THE BREEDING BIOLOGY

OF THE

AMERICAN ROBIN (TURDUS MIGRATORIUS)

IN SOUTHWESTERN BRITISH COLUMBIA

by

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ABSTRACT

The American Robin (Turdus migratorius) in southwestern British Columbia was studied in regard to timing of reproduction, breeding biology, gonadal changes with time, and the relationship between photoperiod and gonadal condition.

The basic breeding biology is similar to that found for other robins in the eastern and midwestern United States. The only marked difference is the very high nesting success rate of the robins which I studied. The overall success rate was 86.6 percent with 87.8 percent of all eggs laid hatching and 98.6 percent of these fledging.

The onset of the breeding season was marked by the increase in territorial aggressive behaviour of male robins. This increase is a gradual process taking place over a two month period from early February until late March.

The histological pattern of testes development and regression in the robin is the same as that for other temperate zone passerines. The length of the daily photoperiod has a definate effect on the timing of testicular recrudescence. The average testes weights of robins kept on eight, 12, and 16 hour photoperiods for the period of the annual cycle when testicular development occurs in the wild were 9.4 mg., 14.6 mg., and 200.5 mg. respectively.

As well as stimulating gonadal development increasing photoperiod, as opposed to short day lengths, affects migra-

tory behaviour as evidenced by Zugunruhe or night restlessness.

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INTRODUCTION

The American Robin (Turdus migratorius) is one of the most abundant and widespread North American passerines. It ranges throughout the breadth of the North American continent and breeds from the northern portions of the United States northward to the treeline in Canada and Alaska. It nests in deciduous and coniferous forests and also in the centre of urban developments. The robin is a highly adaptable species. Surprisingly, in spite of its relative abundance, very little has been published regarding its reproductive biology. This project is twofold: one facet emphasizes the basic reproductive biology of the robin in field circumstances, and the other, a laboratory study, tests its sensitivity to photoperiod.

The following studies represent the spectrum of work published on the American Robin to date. Two major studies have been completed on the nesting habits and success of the robin. One, by Howell (1942), followed the nesting near Ithaca, New York; the other, by Young (1955), concerned robins near Madison, Wisconsin. The paper by Howell (1942) dealt thoroughly with nest building, clutch size, development of young, and nesting success. He also described certain aspects of parental behaviour and gonadal condition. The latter was at the gross morphological level only. Young (1955) was primarily concerned with parental behaviour and overall nesting success. In addition to these two major papers, there are several others that pertain to my own study. Descriptions of a single nesting effort have been made by Gray (1897); Howe (1898); and Schantz (1939). Hamilton (1935) recorded the growth and development of nestling robins. A nest record card survey of breeding season and clutch size done by Howard (1967) provides information on these subjects for various latitudes on the east coast of North America.

Studies of other aspects of robin biology include one on age and longevity (Farner 1945, 1949) and two on winter and spring robin roosts (Black, 1932; Howell, 1940). There are also many notes of observations of abberrant behaviour patterns, particularly those regarding breeding or nesting (Brackbill, 1944, 1947; Kress, 1967).

The European members of the family Turdidae have received far more detailed consideration from ornithologists. Studies of the English Robin (Lack, 1943) and Blackbird (Lack, 1949; Lack and Light, 1941) are primarily oriented to the ecological significance of clutch and brood size in these species. Nest record card surveys of breeding seasons (Myres, 1955), clutch size (Snow, 1955a) and nesting success (Snow 1955b) discuss these topics for the Blackbird, Song Thrush, and Mistle Thrush. These are the European turdids most closely related to the American Robin. While there is abundant information on nesting habits and success there is very little on gonadal condition or the effect of photoperiod on the annual cycle of European thrushes.

The lack of information on the annual gonadal cycle of the turdids, in general, and the American Robin, in particular, has been the impetus behind the choice of the American Robin for this study. The study itself deals primarily with the reproductive biology of the robin, including the nesting parameters such as breeding season, nest location, clutch and brood size, and success. I have examined this with reference to the annual gonadal cycle, and both are considered in terms of photoperiod. My results on the nesting cycle are compared to those published accounts for robins under different conditions of latitude, longitude, and habitat. The effect of photoperiod on gonadal cycle and breeding season is also compared to the results for closely related passerine species.

METHODS AND MATERIALS

My study of the nesting habits of the American Robin was located on the University of British Columbia campus, $123^{\circ}90'$ west longitude and $49^{\circ}18'$ north latitude. This work was done from September, 1967, through December, 1969. The campus provided a 200 acre garden habitat with many deciduous and coniferous trees and shrubs interspersed with large expanses of grass; the area was an ideal nesting habitat.

During the 1968 breeding season of the robin I located 22 nests, most of which had young that were already hatched. In the 1969 season I made a systematic weekly search of an area of the campus (fig. 1) and located 72 nests. To verify the thoroughness of the search I checked the area again in October when the deciduous trees had lost their foliage, leaving the nests exposed. I found five nests not previously recorded. No attempt was made to determine what percentage of nests in coniferous trees were missed.

Each of the nests located during the 1969 season was revisited at three to seven day intervals, the shorter period for active nests. Nests were also checked on the expected day of hatching and fledging. The number of eggs and/or young, the dates of laying, hatching, and fledging, the tree species, nest height, nest construction material and the amount of cover afforded the nest were recorded for each nest. I determined the latter subjectively by noting whether the nest was completely exposed, covered from below, from above, from

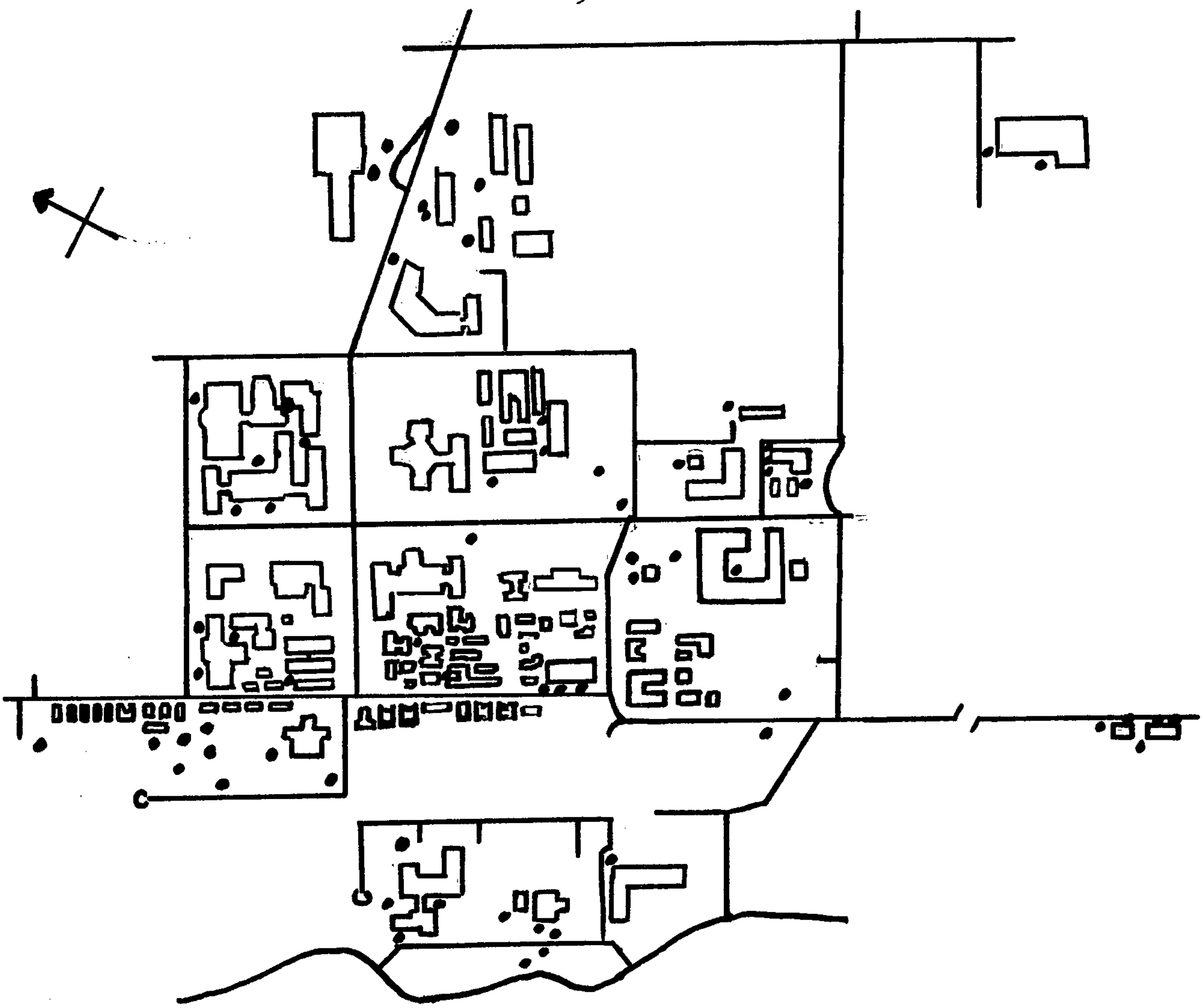

Figure 1. Map of the study area on the University of British Columbia campus. The solid dots indicate nest sites. The scale is approximately one inch to 200 feet.

the side, any two of the last three, or completely concealed. Cover consisted of the trunk, branch or foliage of the tree or of part of a building. I also observed the behaviour of the parents, their relationships with each other, with their young, and with conspecifics.

The data from the field observations were coupled with information obtained from a histological examination of the gonads of robins collected on a blueberry-cranberry farm in Richmond, British Columbia, 123° 10' west longitude, 49° 13' north latitude, approximately 30 miles southeast of the campus. The farm, comprising 400 acres, was bordered on three sides by deciduous shrubs, vines and trees and on the fourth side by a hay field. Road and window kills of robins were also obtained from various sources in the Vancouver area and the Canadian Wildlife Service contributed six specimens which they collected in the vicinity of Richmond. I collected on a weekly basis from March through July and September and October of 1968 and 1969. A total of 240 birds were sampled: 171 the first year and 69 the second.

Body weight to the nearest 0.5 gram, and total body length and greatest wing primary length to the nearest millimeter, were recorded for each specimen.

With minor exception, each bird was dissected within ten minutes of death. The amount (non, slight, extensive) and location (subcutaneous, peritoneal) of fat was noted as well as the obvious presence of parasites. The gonads were removed, measured for greatest length and width to the nearest millimeter, and placed in Bouin's solution. All testes were cut open to increase the speed of penetration by the preservative. Specimens which had been dead for more than 45 minutes were treated as the others except that no attempt was made to preserve the gonads. After 24 to 48 hours the gonads were transfered to 70 percent alcohol. They were weighed to 0.1 milligrams on a Sartorius four decimal place analytical pan balance after thorough preservation and decolouration.

One testis from each bird was embedded in paraffin, sectioned at 7 mu. and stained with Delafield's haematoxylin and eosin. The slides were analyzed for tubule diameter and the presence or stage of development of sperm. The number and size of follicles were recorded for each ovary. When follicles were obviously post-ovulatory or regressing (Davis, 1942a, 1942b, 1942c) I noted them as such, but gross differentiation of developing and regressing ones was not always possible.

The collection of material for gonadal analysis was continued during the non-breeding season on a monthly basis, the purpose being to determine the histological condition in full regression and to determine the onset of gonadal development. This work was correlated with field observations made during the winter months in the expectation that conspicuous differences between nesting behaviour and winter behaviour of robins would provide external clues to the timing of the shift between the active and inactive stages of reproduction. Such observations were concerned solely with the presence of robins in winter flocks or as single or paired territorial birds. Field studies were conducted on an intermittent schedule from November through January, totalling approximately 40 hours during the winter of 1968-69. Beginning in February, a rigorous weekly observation period of a minimum of two and a half hours per week was established. This time was spent searching for and/or observing robins. The work was again primarily carried out on the campus of the University of British Columbia but it became necessary on occasion to make observations on the nearby golf courses of south Vancouver, as well, in order to locate robins.

