationship between gonadal activity and incidence of pairing. All four unpaired, three-year geese autopised (two males and two females) were physically mature. On two separate occasions the reproductive tracts of paired two-year geese were examined and the female in both cases did not show mature gonadal development. It is for this reason that the incidence of pair formation is not presently believed to be a reliable means of determining the probable size of the breeding population.

The use of the hormone treatments previously mentioned may have increased the incidence of pairing in two-year geese. Considering jointly both Groups I and II, including both trials of Group II, seven of 27 control geese and 20 of 41 pituitary-treated geese were paired during the period (Tables 3 and 4). A statistical analysis of these data by chi-square resulted in a value of 7.10 with one degree of freedom. This value is significantly different at the .01 level, but not at the .005 level. In these tests, both members of the pair were considered individually since no attempt was made to segregate the treatment groups, and any given individual could pair with either a treated or untreated mate.

Undoubtedly, some pairs existed within the groups before the test period and probably a greater percentage of these previously established pairs were incorporated into the pituitary-treated group than would have occurred by chance alone. Selection for treatment was based on the order of capture during the process of handling. Since pairs tend to remain together even when in the flock, and the treated birds were selected first, the capture of one member of a pair increased the probability of capture of the other at that time. The results would bias the figures in favor of the treated group and give reason to doubt the validity of the conclusions.

Exposure to the area before the breeding season and for a two-week period prior to treatment did not induce any increase in the rate of pairing. In the single test, Group II, Trial II (Table 5), two of 13 geese exposed to the area and four of 11 not exposed were known to have paired.

Even though sexual activity is minimal during the summer and fall, the bond between individuals in a pair remains and indeed some pairing takes place.

At the conclusion of the test period with Group II in the spring of 1960, the 20 remaining geese were combined into a single flock and penned together from early summer until the following spring. During this period it was observed that even though there was no apparent defense by the pairs, when the flock was disturbed they would arrange themselves in definite groups of pairs. If they were cornered and allowed to escape in singles and pairs, the same combinations would be together each time. In many cases (six of ten pairs), these pairs were together during the previous spring. The other four pairs were established sometime between June and September. Of the four pairs, one resulted from the loss of the female and the acceptance of another by the male, pair 1; another was the combination of two previously unmated birds, pair 4; the third resulted when the female accepted a new male even though the other was still there, pair 3 (this male was defeated by still another the following year); the fourth was the combination of a male from one flock and a female from the other, pair 10 (Table 6).

With the start of the breeding season in 1961 these ten pairs adopted the typical behavior patterns of mated pairs as described by Kossack (1950). Seven of these pairs nested during that season (Table 9). The penning and handling of these for purposes of hormone treatment (see Endocrine Causes of Reproductive Failure), possibly contributed to the lack of success of some of these pairs. It should be noted here that of the four pairs believed to have been formed during the summer only one pair nested the following spring, while five of the other six pairs formed in 1960 nested.

Of the remaining 12 geese in the flock of 32, six escaped or were killed. The other six, which were a part of the flock during the entire period, consisted of three males and three females. These birds were not paired (although RR was paired the previous spring) during this study period and did not pair during the breeding season even though they acquired the other normal behavior patterns.

Records at the Mason Game Farm and observations during this study seem to indicate that pairs formed while one or both of the individuals are still immature tend to last. These pairs are, of course, subjected to the same disruption factors as adult pairs, but if given the opportunity they tend to remain together.

Of the ten pairs in this study which were formed at two years of age or younger and kept together for at least two years, only one change was observed. This was the female UU which was originally paired with RR (Table 4) and then paired with a different male each of the next two years, E as pair 3 in 1961 and with number 22 in 1962 (Tables 6 and 7).

It should be stressed that although pairing is an intricate part of reproduction, its occurrence should not be misinterpreted as a sign of maturity. Also the period of quiescence of the reproductive system does not necessarily destroy the bonds between individuals in a pair or prohibit pair formation.

Figure 2. A pair of geese in normal repose. This pair was nesting and were not disturbed at the time. Photo by Dr. M. D. Pirnie.

Figure 3. The male in a defensive position. The female is sitting on the nest in the background and the male is showing the characteristic attitude of territorial defense. Photo by Dr. M. D. Pirnie.

Figure 4. Another example of the defensive attitude of a pair when disturbed by man. Defense of this type normally preceded a nesting attempt, but a lack of it did not mean that nesting would not occur. Photo by Dr. M. D. Pirnie.

Figure 5. A mated pair excitedly "talking." This type of behavior is a part of the precopulatory display and also is a typical response to disturbance regardless of the season of the year. Photo by Dr. M. D. Pirnie.