In addition to these field studies, robins were captured from January and March of each year for laboratory experiments on the effect of photoperiod on the timing of the gonadal cycle. Also I wanted to determine if a Zugunruhe effect was produced, since the robin is known to be a night migrant.

The first set of experiments was conducted from January to April of 1969 using a total of 21 birds obtained from the golf courses and Richmond. The birds were housed in groups of from three to five in wire cages four feet by two feet by two feet. Each cage was provided with one perch, one food dish, and one water dish. The feed was a mixture of a commercial chick starter and ground beef. Once one bird in each cage discovered the food the others rapidly accepted it. Both food and water were provided ad libitum.

The cages were enclosed by a heavy black vinyl plastic which effectively blocks all natural light. Illumination was provided by a single 60 watt cool white flourescent light for each cage. There were three experimental groups on eight, 12, and 16 hours of light, respectively, in a 24 hour day. There was some light leakage to two of the groups. A very small amount of light, both in quantity and intensity, penetrated through several pinholes in the plastic and exposed the eight-hour groups, and considerably more sunlight reached the sixteen-hour group. In the latter case, however, it occurred only at times when they were already under artificial lighting.

For the second set of experiments, which ran from February through May, 1970, 14 birds were collected in the south Vancouver and campus areas. Six of these were housed individually in cages 14 inches by 15 inches by 15 inches fitted with one food dish and one water dish. Each cage also had one perch which was connected to a microswitch such that the switch was tripped each time the bird hopped on or off the perch. The switch was connected to an Esterline-Angus 20 channel event recorder. Blocks of three cages were kept together on one photoperiod. Three robins on an eight-hour light, sixteen-hour dark photoperiod were illuminated and protected against interfering light by the same means as those on the previous experiment. These three were tested against three on natural photoperiod, which ranged from 12 to 16 hours of light per 24 hour day.

Birds mist-netted for both experiments were maintained for approximately one week under natural light conditions to allow them to settle in and become accustomed to the food. In the second set of experiments this was done in communal cages and then they were transfered to individual ones. No attempt was made during either set of experiments to control the temperature.

At the end of the experiments all the birds were sacrificed and their condition recorded as for the collected specimens. Similarly, their gonads were preserved and prepared for histological examination.

RESULTS

Non-breeding Season

Field Behaviour

The American Robin, as observed on the campus area, is a gregarious species during the non-breeding season, and sightings of lone individuals are rare. Several thousand birds of all ages and both sexes share the same evening roost (Black, 1932; Forbush and May, 1955). During the day the birds are found in smaller groups of highly variable numbers. The groups I observed had from five to approximately 40 members, with 12 to 15 being the most common number. The flock size was extremely labile as groups split and rejoined throughout the day. Once I located a group of robins I could rely on finding them in the same place as long as the food supply lasted, usually one to three days. Their food consisted primarily of soft fruits, especially the berries of the Mountain Ash (Sitka sitchensis) and holly (Ilex sp.), although they appeared to eat insects when available.

There were several exceptions to this general pattern of gregarious behaviour. In January and February of 1969 I observed lone birds on the University of British Columbia campus on 10 occasions, at which times I did not locate any robins in groups. This was a very severe winter with the ground being frozen and/or snow-covered for 41 days, beginning December 26. By mid-January food was very scarce since many of the berries had frozen and rotted on the trees. Each lone bird seemed to be defending a food source, either a bush with a few berries or garbage. On two occasions I witnessed one robin approach another that was feeding. Both times the feeding bird immediately attacked the other and pursued it until it retreated out of sight. Flocks of five to 12 robins were still present in the south Vancouver area primarily around holly trees which still had berries and near feeders that had been put out by residents of the area. I autopsied nine of the many birds which died during this period. All were abnormally light, averaging 63.7 gm. which is approximately 20 gm. lower than normal. They had no fat deposits and had a dark bile-like fluid in the gut which was not present in birds I autopsied at any other time. Steve Johnson (pers. comm.) observed a similar fluid in starlings (<u>Sturnus vulgaris</u>) dying at this time. When the snow started to clear (February 3 - 10) the robins regrouped into flocks which did not break up again until March.

I also observed an unusual behaviour pattern on December 7 and 9, 1967, both cloudy, rainy days. On each occasion I heard a robin giving the typical mating song. In each case it took place in mid-afternoon and the bird was part of a flock of five to 10 robins all sitting in the same tree. The singing bird was showing part of its mating season behavioural pattern at an abnormal time and under abnormal social conditions.

Gonadal Analysis

The reproductive state of the robins which I collected during the fall and winter is represented in Figure 2 for males and Figure 3 for females. The gonads are extremely reduced from October through February. The testes of 20 specimens collected during this period averaged 2.4 mg. in weight, ranging from 1.0 to 4.3 mg. They are a pale grey to black in colour in contrast to their opaque white colour in the breeding season. Histological examination showed no mature or developing sperm present. Seminiferous tubule diameter averaged 23.34 mu. ranging from 7.50 to 24.68 mu.

The left ovary during this same period ranged from 17.8 to 33.1 mg. in weight, averaging 23.7 mg. It is a very small compact organ with all follicles less than 0.5 mm. in diameter and none showing any increase in size over the others.

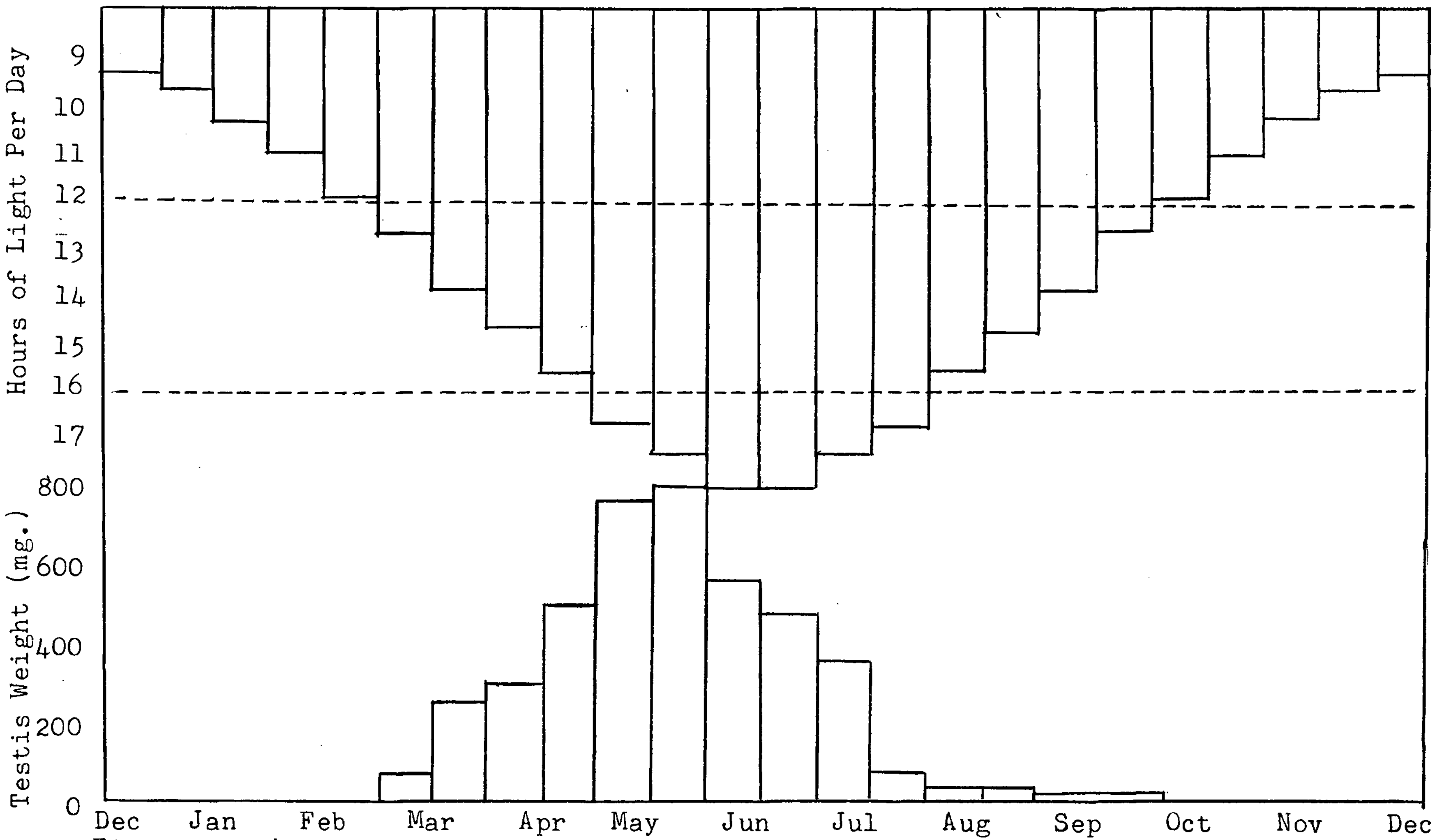

Figure 2. Average testis weight compared to the average hours of light per day for each half month period during the year.

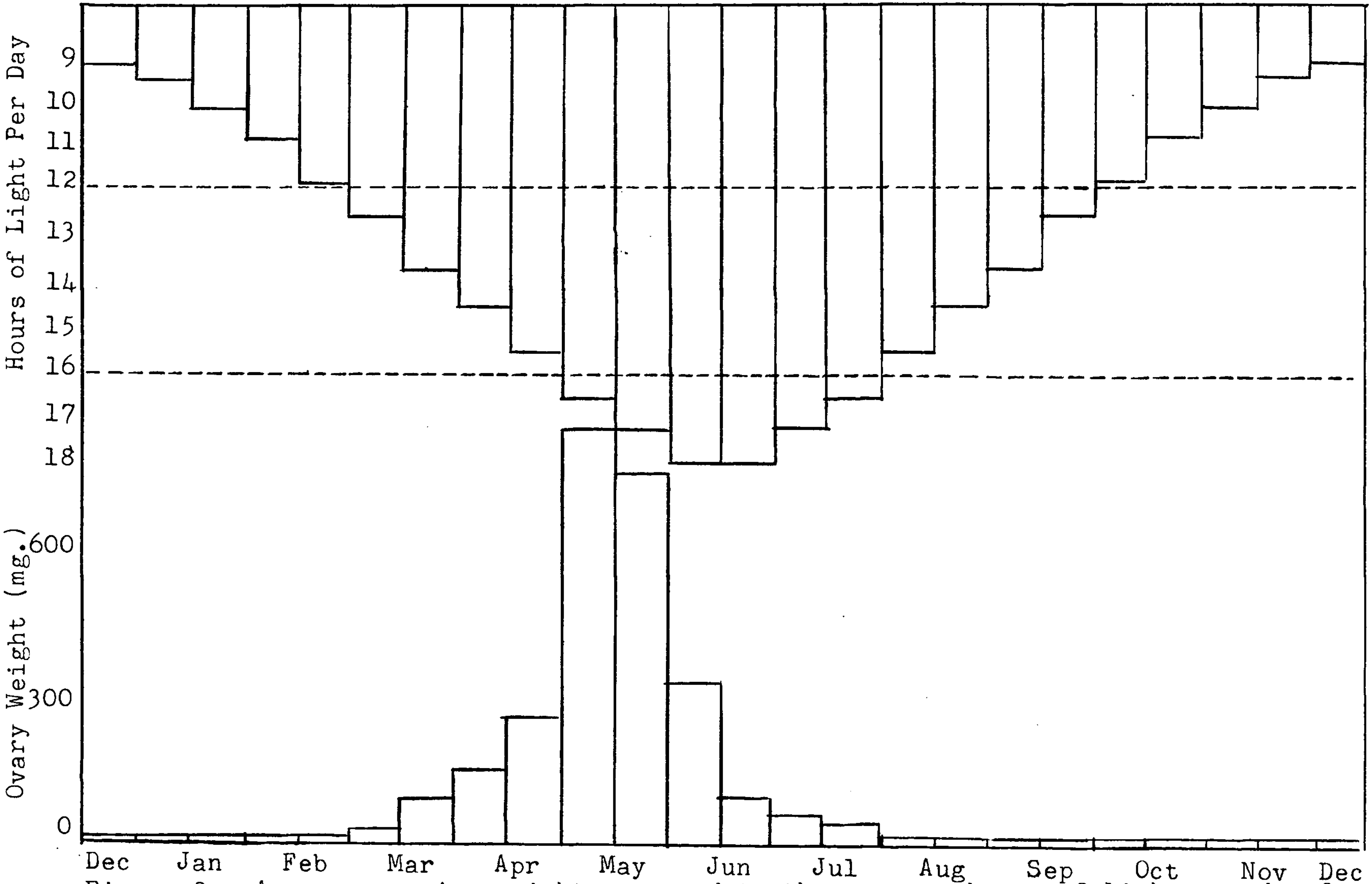

Figure 3. Average ovarian weight compared to the average hours of light per day for each half month period during the year.

Prelude to the Breeding Season

Field Behaviour

In February and March the social organization begins to shift from the nomadic flock structure towards the aggressive, territorial mating behaviour. Table I compares the number of sightings of lone or territorial birds to those of flocks. The shift is a gradual one, not only for the species as a whole but also for every individual. The first indication of the change in behaviour is a decrease in the number of large flocks. After February 1st I never saw a group of more than 15 robins on the campus, except in the evening roosts, and after March 1st never more than five.

The feeding habits and associated behaviour of the robins also changes at this time. They spend an increasingly greater amount of time feeding on earth worms and insects than on berries so they are on the ground more frequently than in trees. Robins, when feeding on the ground at any time of the year, exhibit a spacing behaviour. Price (1933) describes the tenacity of certain individuals for a particular part of the area on which the group is feeding. For the two birds which he could recognize the territories averaged 400 yards square. The resident chased away any other robin which intruded onto it. I have observed the same sort of behaviour during the non-breeding season but restricted to a much smaller area, 50 square yards maximum. These birds never displayed the behavioural patterns which are commonly associated with

Dates	Single or Paired # Sightings	Groups of 3 or More # Sightings	Hours From Civil Dawn to Dusk
Jan 1-15	2*(0,2)	2*(2,0)	9.5
Jan 16-30	3*(0,3)	2*(1,1)	10.0
Jan 31-Feb 14	4*(2,2)	5*(4,1)	10.6
Feb 15-Mar 1	4*(1,3)	2*(2,0)	11.5
Mar 2-16	4	7	12.5
Mar 17-31	9	5	13.3
Apr 1-15	16	1	14.5
Apr 16-30	14	0	15.3
May 1-15	20	1	16.3
May 16-30	17	0	17.0
May 31-Jun 14	14	1	17.6
Jun 15-29	21	0	18.0
Jun 30-Jul 14	5	0	17.6
Jul 15-29	5	3	17.0
Jul 30-Aug 13	3	7	16.25
Aug 14-28	0	0	15.3
Aug 29-Sep 12	0	2	14.5
Sep 13-27	1	1	13.5
Sep 28-Oct 12	0	6	12.5
Oct 13-27	0	2	11.5
Oct 28-Nov 11	0	2	10.6
Nov 12-26	0	4	10.0
Nov 27-Dec 11	0	2	9.5
Dec 12-27	1	3	9.3
Dec 27-31			

Table I. Numbers of sightings of lone or paired robins versus flocked robins on the campus and south Vancouver areas, based on 10 hours of searching per 14-day period. Numbers in parenthesis after asterisk denote breakdown of totals into 1968 and 1969 seasons, respectively.

defending a nesting territory, such as singing from a conspicuous perch and fighting other trespassing robins. Nor did the chases ever result in fights, since the intruder always left and often both birds involved would just move away from each other. This behaviour could more properly be considered an individual distance rather than a true territory, such as that established early in the breeding season. This spacing while ground feeding is not evident when the group is feeding in trees. In the latter case all the members of one group will feed in the same or adjacent trees.

Changes in spacing while ground feeding are another indication of the onset of breeding behaviour. The males patrol a larger feeding area and become more aggressive in their defense of it. The resident bird chases the intruder further, pecks at the intruder and gives a loud, harsh call, none of which occurred earlier in the winter when robins were ground feeding. For example, on March 12 I observed a group of five robins (three males and two females) feeding on a lawn approximately 30 yards by 20 yards on the campus. One of the males attacked any other robin which came within five yards of him. He pecked at the intruder rather than just chasing him and pursued him out of the group feeding area. As soon as the attacking male returned to his feeding area the ousted bird would return to the group area. Two days later I saw a group of four birds (three males and one female) on this same area with one male occupying the same part of it as did the territorial male described above, except that he was defending about a 150 square yard area, almost three times the size of that defended on the previous occasion.

During March males start ot leave the groups entirely. At first they depart for one or two hours in the early morning and evening, at which time they sing the mating or territorial call as described by Howell (1942) and Young (1955), and they are extremely aggressive. This singing is usually done in or near what is to become the male's territory. The habitat of the nesting area is either of the mixed garden type near buildings with shrubs, bushes and trees interspersed with grassed areas, or in a densely wooded area that is bordered by large grass and field areas. As the male chooses his territory he spends increasingly more time on it and defends it to the point of fighting with other males that intrude within it.

Whenever one male enters another's territory the resident male immediately gives a loud harsh call and flies at the intruder. If the latter flees, as I observed in three of 16 cases, the owner pursues him for several yards and then lands. The intruder stops a few feet away. If the intruder does not flee (13 of 16 confrontations) they attack each other with feet and bills as described by Howell (1942). These fights last three minutes at most, being terminated when one bird moves several yards away. None of the battles I witnessed resulted in any physical damage other than the loss of a few feathers. Simple chases, without fights, occur throughout the breeding season but I witnessed only one fight after mid-May and that was on July 3.

The territorial males do not spend all day on their territory but spend part of it on group feeding areas. These are generally large, grassy areas such as small parks, fields, or large lawns that are not within breeding territories. The males also return to the large communal roosts at night.

As the males establish their territories the females also leave the groups, i.e. the groups are disintegrating. They choose a male and/or his territory and aid him in patrolling the territory and in chasing intruders. Like the male they do not spend all their time on the territory but do some of their feeding on the group areas and roost with the other robins. The birds have reached this stage by early April and are ready to begin the breeding cycle. It is important to note (Table I) that this shift takes place over a long period of time, and that the hours of light per day have increased from just under 12 to almost 14.

Gonadal Analysis

A dramatic increase in the size of the gonads begins in March, after the daily photoperiod exceeds 12 hours per day. For the first half of March the testes weights average 52.9 mg., ranging from 3.5 to 313.2 mg. for 11 specimens (fig. 2). Of these 11, five were collected in the Richmond area in 1969 and average only 9.5 mg., whereas the remaining six were collected on the campus in 1968 and average 89.3 mg. in weight.

The seminiferous tubule diameter also increases greatly during the first half of March (fig. 4). The males collected in the Richmond area had an average tubule diameter of 32.82 mu. ranging from 25.65 to 38.40 mu. None of these specimens contained mature or developing sperm. Those collected on campus still had no developing sperm even though the tubule diameters averaged 65.95 mu., almost twice the diameter of those collected in Richmond. The range in diameter for the campus groups was from 37.28 to 107.70 mu. The overall average of seminiferous tubule diameter in robins from both areas was 50.89 mu.

During the second half of March the testes increased markedly in weight to an average of 257.1 mg. for eight specimens, ranging from 10.6 to 487.8 mg. (fig. 2). The dichotomy between samples collected in Richmond and on the campus was still evident, for the two males from Richmond averaged 18.5 mg. (range of 10.6 to 26.5 mg.) and six from the campus averaged 336.7 mg. (range of 20.2 to 487.8 mg.).

All of the testes of birds taken on the campus during the second half of March showed developing sperm and one contained a few mature sperm. Histological examination of the Richmond specimens showed no developing sperm. This difference was reflected in the tubule diameters which averaged 141.69 mu., ranging from 129.45 to 154.20 mu. for campus birds, and 45.27 mu., ranging from 41.78 to 48.75 mu. for those from

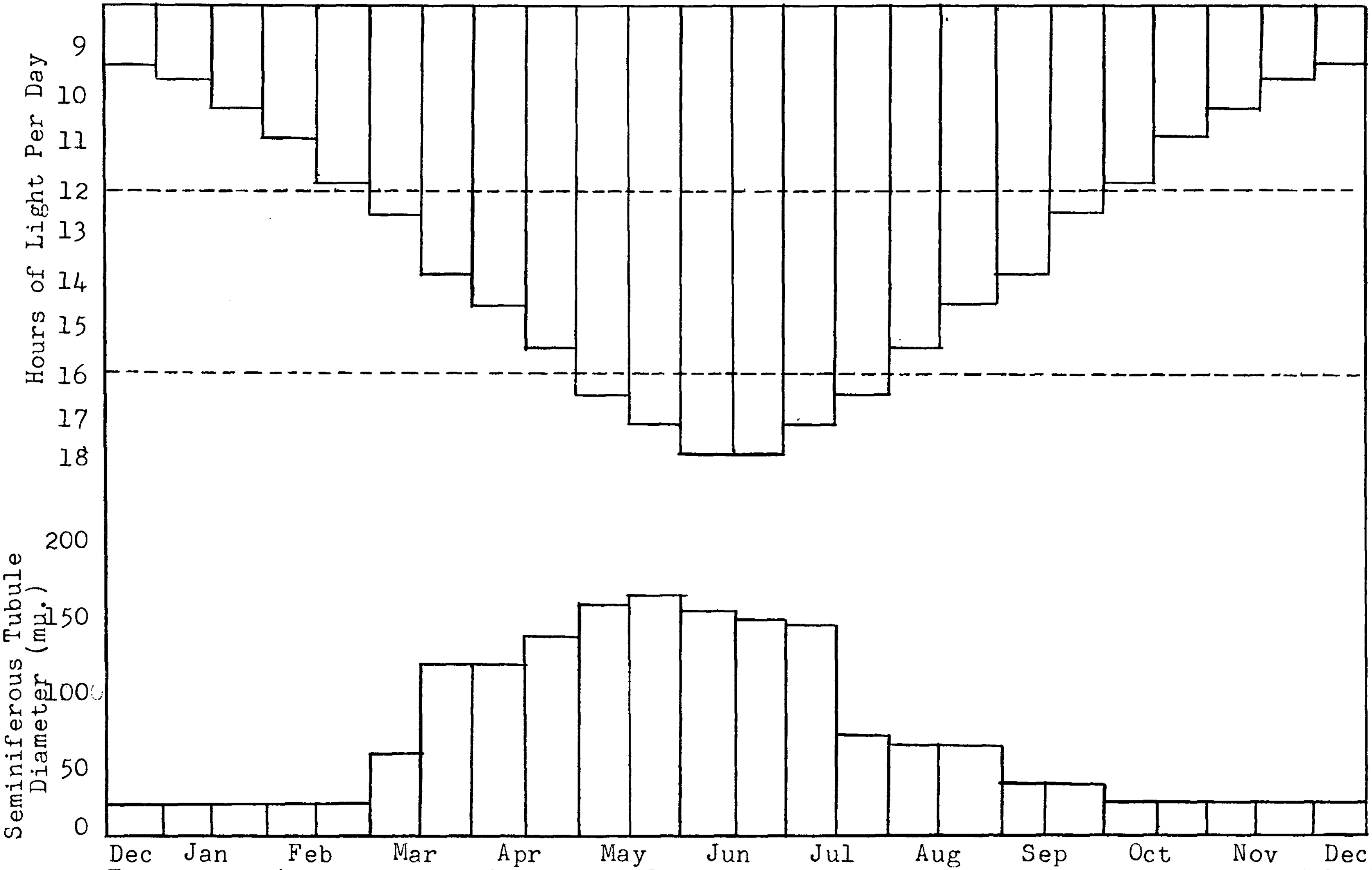

Figure 4. Average seminiferous tubule diameter compared to the average hours of light per day for each half month period during the year.