Table 9

Nesting Record for Experimental Flock in 1961

Pair no.	Date First egg	No. of eggs	Date incubation started	Comments
14	April 2	4	--	Eggs gathered**
15	April 2	6	--	Eggs gathered**
16	April 5	5	--	Eggs gathered**
11	April 4	5	April 10	Hatched 4 young 5-8
2	April 4	4	April 9	Abandoned 4-27*
1	April 12	3	Abandoned	Did not begin incubation*
12	April 13	3	April 17	Hatched 2 young 5-15
9	April 21	4	April 25	Hatched 4 young 5-23
6	April 24	5	April 30	Abandoned*
7	April 25	4	May 1	Abandoned*
5	April 27	3	May 1	Abandoned*
13	May 5	2	May 7	Abandoned*

*Eggs examined, were fertile, and, except for pair 1, contained developed embryoes.
**This was the general practice for all nesting pairs at the Mason Game Farm.

Table 10

Nesting Record for Experimental Flock in 1962

Pair no.	No. of eggs	Start of incubation	Disposition
1	5	April 10	Hatched 5 (5-8-62)
2	6	April 8	Hatched 6 (5-5-62)
17	4	April 14	Hatched 3 (5-12-62)
4	5	April 12	Hatched 4 (5-10-62)
6	5	April 19	Hatched 3 (5-17-62)
5	6	April 14	Abandoned
13	5	April 14	Hatched 4 (5-12-62)
15	4	April 19	Hatched 3 (5-17-62)

Normal Reproductive Development

The following account of the reproductive development of the Canada goose is based on the macroscopic and histological examination of 20 individuals. This group was comprised of two one-year birds, nine two-year birds, eight three-year birds, and one four-year bird (Figures 6-10).

One-Year--Both sexes of Canada geese in the first year were found to be immature. The ovaries showed slight follicular development, but all follicles were in the very early stages of development (less than .15 cm.). There was little gradation in the stages of development of these follicles and deterioration of these cells and irregularity of contour in some of them indicated that they would probably not develop much beyond these early stages. The oviduct appeared to be in the early stages of development, consisting of single cell layers and lacking convolution. The epithelium consisted of a single layer of cells and there were no tubular glands present.

In the male the secretory cells of the epididymis were not developed, the seminiferous tubules of the testes were of the solid cord type, and the interstitial tissue was sparse. The lumina of the tubules were not developed although in some instances a partial cellular evacuation of the central portion of the lumina was noted. There was no evidence of spermatogenesis even in its early stages. The ductus deferens consisted of single cell layers, was not convoluted, and showed no indication of stimulation. There were interstitial cells present in these testes, but these were sparse and appeared inactive.

Although there are reports of geese reproducing in their first year, no instances have been reported from flocks where the birds were individually marked and the ages were known.

Two-Year--The ovary of the goose in its second year appears to be somewhat intermediate in size between those of the one- and the three-year birds. The increase in size over the ovary from the one-year bird is mostly due to increased proliferation of follicles, both in size (up to .91 cm.) and quantity (Figure 7). Although there were some larger follicles on the two-year ovaries, they were few in number and there was a noticeable lack of even distribution in the gradation of follicular development as compared to the mature ovary (Table 11). In general, these ovaries are immature. The oviducts were more developed than in a first-year goose containing a multiple-layered epithelium, but showing no signs of estrogen stimulation. The epithelial linings were in the rudimentary stages of development and the tubular glands of the magnum were not evident.

Unlike the females, the two-year males examined appeared to be sexually mature. The seminiferous tubules were normally developed and spermatogenesis was evident. The interstitial tissue was abundant and the Leydig cells appeared to be active. The secretory cells of the epididymis and the ductus deferens were normally developed and sperm were present throughout the tract.

The semi-domesticated Canada goose in its second year is apparently on the verge of sexual maturity since some do reproduce. However, the percentage is probably very low. On the average, less than 5 percent of all two-year semi-domesticated geese succeed in reproducing. Kossack (1950) lists the percentage as 7.8 and Balham (1950) found 1 percent or less. At the Mason Game Farm the percentage of two-year birds that reproduce rarely exceeds 5 percent.

Hanson (1950) reported that definite information on Canada geese breeding in the wild at two years of age is lacking, but wrote that if the presence of an open oviduct is a sign of sexual maturity or an indication that eggs have been produced, then the Horseshoe Lake data indicate that practically all females are productive at two years of age. The results of this study show clearly that the presence of a prominent oviductual opening is not necessarily a criterion of sexual maturity. As Hanson found, most two-year birds examined had open oviducts during the second fall, but all of them examined histologically during the reproductive period were definitely immature. Although the presence of this prominent opening may result from a response to hormonal stimulation, its existence does not insure reproductive maturity.

<u>Three-Year</u>--The condition of the reproductive organs of the male in its third year were about the same as described for the two-year old. The testes of the three-year males were larger (Table 12), but this may have been due to individual variation or perhaps an earlier photoperiod response by older individuals.