Richmond.

The ovaries also increase in size during March but the change is not as sharp nor as early as that of the testes. Nor is there a noticable difference in amount of ovarian development between females collected in Richmond and those collected on the campus. Eight specimens collected during the first half of March averaged 33.6 mg. in ovarian weight, ranging from 25.4 to 46.6 mg. (fig. 3). None of these showed any follicular development.

For 10 specimens collected in the second half of March the ovaries averaged 85.1 mg. in weight, ranging from 48.3 to 117.6 mg. Of these all but one had some follicles which were enlarging and three had one follicle each that had increased to at least 2.0 mm. in diameter.

The rapid increase in gonadal size continues throughout April, although it is not as marked in the first half of the month as it is in the second portion. The average testis weight for the first half of the month is 300.5 mg., ranging from 8.1 to 611.3 mg. (fig. 2). Again, the Richmond birds seem slower to develop than those from the campus. The average weight for the testes of eight of the former is 199.8 mg., ranging from 8.1 to 361,3 mg. The campus birds average 362.6 mg. for 13 testicular specimens, ranging from 123.0 to 611.3 mg.

The males collected on campus during the first half of April all had developing spermatocytes and six showed mature sperm. The diameter of the seminiferous tubules had not increased noticeably since that at the end of March (fig. 4), averaging 130.19 mu. and ranging from 106.09 to 168.54 mu. All those with mature sperm were greater than 120.00 mu. in diameter. The birds collected in Richmond during this same period, however, showed no mature sperm. They averaged 88.00 mu. in diameter, ranging from 30.00 to 121.65 mu. All those over 85.00 mu. in diameter did show developing sperm, including spermatids.

By the end of April the daily light phase of the photoperiod has increased to 15.5 hours, the gonads have taken another sharp increase in size, and differences in the development of males from Richmond and the campus disappeared. The testes now average 494.2 mg. in weight, ranging from 292.4 to 941.5 mg. for 11 specimens. The seminiferous tubule diameters range from 120.97 to 148.8 mu., averaging 131.14 mu. All testes contained some mature sperm.

The average ovarian weight for 15 samples taken in the first half of April was 148.6 mg., ranging from 27.9 to 556.0 mg. (fig. 3). Of these, six showed no follicular development and five had one follicle greater than 2.0 mm. in size. One ovary, weighing 90.8 mg., had a follicle measuring 2.8 mm. while another ovary, weighing 556.0 mg., had one measuring 2.9 mm. Those showing no development weighed from 27.9 mg. to 138.6 mg.

In the second half of April the ovaries increased to

252.13 mg. in weight on the average, ranging from 40.5 to 535.1 mg. for eight specimens. Of these one, at 40.5 mg., showed no development, and the rest had from 1 to 12 follicles clearly enlarged. Of the latter, the largest was 4.3 mm. in diameter on an ovary weighing 535.1 mg. and having nine developing follicles.

Thus, during April the gonadal state of the males and, to a lesser extent, that of the females indicates readiness for breeding. The birds are in full breeding plumage. The males have a jet-black head, yellow bill and bright red breast, with the back and wing contour feathers being black. The females have the same yellow bill but are somewhat paler in all other colouration. Both sexes exhibit the same plumages as described by Forbush and May (1955) and Godfrey (1966). They are pairing and commencing the nesting cycle (fig. 5).

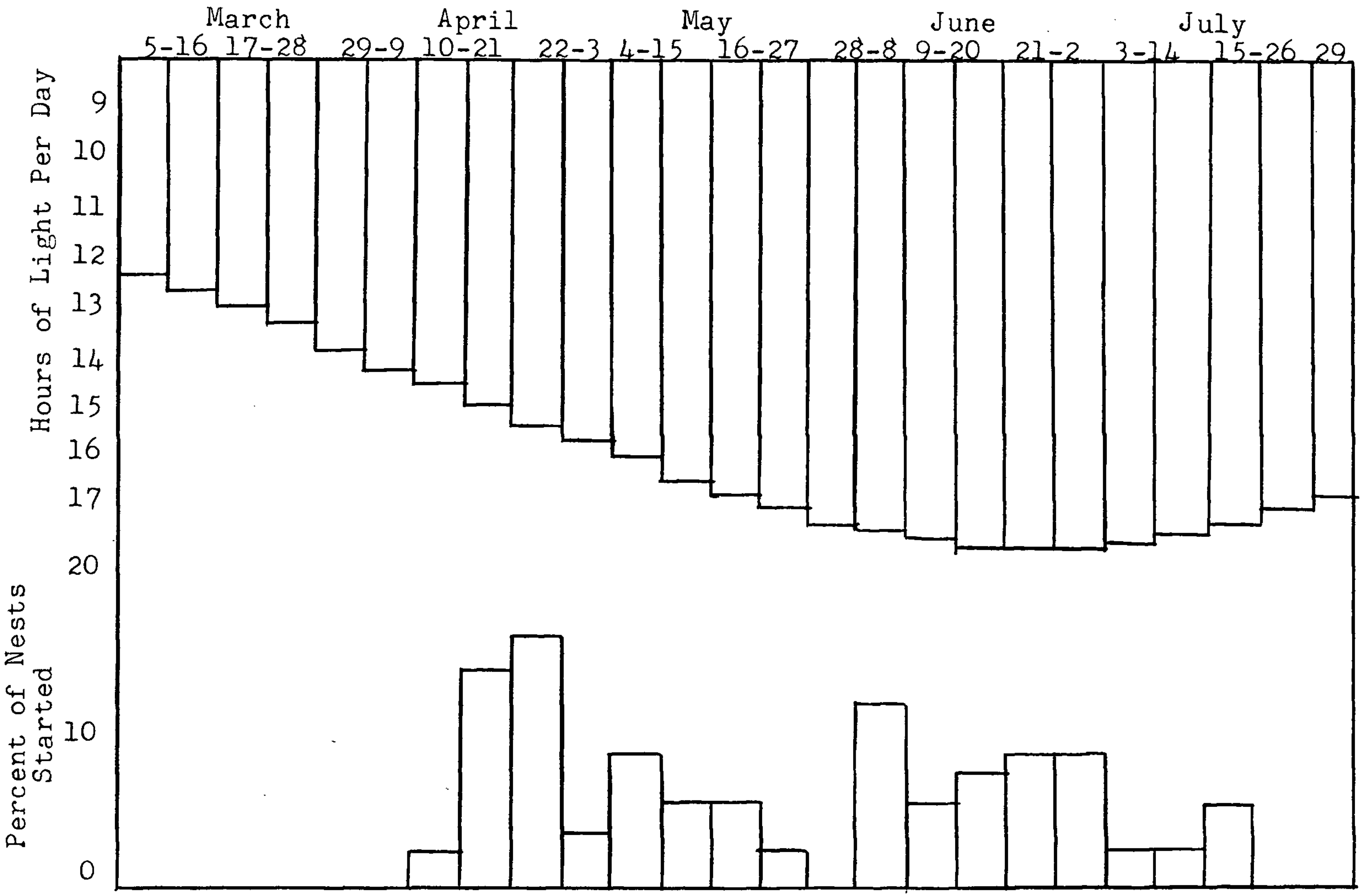

Figure 5. The percentage of the total number of nesting efforts which were started in each time period compared to the average hours of light per day for that period.

Breeding Season

Field Behaviour

Pair formation is an exceedingly undemonstrative procedure for robins. The male has already established his territory and seems to make no effort to attract the female. I never observed movements by the males which could be construed as courtship display or courtship feeding, although Brackbill (1944) describes a rare occurrence of inverted courtship feeding. Of 14 copulations which I witnessed the male always chased the female for several seconds to a minute and then mounted her. No special desplay followed copulation. At this stage of the nestling cycle the pair is feeding both within and without their nesting territory and is returning to communal roosts at night.

Both sexes are involved in choosing the nest site (Brackbill, 1947). Contrary to the evidence of other workers (Howell, 1942; Young, 1955) there was no preference for evergreen over deciduous trees at the beginning of the nesting season or for the season as a whole. The total of 28 evergreen and 44 deciduous tree nests was not significantly different using either a chi-square or a one-sample runs test. The height of the nests ranged from 1.5 to 30 feet above ground level, the average for 72 nests being 10.7 $\pm$ 6.8 feet. There did not seem to be any preference for high or low nests at any particular time of the year. The nest site seemed to be selected, however, on the basis of the amount of cover provided. Of the 72 nests, seven were completely exposed, one was hidden only from below, 22 were protected from above, one from the side, 23 from two directions and 18 were completely hidden. Both Kolmogorov-Smirnov and Chi-square tests show a significant difference amoung these groups at 0.05 level. This indicates that robins prefer nest sites which offer cover.

Once the site was chosen the female began nest construction. She alone did the building but the male was often nearby. Total time from start to finish averaged 7.6 days, ranging from five to 21 days. The female first built a shallow mud bowl reinforced with small twigs and/or straw. This was elaborated with more twigs, straw, grass, string etc. into the open cup thickwalled shape that is characteristic of the robin's nest. In the final stage of construction the female lines the nest with grass and/or shredded paper and shapes it to fit her body. The female does not necessarily work every day but may pause for several days, usually between stages (Young, 1955). I have noticed no change in nests for from three to five days but never longer unless the nest had been deserted. The latter was the case in 10 of 48 nests and none of these had reached the lining stage.

After the nest is completed egg laying may begin immediately or may be delayed as much as a week. Generally, the female lays one egg per day on consecutive days sometime in the morning. I found only one instance of a missed day, this between the second and third days of a three-egg clutch. The female does not begin to incubate until she lays the last egg, but from that time on she stays on or near the nest 24 hours per day. She will be off the nest for a maximum of 20 minutes at any given time, but usually for only three or four minutes. She remains on the nest at night while the male returns to the communal roost. I twice observed what I assumed to be males (on the basis of their plumage colouration) sitting on the nest, although other workers (Howell, 1942; Young, 1955; Howe, 1898) report that only the females incubate. In one of the cases the female was nearby feeding, when she returned the presumed male left the nest immediately and she settled on it. In the other case no other robin was seen in the vicinity. For those nests for which I know the exact date of laying and hatching the egg incubation period lasted from 12.5 to 13.5 days. In ten cases one egg hatched a day later than the rest.

During the nestling period both parents are in constant daytime attendance. For one to three days immediately following hatching the male is almost the sole provider of food, since the female still spends the majority of her time incubating the young, especially if the weather is cool or rainy. On may 16, 1969, the weather was overcast with an almost constant drizzle and the temperature was approximately 60°F when I observed a female brooding her three one-day-old offspring. Over a three-hour observational period she stayed with them for 10 to 20 minute intervals, averaging 13 minutes. She left the nest for a maximum of three minutes at a time and fed while she was away but never brought food to the nest. The male brought food to the young six times while I was observing them. When the female was off the nest he stood right beside it but did not afford the nestlings any protection from the rain.

As the young grow older, consequently developing more feathers and larger appetites, both the male and the female spend all day feeding them. The food consists primarily of earthworms, caterpillars and adult and larval insect stages. The porportion of any one item in the diet depends on whatever is most plentiful at the time of greatest demand. For example, in 1969 there was an extremely abundant crop of tent caterpillars on campus whose appearance coincided with the hatching of the young of first nesting efforts that season. These nestlings were fed caterpillars almost exclusively.

The female continues to incubate the young at night until they leave the nest. The male, however, stays with his family only until dusk when he departs, presumably for the communal evening roost. He is apparently not in the vicinity of the nest since he does not respond to the alarm call of the female, whereas during the daytime the male always appears immediately if the female gives the call. This pattern of care continues until the young are ready to leave the nest or are forced out.

The average period of time the young remained in the nest was 12 days, ranging from 11 to 14 days. The natural fledging time appears to be closer to 13 days, for any disturbance after 11 days seems to cause the young to leave the nest. The was the case in the four instances of 11-day nestling periods that I observed, for during my efforts to ascertain the presence and number of young they left the nest.

When the young fledge their heads, backs, and upper wing surfaces are a grey-brown colour; their bills are a dull grey-black with, at most, a trace of pale yellow near the head. They frequently still have tufts of down feathers protruding from their juvenile plumage, especially in the head region and they have a very short tail.

They are not fully capable of caring for themselves when they leave the nest regardless of whether they take 11 or 14 days to fledge. They are incapable of flights of more than a few feet and, because of their short tails, have poor directional ability and stability. Nor can the fledgings feed themselves for the first several days; hence they follow their parents and beg for food.

For the first few days the family remains very close to the nest site. Other investigators (Howell, 1942; Young, 1955) report that the young may return to the nest for the first and perhaps second night. I found no evidence of this, although I searched eight nests just prior to sunset of the day on which the young fledged. They could, however, have returned later.

As the young learn to feed themselves the family group starts to break up and the female prepares another nest for a second clutch. The male continues to watch over the young for approximately one more week, by which time the female may be incubating another clutch.

From the end of the first nesting effort in mid to late May until August I observed large groups of robins, composed entirely of juveniles. All such groups occurred apart from areas of nesting activity and my observations of them were confined to the vicinity of the blueberry farm in Richmond.

Nesting Success

The average clutch size for the 1969 season was 3.04 ± 0.59 eggs, ranging from two to four, for 27 nests that I followed from the stage of nest construction to that of fledging of the young. Of these, 2.67 ± 1.12 hatched and 2.63 ± 1.13 fledged. This is a fairly high success rate. The decrease from egg to nestling stage represents the loss, in every case, of the entire brood. The drop between nestling and fledging stages was due to a partial loss of one brood.

In 1968 I traced eight nests from the egg stage through to fledging. The average clutch size for these was 3.25 ± 0.71 eggs, and there was 100 percent recruitment to the nestling and fledging stages. A Mann-Whitney U test applied to the clutch sizes for both years showed no significant difference between them.

Success can also be measured in terms of total numbers of eggs laid, hatched, and young fledged. In 1969 82 eggs were laid in the 27 nests followed for the entire nesting period. Of these, 72 young hatched and 71 fledged. This gives an overall success percentage of 86.6. Of all the eggs laid 87.8 percent hatched and of these 98.6 percent fledged. It is interesting to note, however, that of 53 nests observed during building only 58.5 percent produced any young. Of the other 41.5 percent, 12 nests, or 22.6 percent never had more than one egg laid in them. Hence, females had spent time and energy building nests that were never productive. Of the 10 nests which failed during the nesting cycle one was the result of predation by a Cooper's Hawk (Accipter cooperii) which took the female. One other failure could be attributed to competition with a pair of Brewer's Blackbirds (Euphagus cyancephalus) that harrassed the female robin daily while she was building and laying eggs. She never completed incubation of them. The reasons for the failures of the other eight nests are unknown. Human interferance was a factor in four of the 12 nests which were not used after building. The factors affecting the remainder are unknown.

An attempt was made to determine if any of the physical factors of nesting such as nest site and timing had any effect on success. Nest height did not have any significant effect (based on a Mann-Whitney U test using the normal distribution which produced a value of $z = 0.027$). There was also no differential effect between nesting in either an evergreen or a deciduous tree; (the chi-square resulting from a 2 X 2 contingency table was 0.013, not significant). Nor was cover an important factor (determined by a chi-square test done by lumping the three categories that included cover from one direction only; the chi-square was 5.8460). Whether a nest was started early or late in the season also had no effect (shown by a one-sample runs test and a chi-square test on a 2 X 2 contingency table). For the latter an early/late classification was used based on the grouping of nesting activity shown in Figure 5. All nests started before the May 28 - 30 break are classified as "early" nests and all those after as "late". It is also interesting to note (fig. 5) that no nests are started after mid-July although the daily photoperiod is still in excess of 16 hours of light.

Gonadal Analysis

The gonadal condition reaches its peak and then declines rapidly during the breeding season. The testicular weight ranges from 476.4 mg. to 901.7 mg. and averages 762.8 mg. for 18 specimens collected in the first half of May, during which the daily light period exceeds 16 hours. For the second half of May the average for 10 males was 807.7 mg., ranging from 696.7 to 880.7 mg. During this month the seminiferous tubules reach their greatest diameter. The average diameter is 151.70 mu. for the first half of the month, ranging from

132.60 to 164.33 mu. For the latter part of the month the average is 157.83 mu., ranging from 152.70 to 164.03 mu. All specimens had mature sperm present.

During June the testes start to regress in terms of both weight and size; however, all specimens still show mature sperm present and there is little change in the structure of the seminiferous tubules. It is also during this month that the total hours of light per day reaches its maximum of just under 18 hours. The testes average 554.2 mg. weight, ranging from 295.4 to 865.3 mg., for 10 specimens collected in the first half of June. For the same period the seminiferous tubule diameter averaged 147.39 mu., ranging from 128.85 to 174.38 mu. In the second half of the month the six testes collected averaged 483.1 mg., ranging from 337.9 to 791.4 mg. The average tubule diameter was 142.15 mu., ranging from 129.60 to 147.15 mu.

The ovaries showed very marked size changes during the height of the breeding season. In the first part of May the average weight for the ovary from each of seven specimens was 813.9 mg., ranging from 341.6 to 1265.5 mg. All but one specimen had more than five enlarged follicles, with 10 being the largest number. The largest follicle measured 12.4 mm. This was on the 1265.5 mg. specimen which also had one post ovulatory follicle. For the second half of May eight ovaries averaged 733.2 mg., ranging from 100.3 to 2544.9 mg. Again all ovaries showed developing follicles, the number ranging from two on the lightest ovary to nine on one weighing 522.8 mg. The heaviest specimen had the largest follicle (diameter 12.3 mm.). This specimen had only four developing follicles but all were greater than 9.0 mm. in diameter, and this bird also had an egg in the lower part of the oviduct.

In June the ovaries, as well as the testes, begin to regress. Each ovary averages 317.5 mg. in weight, ranging from 73.5 to 1726.9 mg. for the eight specimens collected during the first half of the month. This drops to 89.7 mg. average for five specimens collected in the second half of June which ranged from 66.5 to 196.0 mg. Two of the specimens collected during early June showed no enlarged follicles. With the exception of that of the 1726.9 mg. specimen, the largest follicle was 2.6 mm. in diameter. The large ovary had three enlarged follicles, ranging from 8.4 to 12.6 mm. in diameter. By the end of the month only two specimens showed any follicular enlargement and that consisted of three follicles (two on one, one on the other), the largest of which was 2.7 mm. in diameter.

Onset of the Non-Breeding Season

Field Behaviour

During the breeding season most pairs have attempted to nest at least twice and some, three times. The latter are starting their last attempt in July. Some pairs reuse the same nest and some build new ones but remain in much the same area or territory even if they change their nest site. As the young from the final nesting effort fledge both parents stay with them feeding and caring for them until they are completely capable of caring for themselves. Even then the young stay with both parents, so small groups are evident in areas which were formerly restricted to breeding birds. As more pairs complete nesting more groups are in evidence. This occurs throughout July and early August while the daily hours of light are still in excess of 16 but less than the maximum of 18 reached in June.

Some of these family groups may join together but the groups generally remain small, ranging from five to 12 members. For the last part of August no robins were observed on campus. They returned in September in somewhat larger groups, as high as 20 members, and family groups could no longer be distinguished. From this time on the behaviour of the robins was typical of the winter, or non-breeding season, patterns described previously.

Gonadal Analysis

By July far fewer nests are being started and the gonadal conditions are regressing rapidly. During the first half of the month the average testis weight is 373.1 mg., ranging from 104.1 to 550.5 mg. for seven specimens. Two of the specimens showed mature sperm. The rest had a few sperm present but the seminiferous tubule structure was degenerating. The average tubule diameter was still quite large, 139.71 mu., ranging from 125.63 to 154.43 mu.

In the second half of the month the testis weighed 94.3 mg., ranging from 14.4 to 291.6 mg. for seven specimens. On microscopic examination none of the specimens showed any sperm present or developing. The average tubule diameter had decreased to 66.55 mu., ranging from 38.25 to 116.19 mu.

In July the ovaries become fully regressed. None of the 12 specimens collected during the month showed any enlarged follicles. The average weight of the ovary of six specimens collected in the first half of the month weighed 57.6 mg., ranging from 31.8 to 70.1 mg. In the latter part of July the average weight was 39.8 mg., ranging from 25.6 to 82.3 mg.

Throughout August seven male specimens were collected. The average testicular weight was 41.6 mg., ranging from 17.4 to 84.5 mg. The tubule diameter averaged 57.20 mu., ranging from 35.46 to 72.91 mu. with no sperm being present in the seminiferous tubules.

In September eight specimens showed a testes weight which averaged 21.7 mg., ranging from 8.6 to 44.6 mg. The seminiferous tubule diameter from this period was 32.51 mu., ranging from 18.72 to 42.66 mu.

The ovaries averaged 20.6 mg. weight ranging from 10.8 to 36.0 mg. for six specimens collected in August. In September the average was 22.6 mg. based on nine specimens and ranged from 12.2 to 31.4 mg.

Figure 6 shows the relationship between the development and regression of the male and female reproductive systems for the entire breeding season.

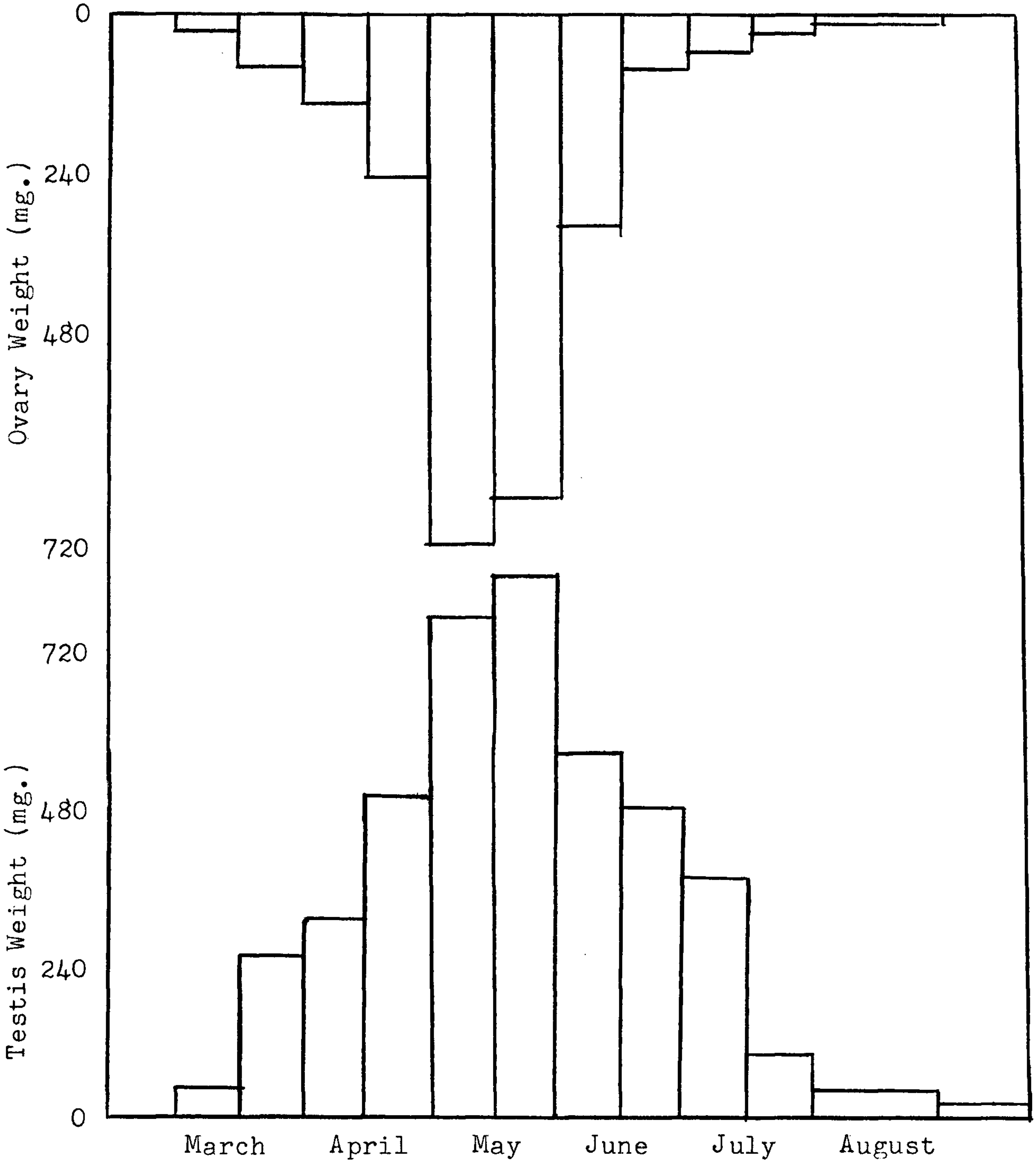

Figure 6. The relationship between the development of male and female reproductive organs.