The reproductive organs of the three-year females examined appeared to be both mature and stimulated. The ovary exhibited typical gradation in follicular development (Table 9). The largest follicle present was not mature, but showed no signs of atresia. The most evident differences between mature and immature birds were in the condition of the oviduct. Under estrogen stimulation the tract becomes thick and very vascular. The uterus or shell gland area becomes pouch-like. Examination of sections of the magnum revealed that the epithelium was highly fimbriated and that the cells lining the lumen were simple-columnar and ciliated. The periphery contained large numbers of tubular glands.

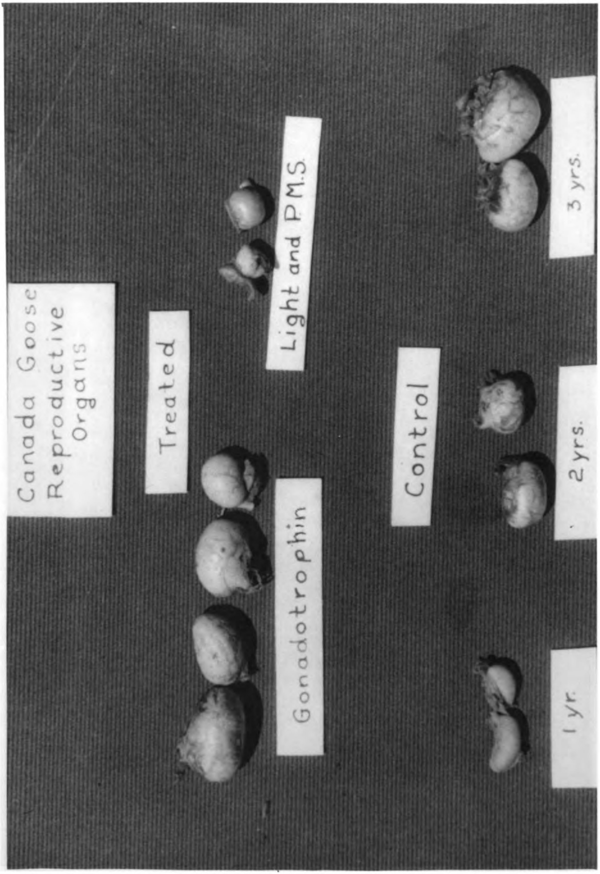
In general, the mature male and female reproductive systems appear to be structurally very similar to those of the chicken as described by Sturkie (1954). The oviduct in Figure 9 shows clearly the infundibulum, magnum, isthmus, uterus or shell gland area, and vagina. The ovary of the mature female contains a gradation in follicular development (Figure 7), but this gradation is interrupted during the later stages of development when there is an evident difference in size between the follicles which will presumably be ovulated and those which will not (Figure 9). Apparently at this time the larger follicles which are not to be ovulated regress. In Table 11 the three follicles immediately below the "break" in follicular gradation were all atretic.

Follicular atresia is apparently normal in Canada geese during all stages of reproductive development and, therefore, by itself is not indicative of reproductive inhibition. Atretic follicles are present on the ovary in Figure 9, even though she was actively reproducing as shown by the presence of the egg in the uterus. Atresia in very large follicles or large numbers of atretic follicles during the early part of the breeding season, however, may indicate reproductive problems.

Barry (1962) states that he observed a relationship between atresia and lateness of breeding season in brant and blue and snow geese. He postulates that there may be some relationship between the incidence of atresia and reduced clutch size or reproductive failure. However, any follicle which is not ovulated ultimately must become atretic. Most certainly this is true during the period of gonadal regression. Atresia is not an anomoly, but is rather the result of normal physiological phenomena. The importance therefore is not in the act of the follicles becoming atretic, but rather in whether it is due to normal gonadal regression or as a result of some malady.

For the incidence of follicular atresia to be of practical use in determining the effects of reproductive problems, it must be presumed that in determinant laying birds not only the number of follicules but also the precise follicles which are to be fully developed and ovulated are predetermined. This has not yet been proved. In addition, it would be necessary to be able to identify the precise follicles which would have been ultimately ovulated and this is presently impossible.

Figure 6. The gonads from sacrificed male Canada geese showing normal development and the responses of two-year birds to various hormonal treatments (approximately life size).



Canada Goose Reproductive Organs
Treated
Light and P.M.S.
Gonadotrophin
Control
3 yrs.
2 yrs.
1 yr.

Figure 7. The reproductive organs from sacrificed female Canada geese showing their normal development and the responses of two-year birds to various hormonal treatments, April 5, 1959 (approximately 1/2 life size).

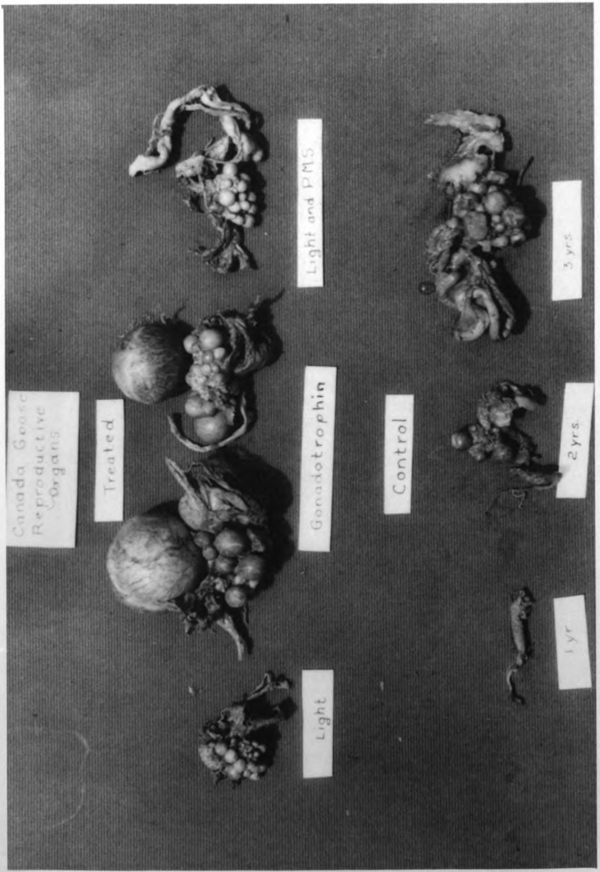

Canada Goose
Reproductive
Organs
Treated
Light and PMS
Gonadotrophin
Light
Control
3 yrs.
2 yrs.
1 yr

Figure 8. The reproductive organs from three-year female Canada geese showing a lack of response to gonadotrophic stimulation. Note the presence of atretic follicles (approximately 1/3 life size).


TREATMENT:
CONTROL
Age: 3 years
Sex: female
Date: 3/21/61
TREATMENT:
5 PITUITARIES PER BIRD
C.
Age: 3 years
Sex: female
Date: 4/3/61
TREATMENT:
3.5 + 5 PITUITARIES PER BIRD

Figure 9. The reproductive organs from a mature actively reproducing female Canada goose. Note the presence here also of an atretic follicle (approximately 1/3 life size). O -Atretic follicle.

Figure 10. The reproductive organs from three-year male Canada geese showing a lack of response to gonadotrophic stimulation (approximately 1/3 life size).


Date: 3/21/61
TREATMENT:
CONTROL
Date: 3/21/61
TREATMENT:
5 PITUITARIES PER BIRD
Date: 4/3/61
TREATMENT:
3.5 + 5 PITUITARIES PER BIRD

Table 11

Diameters in Centimeters of 10 Largest Follicles
on Ovaries of Sacrificed Canada Geese

Rank	1 yr. old	2 yr. old	Light treated 2 yr. old	Chicken pituitary treated 2 yr. old	Chicken pituitary treated 2 yr. old	P.M.S. treated 2 yr. old	3 yr. old	4 yr. old
1	--	.91	.53	3.58	2.70	.54	1.92	5.23
2	--	.83	.51	2.86	2.34	*.53	1.06	4.17
3	--	.48	.50	2.41	1.94	*.50	.98	3.95
4	--	.37	.49	1.85	1.62	*.48	.97	*.65
5	--	--	.23	1.40	1.23	.46	*.87	*.64
6	--	--	.22	1.26	1.01	*.45	.78	*.63
7	--	--	.18	.98	.92	.32	.72	.55
8	--	--	.15	.87	.79	.29	.61	.54
9	--	--	--	.75	.62	.28	.57	.47
10	--	--	--	.66	.55	.26	.52	.40

- Indicates to small to determine size gradiant.
* Atretic.

Table 12

Length and Diameter in Centimeters of Testes from Sacrificed Canada Geese

				Chicken pituitary treated		P.M.S. treated	
		1 yr. old.	2 yr. old	2 yr. old	2 yr. old	2 yr. old	3 yr. old
Left	Length	1.80	2.20	2.94	2.45	1.37	2.73
testis	Diameter	.86	1.37	1.92	1.68	1.01	1.60
Right	Length	1.42	1.75	2.23	1.92	1.00	2.28
testis	Diameter	.82	1.34	1.69	1.34	.84	1.29

Influence of Hormonal Treatment on Reproductive Maturation

The subcutaneous injections of chicken pituitaries and Pregnant Mares Serum (PMS), in combination with an artificially increased photoperiod, instigated a variety of responses. The lengthening of the photoperiod by itself or in combination with other treatments did not apparently increase gonadal development. Since natural light at that time of year was sufficient to induce gonadotrophic stimulation in mated pairs at the Mason Game Farm (mating had started), this result is understandable.

Treatment with 1.5 chicken pituitaries per bird resulted in a marked increase in follicular development at the end of 13 days (Figure 7). The ovaries of these geese appeared mature and in one case there was a mature follicle present. The absence of atretic follicles on these ovaries indicated that they had not passed the peak of gonadotrophic stimulation. The oviducts from these birds were immature and showed no indication of estrogen stimulation. Thus from this observation, it appears that in 13 days either the oviduct did not have sufficient time to respond to increased estrogen or the maturation of the ovary did not result in normal increased estrogen secretion.