Photoperiod Experiments

Two sets of controlled photoperiod experiments were conducted, one from January to April of 1969 and the other from February to May of 1970. Both were designed to demonstrate the effect, if any, of increasing photoperiod on gonadal development and on migratory behaviour as evidenced by *Zugunruhe* or night restlessness.

In the first experiment 21 robins were maintained, in groups of three to five birds, on three different light regimes. One group had an eight-hour light, 16-hour dark day, less light than would be normally received at the latitude of my study area at any time of the year. Another group was maintained on a 12-hour light, dark cycle, similar to the photoperiod experienced on campus in the latter part of February. The third group received 16 hours of light and eight of darkness in each 24 hours. This compares to the photoperiod of early May, during the height of the breeding season on campus. I originally intended to use only males for both these experiments, however, when the robins were sacrificed at the conclusion of each experiment several of the males proved to be females.

During the first experiment six robins (four males and two females) were kept on the short day length; eight robins (seven males and one female) on the 12-hour daylight and seven robins (six males and one female) on the long day cycle.

Actual experimental conditions began February 1, 1969 after all the birds had been in captivity under natural photoperiod conditions for at least one week. The birds were sacrificed on April 19, 1969 when the natural photoperiod was approximately 15-hours light, nine-hours dark.

The changes in testicular development on the different photoperiods are summarized in Table II. Those males on the short day length treatment had an average testicular weight of 9.4 mg., ranging from 4.1 to 20.7 mg. The average seminiferous tubule diameter was 39.38 mu., ranging from 37.80 to 41.25 mu. The males on 12-hour days had an average testicular weight of 14.6 mg., ranging from 5.0 to 33.9 mg. and a mean tubule diameter of 45.03 mu., ranging from 30.98 to 72.83 mu. Neither of these two groups of males showed any histological testicular development. The average testicular weight of those males on 16-hour daylight was 200.5 mg., ranging from 77.8 to 313.8 mg. with a tubular diameter averaging 110.25 mu., ranging from 82.95 to 143.1 mu. The testes of this group did have developing spermatocytes but no sperm. These results can be compared to the gonadal development of birds in the wild state. Four males, collected in January at the same time that the experimental birds were captured, had an average testicular weight of 2.9 mg., ranging from 2.0 to 3.9 mg. and an average tubule diameter of 16.38 mu., ranging from 7.58 to 21.90 mu. The testicular state of robins collected in Richmond and on the campus during April, i.e. at the

		First Experiment			Second Experiment	
Photoperiod (Hours)		8	12	16	8	natural
Testes Weight (mg.)	Average	9.4	14.6	200.5	25.0	366.9
	Range	4.1-20.7	5.0-33.9	77.8-313.8	17.0-32.9	271.4-414.8
Seminiferous Tubule Diameter (mu.)	Average	39.38	45.03	110.25	44.14	124.65
	Range	37.80-41.25	30.98-72.83	82.95-143.1	36.22-52.05	121.13-126.68

Table II. The testes weight and seminiferous tubule diameter at the conclusion of the experiments for the robins maintained on different photoperiods.

same time that the captive birds were sacrificed, has been given previously, as has the gonadal condition of those collected in May when the photoperiod was comparable to the 16-hour light that the experimental birds received.

The females also showed different amounts of gonadal development under different photoperiod conditions. The two birds on short day length had ovarian weights of 26.8 mg. and 40.9 mg. and showed no follicular development. The ovary of the one female on a 12.-hour light, 12-hour dark cycle weighed 56.8 mg. and similarly showed no development. The ovary of the female on long day length, however, weighed 183.1 mg. and had nine enlarging follicles, two of which were over 2.0 mm. in diameter. Like the males the development of the captive females can be compared to that of females collected in Richmond and on the campus.

The second set of experiments was designed to show the effect of photoperiod on behaviour, particularly migratory behaviour, as well as on gonadal development. For these experiments, run the following year from March 6 to May 5 using birds captured in late February, the robins were housed individually. This was done primarily to permit the measurement of each individual's night activity and also to reduce any effect, on both activity and gonadal development of aggression or the social dominance of one bird in a cage over the others. For this experiment only two photoperiods were maintained: one was an eight-hour light, 16-hour dark cycle experienced by two males and one female, and the other was the natural photoperiod of the University of British Columbia for the duration of the experiment. Three males were kept on the latter treatment.

The two males on an eight-hour photoperiod had testes weights of 32.9 mg. and 17.0 mg., averaging 25.0 mg. at the conclusion of the experiment. Their tubule diameters measured 52.05 mu. and 36.22 mu., averaging 44.14 mu. (Table II). No development of secondary spermatocytes or spermatids was evident. The female in this treatment had an ovary which weighed 28.3 mg. and had no developing follicles.

The three males kept under natural photoperiod conditions had an average testicular weight of 366.9 mg., ranging from 271.4 to 414.8 mg. The seminiferous tubule diameter averaged 124.65 mu., ranging from 121.13 to 126.58 mu. These specimens did show developing spermatocytes and spermatids.

The activity of the two groups of robins is shown in Figures 7a to 7h. The period from 4 pm one night to 8 am the following morning represents the dark phase of the birds on short photoperiod. The average of the activity of these birds is shown by the solid line. For the three males on natural photoperiod the dark phase of their daily cycle is shown at the top of each figure and the average of their activity by the dotted line. The figures are for one day of each week for the eight weeks of the study. The night activity or

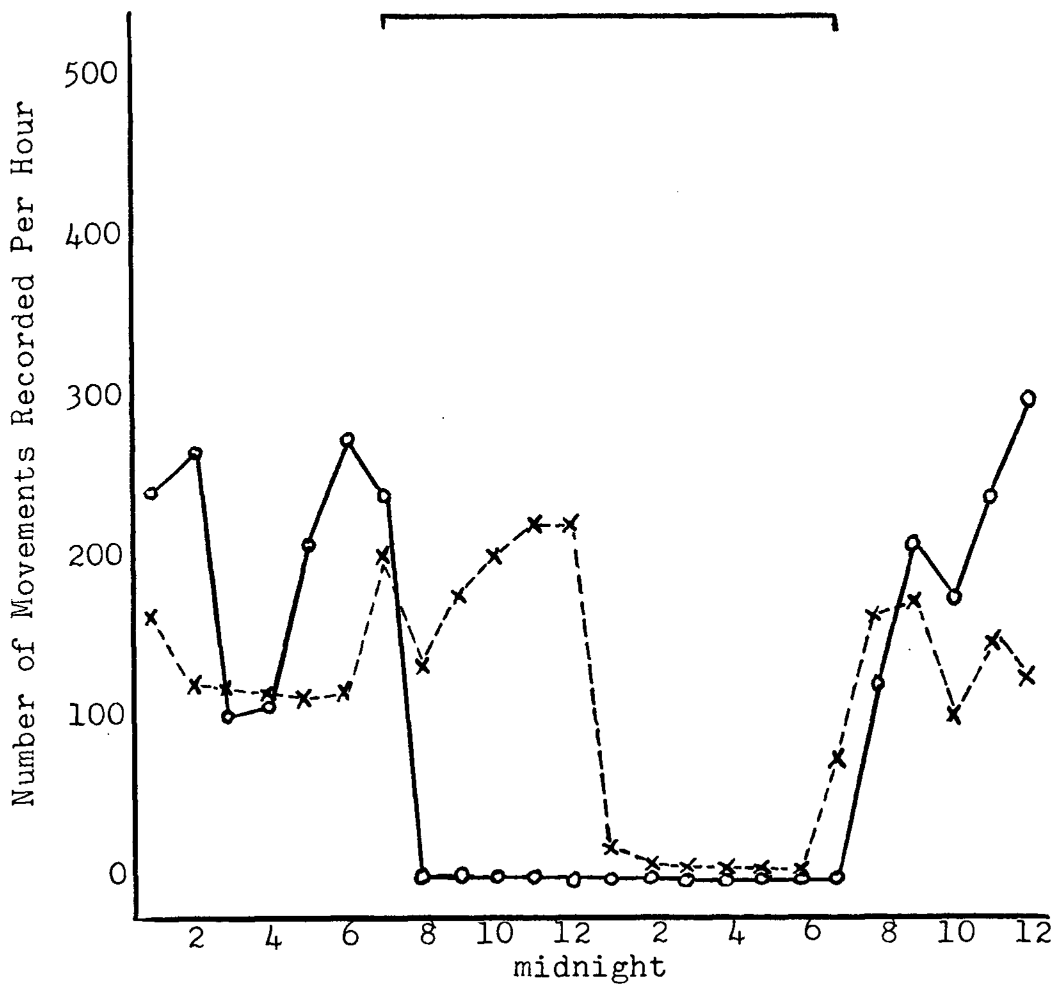

Figure 7. The average hourly activity of two groups of robins housed under different photoperiod conditions. The dotted line represents those exposed to natural photoperiod with the line at the top of the graph showing the period of darkness for these birds. The solid line represents the activity of birds kept under short photoperiod which were in darkness from 4 pm to 8 am each day.

7a. The activity for March 9/10.

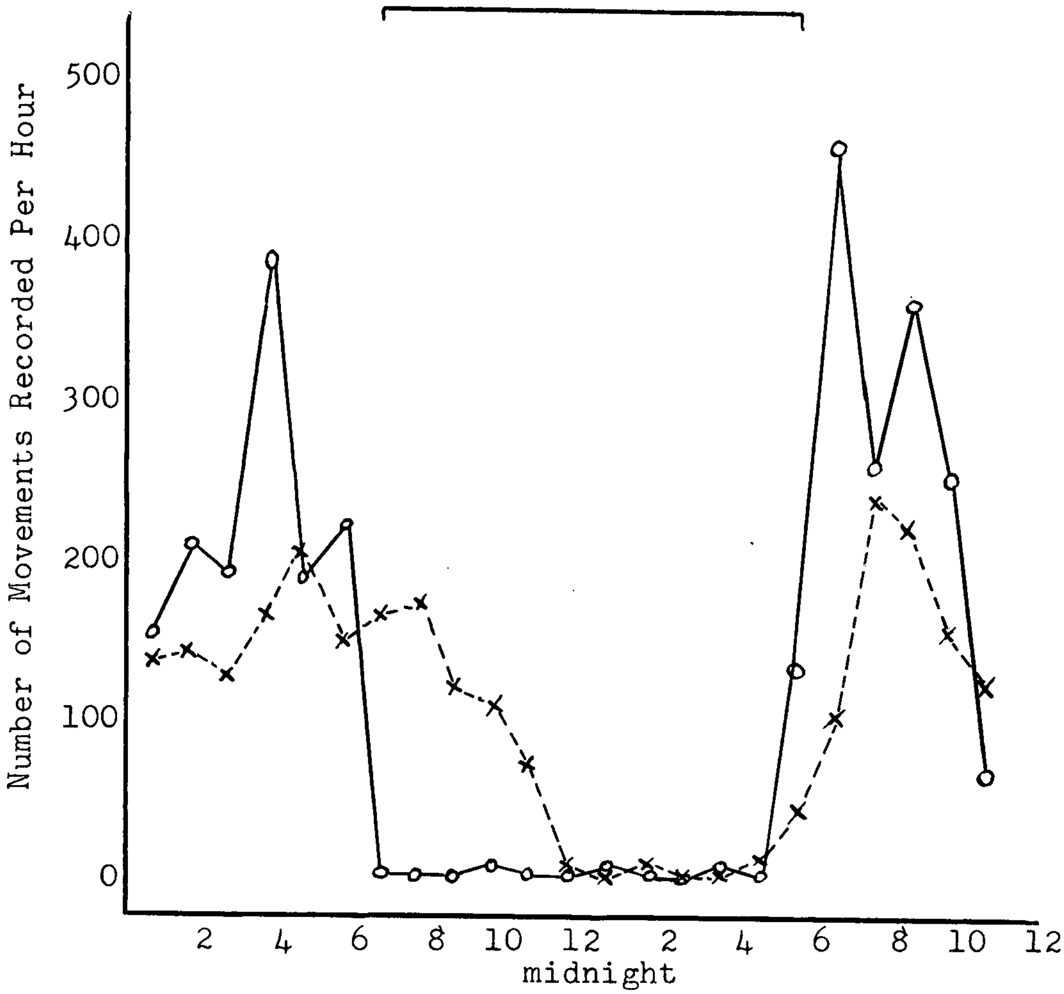

Figure 7b. The activity for March 16/17.