Nalbandov (1958) reported that FSH alone, while causing an increase in ovarian weight, does not cause an increase in uterine weight in rats, which suggests that follicles produced with FSH alone are not capable of secreting estrogen. Perhaps this result suggests an LH deficiency in the chicken pituitaries being used, as previously suggested. This apparent LH deficiency can be explained in several ways, among which are: that handling for slaughter may have produced this effect; that since the chickens being used were "culled layers" they could be expected to have lower amounts of LH stored in the pituitaries; in addition, it is also possible that Canada geese are not responsive to the LH produced by chickens.

When diethylstilbestrol pellets were implanted one week prior to treatment with 2.5 chicken pituitaries (Table 4), maturation of the oviduct resulted, but the ovary was suppressed. The results were a mature oviduct and an immature ovary. An increase in dosage from 1.5 to 2.5 pituitaries per bird without stilbestrol implants did not appear to alter the response.

The treatment of two-year males with either 1.5 or 2.5 chicken pituitaries per bird did not result in any significant changes in the reproductive organs. There was a slight increase over the controls (Table 12) in the size of the testes, which may have been due to individual response variation. Histological examination showed that they were mature, spermatogenesis was occurring, and that they were not different than the untreated two- and three-year geese examined.

The subcutaneous injection of PMS gave very striking results in both the male and female two-year geese. The oviduct of the female was fully mature and functional, but the ovary macroscopically appeared suppressed. Microscopic examination revealed the presence of large numbers of atretic follicles indicating that the peak of development had occurred prior to the day of sacrifice. It appeared that the response to PMS was much more rapid than to chicken pituitaries and that these birds were not able to maintain this artificially-induced maturity after the influence of the treatment was lost.

The male two-year goose treated with PMS showed a complete regression of the reproductive system. The testes were small, wrinkled, and friable. The ductus deferens were small and lacked convolution. Microscopically they were similar to the male in its first year.

The treatment of three-year non-reproducing females with from 1.5 to 5 pituitaries per bird did not result in any significant increase in reproductive development. The use of a double injection of 3.5 pituitaries per bird and 5 pituitaries one week later also produced no significant changes. An explanation of this lack of response may be that maximal stimulation from FSH had been attained normally and the ovaries were thus not responsive to additional exogenous FSH. In addition, if these pituitaries were LH deficient, as previously discussed, final follicular maturation would not be expected to result regardless of the FSH level. There are other possible explanations, but in view of points which will be discussed later, the above seems most probable.

Confinement and Release Studies

There is little information as to the minimum territory per pair necessary for successful nesting. The high density of nesting which has been reported from some areas suggests that when other conditions are satisfactory the area required is very small.

In observations of Group III during the spring of 1961, no exact relationship between extent of available area and nesting success was observed. Two of the first three nests (pair 1 and pair 2, Table 6) were in the smallest pen, approximately 150 feet long by 50 feet wide. The pairs which nested in the largest pen (called the "Long Woods Pond," Figure 1) were the latest nests to be established. In neither area were the nests located at the maximum possible distance apart. In fact, the two nests in the smallest pen and three of the four nests in the largest were located on adjacent islands only 38, 78, and 74 feet from the nearest nest.

An analysis of variance for clutch size and extent of available area per pair in the experimental flock in this study resulted in an F value of .7622 (Table 13). With an F value this low there is no evidence to indicate that size of available area had any significant effect.

Space may become a limiting factor when the individuals involved are extremely unequal in social status. When one or more observed pairs were extremely aggressive or submissive, a greater amount of area was required than when they were nearly equal in social status. This problem was apparently responsible for the suppression of pairs 9, 12, and 13 prior to release from the pens as discussed later.

On the basis of the tests in handling, transporting, and confining of six pairs of geese in Group III which had reproduced the previous spring (Table 6), it was felt that only the confinement seriously affected reproduction. Of these six pairs, three pairs were handled and transported with the experimental flock and then returned to their previous nesting area at Mason Game Farm (pairs 14, 15, and 16, Table 6). These three pairs nested at the normal time and produced normal clutches (Table 9). Three other pairs (11, 12, and 13, Table 6) were handled, transported, and confined in a pen. Pairs 12 and 13 showed no indication of reproductive activity while in the pen. Both pairs established nests soon after being released (Table 9). Pair 11 reproduced normally in the pen.

The onset of secretion of gonadotrophic hormones by the pituitary of birds is dependent upon photoperiodic stimulation of the hypothalamus (Nalbandov, 1958). Since there is a limited period of time during the year when proper lighting conditions prevail, it is reasonable to expect that there is a limited time when reproductive success is possible. Therefore, the date of release in a suitable area might play an important part in reproductive success. The amount of data on this subject obtained during this study was small, but perhaps of value.

Because the first two years of work with the experimental flock (Groups I and II) did not result in any nesting, the influence of the date of release could not be determined.

The release date in 1961 (Group III) was March 11 which coincided with the start of nesting activity in the Kellogg Bird Sanctuary flock. The first egg laying from Group III did not begin until April 4, at which time some Kellogg pairs had begun incubation. Three pairs (14, 15, and 16, Table 6), were transferred at the same time and returned to their former breeding sites at the Mason Game Farm. These began nesting April 2-5, which coincided with the start of the nesting activity at the Mason Game Farm.

Pair 12 escaped from its pen on April 8 and pair 9 escaped on April 15. Pair 13 was released (Table 6). These two dates functionally serve as a type of release date since the pairs involved moved from an area that was apparently unsuitable for them into a more suitable one, since they behavioristically appeared to be suppressed prior to this release and made no attempt to reproduce in the pens.

Two of these three pairs began nesting almost immediately. The first egg from pair 12 was laid on April 13, and the first by pair 9 on April 21, nearly 1-1/2 months after the start at Kellogg. In contrast, the goose of pair 17 did not lay until May 2.

Three of the pairs left on the "release" area (pairs 5, 6, and 7) were apparently delayed in adapting and did not start nesting until the latter part of April. Four pairs did not show any indication of nesting during the study (Table 6).

Four geese from Group III were sacrificed on March 20 and another pair on April 3 (Table 7). Examination of their reproductive systems revealed that they were mature and stimulated at that time but apparently had not copulated during this period. Moulting, a normal indication of gonadal regression, was not known to have occurred in the flock from March 20 to May 31. In view of these facts, the nesting results previously mentioned indicate that the reproductive organs of the mature goose develop very early in the season. The fact that they are maintained at a high level of development was shown by the rapid response of pairs 9 and 12 to the changing of habitat when they escaped from the pens and that the geese examined were naturally stimulated on or before March 20, but did not begin nesting until the first of April.

Tables 9 and 10 reveal that the clutch sizes of the experimental flock, averaging 4.0, were well below the average size for either Mason Game Farm or the Kellogg Bird Sanctuary flocks which were 5.2 and 4.9, respectively. The exact reason for this is not known. However, it should be noted that within this group the size of the clutch did not change significantly from the beginning to the end of the nesting season (Table 14).

An analysis of variance involving the two variables, clutch size, and date of the start of incubation resulted in an F value of 3.10 which is not significant at the .05 level (Table 14). However, the group for May 1 and later appears to have a lower mean and a larger sample size might have shown a significant reduction in the very late clutch sizes. A second analysis of variance was calculated for date and clutch size from the nesting at the Kellogg Bird Sanctuary, 1933 to 1945, recorded by Dr. M. D. Pirnie. The resulting F value was even lower at .2604 though here also the sample size for the late dates was small (Table 15). In view of these results it appears that delaying reproduction does not necessarily result in a reduced clutch size.

In 1961 the last four nests (pairs 6, 7, 5, and 13) were abandoned before incubation was completed. This cannot necessarily be attributed to the lateness of season. Two other pairs (1 and 2) abandoned during the early part of the season. The eggs examined from these abandoned nests all proved to contain developed embryoes. The reason for this abandonment is not known.

Table 13

Analysis of Variance for Clutch Size and Available Area for This Study

	Total Available Area					
	less than .33 acres	.33 acres	1 acre	1.5 acres	no limit	
Clutch Size	5 6 4 3	5 6 5 3	4 5 4 5	5 3 2	3 4 6 5 4 7	
						Total
$n =$	4	4	4	3	6	21
$\Sigma X =$	19	19	18	10	29	94
$\Sigma X^2 =$	86	95	82	38	151	452
$(\Sigma X)^2/n =$	81	90.25	81.00	33.33	140.17	420.76
$\bar{X} =$	4.50	4.75	4.50	3.33	4.83	4.48
$S_b^2 = 1.25$						
$S_w^2 = 1.64$						
$F = .7622$	df. = 4/16					

Table 14

Analysis of Variance for Clutch Size and Completion Dates for This Study

	Date of Completion				
	April 1 - 10	April 11 - 20	April 21 - 30	May 1 -	
Clutch Size	5 4 5 6	3 5 5	5 4 4 4 6 5	4 3 2	
					Total
$n =$	4	3	6	3	16
$\Sigma X =$	20	13	28	9	70
$\Sigma X^2 =$	102	59	134	29	324
$(\Sigma X)^2/n =$	100	56.33	130.67	27	306.25
$\bar{X} =$	5	4.33	4.67	3	4.38
$S_b^2 =$	2.58				
$S_w^2 =$	.8333				
$F =$	3.10	df. = 3/12			

Table 15

Analysis of Variance for Clutch Size and Completion Dates at the Kellogg Bird Sanctuary from 1933 to 1945