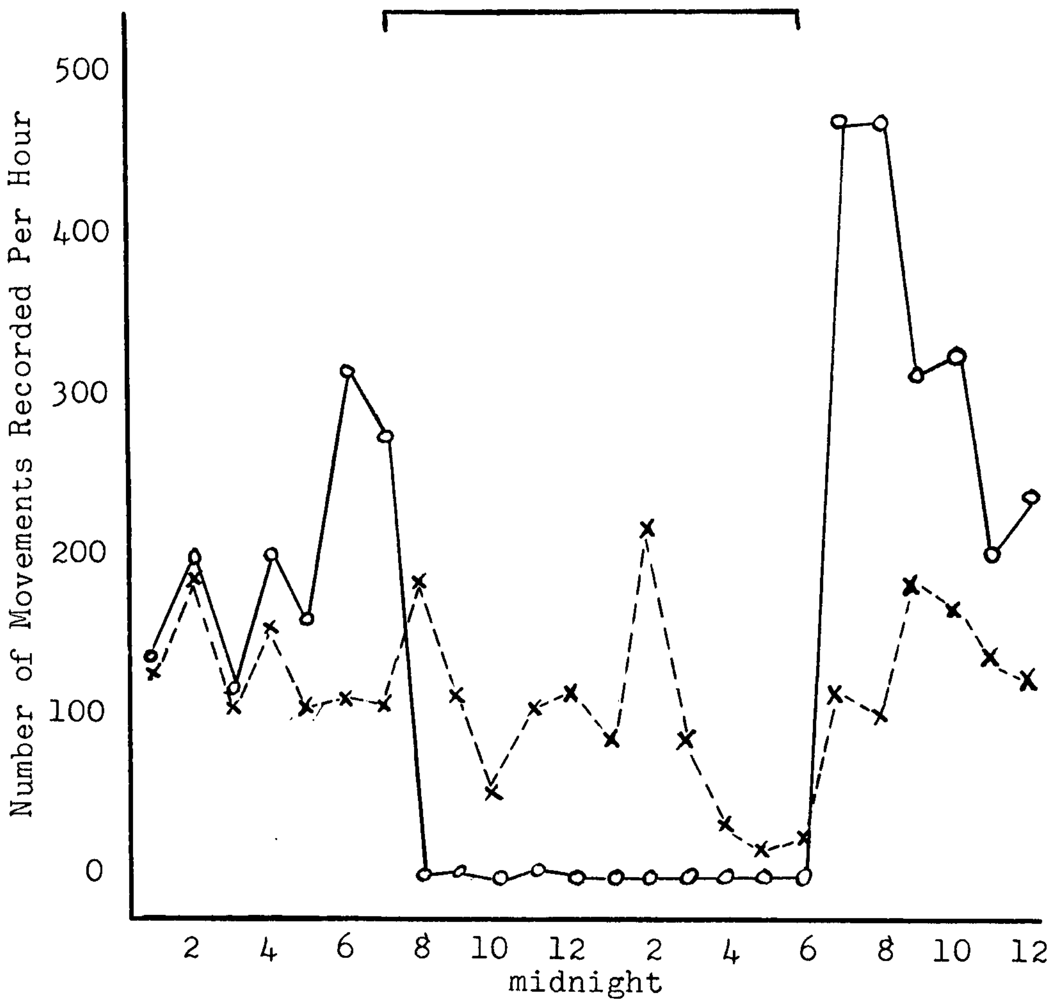

Figure 7c. The activity for March 24/25.

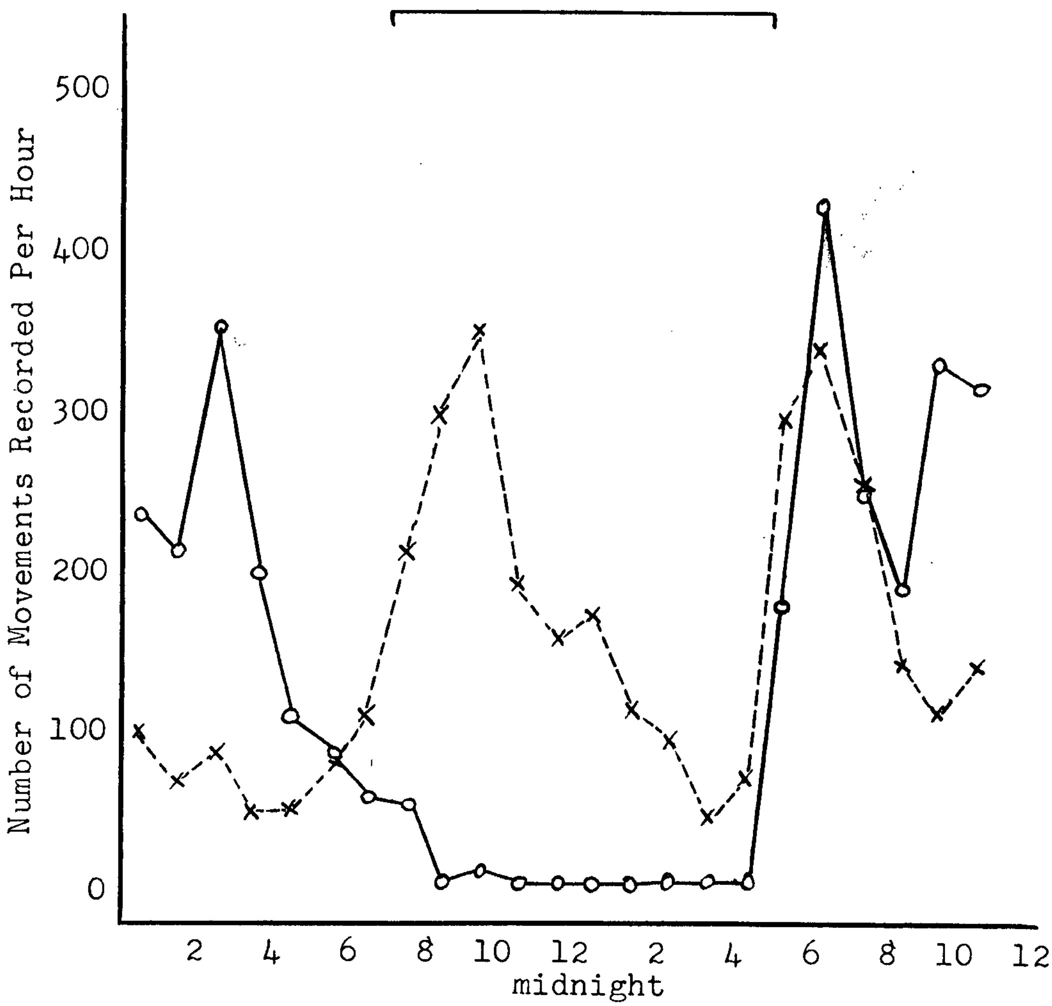

Figure 7d. The activity for March 30/31.

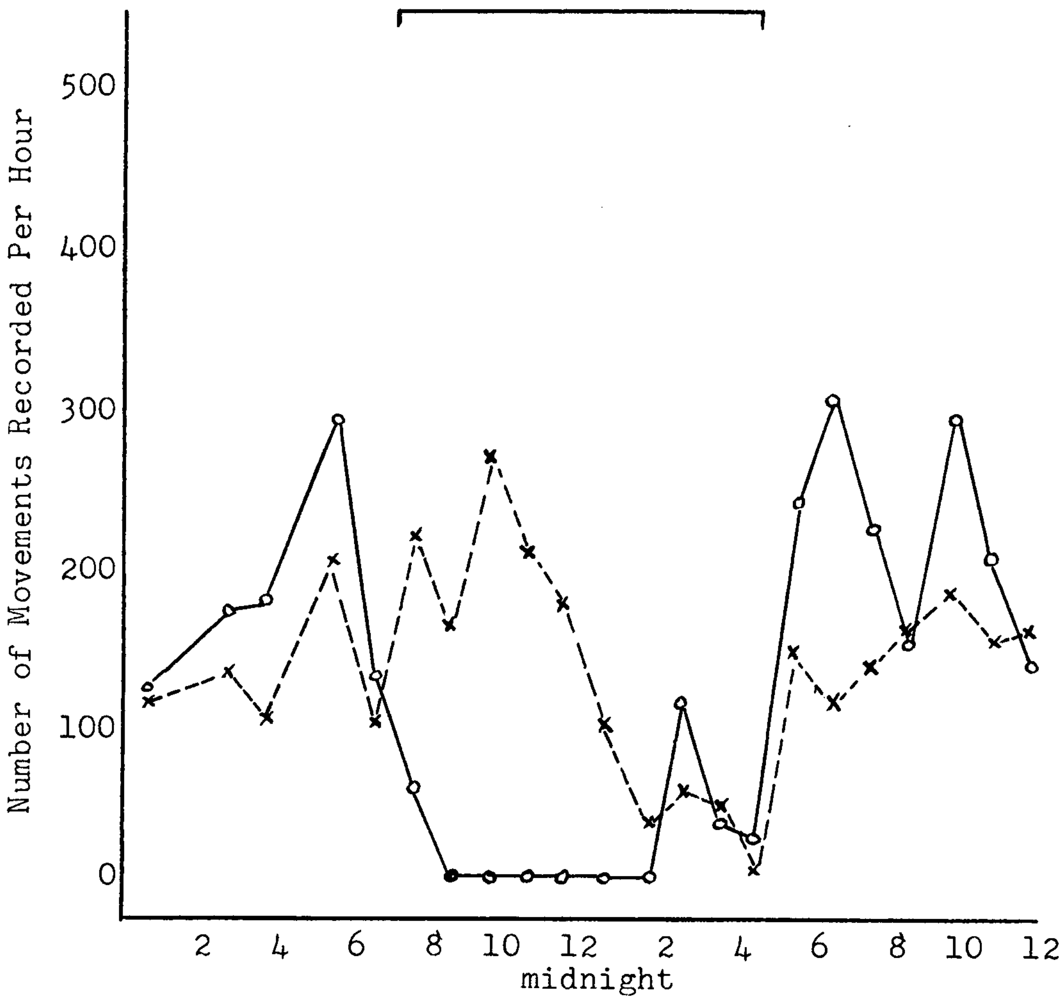

Figure 7e. The activity for April 8/9.