Year	Date of Completion April 1 - 10	April 11 - 20	April 21 - 30	May 1 -
1933	6,6	6,4,4		
1934	3	5,7,5,5,6		
1936	6,6,5,6	6,6	4	
1937	6,5,4,5	6,6,3	4,6,5,4,4	
1938	5,7,3,6,4,4	7,6		
1939		5,5,6,3,5,2,5		
1940	3	6,6,5,3,4	6,5,5,7	
1941	5,5	5,5,5,4,5,6,4 5,5		
1942	5,6,6,4,5	3,3,5	5	6,3
1943	No early records		5	
1945	6,6	6	4	

Table 15 (continued)

	Date of Completion April 1 - 10	April 11 - 20	April 21 - 30	May 1 -	Total
n =	27	40	13	2	82
ΣX =	138	198	64	9	409
ΣX^2 =	736	1034	326	45	2141
$(\Sigma X)^2/n$ =	705.33	980.10	315.08	40.5	2040.01
$\bar{X}$ =	5.11	4.95	4.92	4.5	4.99
S_b^2 =	.333				
S_w^2 =	1.28				
F =	.2604	df. = 3/78			

Endocrine Causes of Reproductive Failure

Even though Canada geese are extremely adaptable, reproduction is often difficult to establish in captive flocks. Changes within an established breeding population and the nesting territory that the flock uses will often result in decreased reproduction. Even when immature geese are introduced, many individuals never do adjust to the new location. Balham (1950) reports that many geese fail to mate their first year after such changes and some never do even under natural conditions.

The ecological reasons for these failures are probably varied and perhaps unique with the individual situation. This current study was mainly concerned with the physiological manifestations of these ecological factors. The results indicate that ecological inhibition of reproduction may be due to a suppression of the release of LH.

The use of injections of chicken pituitaries on three-year non-reproducing geese did not produce significant changes in gonadal development. Based on the results of the examination of the reproductive systems of six geese (Table 7) these birds were mature, stimulated, and the treatments did not alter this condition (Figures 8 and 10). These observations were supported by the fact that no relationship was noted between treatment and nesting success. Of the first ten pairs in Table 6 (pairs which had not previously reproduced), three of the five treated pairs and three of the five untreated pairs nested (Table 8).

If we assume that the sacrificed geese were representative of the whole experimental flock, then most of them were capable of reproduction at the time of release. If this is true, then all of the pairs which did not begin nesting within a few days of April first must have been delayed in their development.

In the previous section, "Confinement and Release Studies," the rapid adjustment of three pairs which escaped or were released from their pens was discussed. It was also stated that no indications of moult were observed at this time. The conclusion drawn from these observations was that the gonads could be maintained at a relatively high stage of development for extended periods of time. Thus external factors which inhibit reproduction appear to do so by inhibiting complete maturation and ovulation of the follicles rather than by suppression of the reproductive system as a whole.

If ovarian follicles are being formed and are developing normally (the condition of the ovaries examined), then FSH is probably present. However, final maturation and ovulation of the follicles is dependent upon LH which is released in "ovulatory peaks" (see Sturkie, 1954). If the release of LH was inhibited and FSH not influenced, then it would be possible to maintain the ovary in a developed stage without realizing ovulation. On this basis it is also possible to explain the apparent LH deficiency of the chicken pituitaries used for this study (see page 52).

Nalbandov (1958) worked with the inhibition of ovulation in chickens by placing a foreign body in the magnum. He succeeded in doing so and in his book says:

> The startling thing was that during this anovulatory phase neither the combs nor the ovaries shrank and the ovaries continued to contain follicles of ovulatory size. There was no atresia, and the follicles that were present in the ovary when the foreign body was introduced into the magnum were maintained. Equally important was the fact that the whole oviduct was maintained in its initial size during this anovulatory period. These observations led to the following conclusions concerning the rates of hormone secretion:
>
> 1. The rate of androgen secretion remains unaltered. Because androgen secretion in the hen is governed by LH acting on an unknown component of the ovary, the undiminishing size of the comb implies that the presence of the foreign body does not completely stop the secretion of LH.
>
> 2. The rate of estrogen secretion remains unaltered. Estrogen is known to be secreted in the hen by ovarian follicles, just as it is in mammals and the rate of its secretion in hens also is controlled by FSH and LH. An undiminished flow of estrogen accounts for the undiminishing size of the oviducts.
>
> 3. The rate of FSH secretion remains the same. This is indicated by the maintenance of ovarian follicles without atresia.
>
> 4. The major change that occurs in the hen after the foreign body is placed in the magnum is cessation of ovulations. Since LH is known to be necessary to ovulation, this observation led to the postulate that there might be a deficiency of LH.
>
> To test this last possibility, the investigators injected LH into hens in which ovulations had been interrupted by the presence of a foreign body in the oviduct: all hens responded by ovulations. In view of the evidence summarized here and the effectiveness of LH in inducing ovulations, the following hormonal relation between the pituitary and the ovary was postulated. It is probable that in the normally laying hen there is a steady and continuous flow of FSH and of some LH. At certain

intervals a quantity of LH above the steady flow is released. These "ovulatory peaks" of LH are responsible for ovulations.

This description of the conditions which resulted when foreign objects were placed in the magnums of chickens very closely resembles those observed among the non-reproducing three-year geese in this study.

In 1962, an attempt was made to force ovulation after suppressing normal reproduction. Twelve pairs of geese (Group IV) were placed in the penned areas at the Kellogg Bird Sanctuary (Table 8). These were purposely crowded in an attempt to inhibit reproduction, and after two weeks seven pairs which behavioristically showed no signs of nesting were selected for treatment.

Four of these pairs were treated subcutaneously with 1 mg. of progesterone in sesame oil. Progesterone was selected rather than LH because the available LH was of the mammalian-type and in view of the response obtained by the use of PMS (see page 53), there was reason to doubt its value without additional work on dosage levels and variation in response. In addition, Rothchild (1949) and others have obtained excellent results from progesterone in similar work on chickens. The remaining three pairs were penned but not treated.

Within a 60-hour period following treatment, six of the seven females laid eggs. These six pairs included three controls and three treated pairs (Table 16) and, therefore, it was not an adequate test of the theory that reproductive failure was due to deficient LH secretion. These results suggest that the different pairs had different tolerance levels to crowding and, therefore, were not all completely inhibited and that behaviorisms are not an adequate means of determining nesting potential.

This experiment did not provide an adequate test for the theory that reproductive inhibition results from a lack of "ovulatory peaks" in the rate of LH secretion. Further work must be done before the validity of this conclusion can be determined. However, the fact that three of the four treated females oviposited only one egg and made no nesting attempt perhaps indicates a response to progesterone treatment. Further work concerning dosage levels may prove to be fruitful.

Table 16

Results of Progesterone Treatment on the Females of Non-reproducing Pairs

Pair no.	Treatment	Response	Pen area
3	Control	Female killed, egg found in oviduct Figure 5	Experimental Pond
6	Control	Began nesting two days later	Farmlane Pond
9	1 mg. progesterone	Laid one egg 55 hours later *	Farmlane Pond
16	1 mg. progesterone	None	Farmlane Pone
18	1 mg. progesterone	Laid one egg, approximately 60 hours later *	Buttonbush Pond
15	Control	Began nesting two days later	Buttonbush Pond
19	1 mg. progesterone	Laid one egg, approximately 60 hours later *	Buttonbush Pond

*Made no nesting attempt.

SUMMARY

Habitat acceptance appears to be a matter of individual response and certainly is not a species-wide trait.

The incidence of pairing is not a reliable index of the reproducing pairs in a flock. Pairing was observed to have taken place during all times of the year and between both mature and immature geese. The pairs resulting from "off season" or immature unions did not appear to be significantly less successful than pairs of mature individuals or those formed during the reproductively active period.

There is reason to believe that libido is in part controlled by the nervous system and is independent of sex hormones, at least in geese. The onset of displaying is not necessarily indicative of sexual maturity and the degree of aggressiveness is not an index of nesting probability. The establishment of a territory likewise does not indicate sexual maturity nor probable nesting.

The semi-domesticated Canada goose seldom attains reproductive maturity until its third year. A small percentage, approximately 5 percent, mature in the second year. Most males appear to be physically mature in the second year, but do not actively reproduce until the following year. Both male and female one-year birds are immature and physically incapable of reproduction.

The reproductive organs of two-year females responded to gonadotrophic treatment and, although a completely mature system was not known to have resulted in these tests, it may be possible with additional study.

Two-year males and three-year males and females did not show any significant development after the hormonal treatments. At no time during this study could any increase in libido be demonstrated to have resulted from these treatments. This may have been due to using LH deficient pituitaries.

Atresia occurs during all phases of ovarian development and this condition is not believed to be an index of reproductive problems. However, the presence of large numbers of atretic follicles during the early part of the season may indicate some difficulty existed for the individuals.

Canada geese appear to be able to maintain their reproductive systems in a developed state for extended periods of time without ovulating when adverse conditions exist. Subsequent release from these conditions may result in a very rapid response of the system and reproduction may occur within a short time. The data indicate that delays do not necessarily result in reduced clutch size until very late in the nesting season.

The significance of size of the territory seemed to be related to the relative aggressiveness of the pairs involved. When pairs of nearly equal aggressiveness were penned together, they nested on relatively smaller areas. The importance of crowding as an inhibiting factor appeared to vary according to individual responses. The data in this study do not indicate any significant changes in clutch size to have resulted from the amount of available territory.

The endocrine cause of reproductive failure appeared to have been a lack of "ovulatory peaks" in the rate of secretion of Luteinizing Hormone. The observed syndrome very closely resembled that described by Nalbandov (1958) and others in chickens, which were attributed to a lack of LH peaks. A single attempt to force ovulation by progesterone treatment did not succeed, but the results suggest that failure may have resulted from insufficient preliminary information on: (a) the amount of crowding necessary to inhibit reproduction in the test geese, and (b) the exact dosage levels of progesterone which should be used.

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