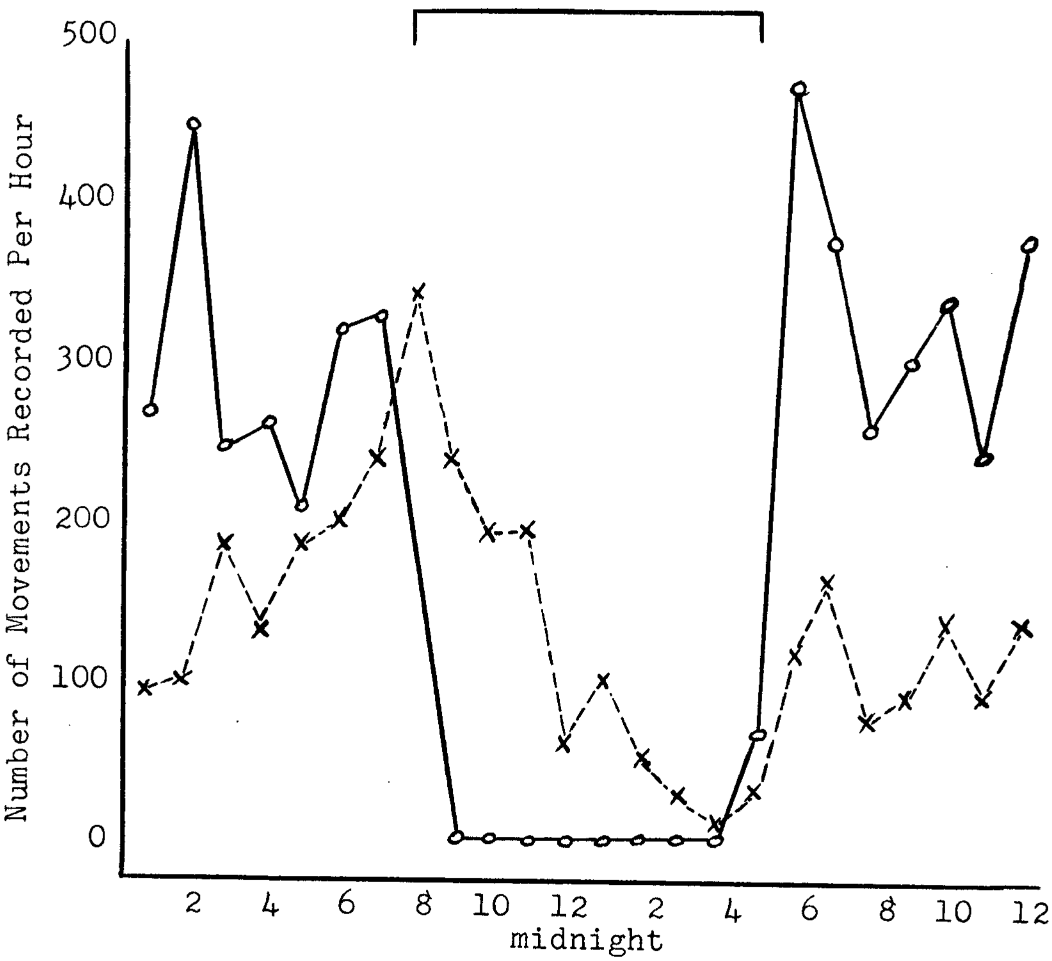

Figure 7f. The activity for April 14/14.

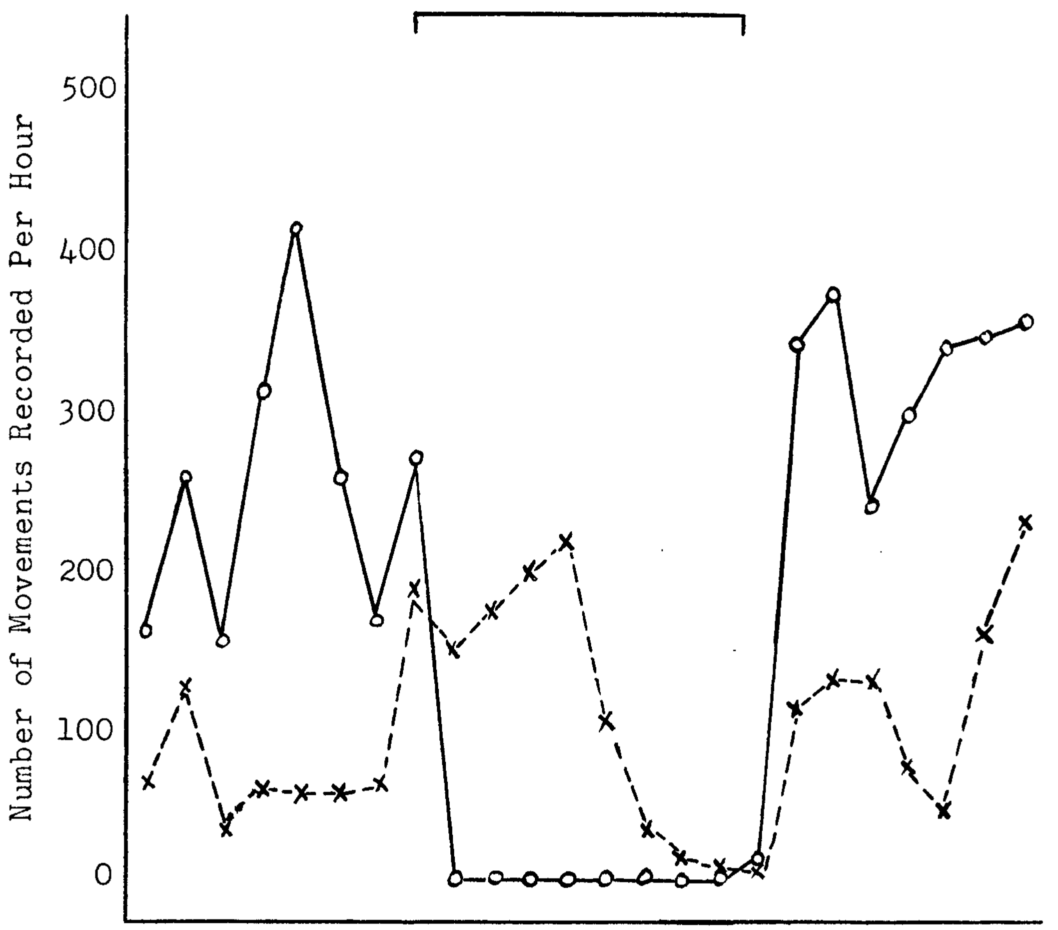

Figure 7g. The activity for April 20/21.

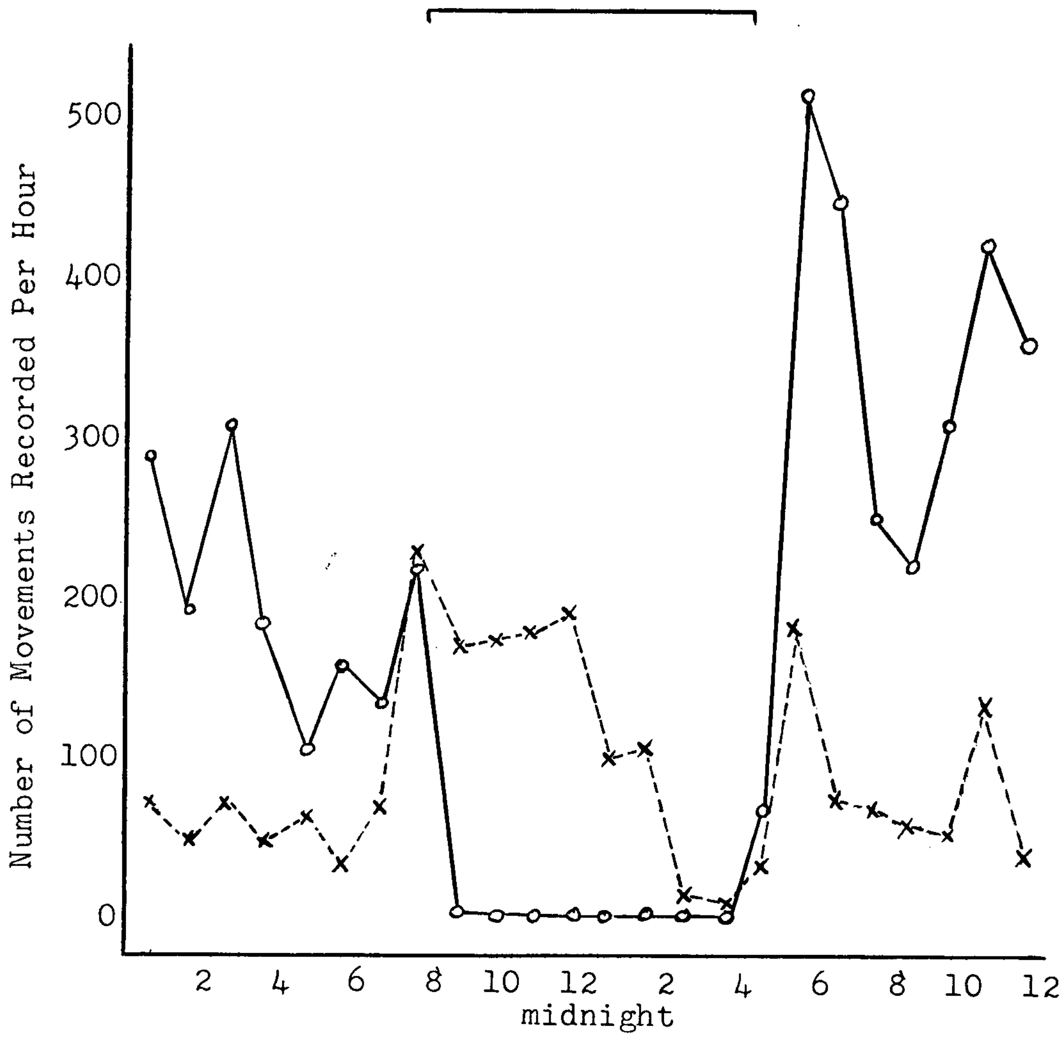

Figure 7h. The activity for April 27/28.

Zugunruhe of the birds on natural photoperiod, which varied from 12.25 hours at the onset of the experiment to 16 hours of light per day at the end of the experiment, is strikingly evident.

DISCUSSION

My study of the American Robin (*Turdus migratorius*) concerns itself with two main aspects of the reproductive biology of the species. One consideration is a study of the nesting parameters of these birds. This includes the roles of the parents from the onset of the breeding season until the last brood is reared, the physical factors of nesting such as location, and the nesting success. The other aspect is the relationship of the increasing day lengths of spring to gonadal recrudescence and the timing of the breeding season. This relationship was studied both by field observation and laboratory experiments. The study was somewhat complicated by the presence of three subspecies of robin (*T. m. migratorius*, *T. m. caurinus*, and *T. m. propinquus*) in the Vancouver area. Unfortunately a workable description of the different subspecies and their habits is not available (Coues, 1903; Forbush and May, 1955; Godfrey, 1966) so I was not able to determine whether or not a given bird was a migrant or resident and to which subspecies it belonged.

Nesting Parameters

The pattern of nesting activities which I recorded for the American Robin is basically the same as that described by Howell (1942), Young (1955) and Howard (1967). These researchers, however, studied populations which were migratory, so their observations begin with the arrival of birds in spring and the establishment of nesting territories by the male. Since my work deals with a partially resident population of robins I was able to observe the early indications of breeding behaviour. I used the shift from gregarious winter behaviour to territorial behaviour as a marker for the onset of the breeding season. There are accounts of winter behaviour in robins (Black, 1932; Price, 1933) but none describing the shift from social flocking behaviour to pairing.

The European turdids, especially the English Robin (Erithacus rubecula), show a territorial behaviour year round (Lack, 1948). The territory established in autumn is in a different place from that established in spring, but Lack (1948) gives no indication of when or how the breeding territory is established. It does seem, however, that the winter territory of the English Robin is more distinct and permanent than the individual spacing behaviour which I noted while American Robins were ground feeding during winter. The spring, or breeding, territory of the English Blackbird (Turdus merula) is not established until after pair formation occurs (Lack and Light, 1941). The latter, however, takes place in early February, so it may not coincide with gonadal recrudescence whereas territory establishment may. Unfortunately there is no information on the gonadal cycle of this species. The Blackbird on the Shetland Isles of Britain winters in loosely aggregated groups near, and occasionally in, the breeding area (Venebles and Venebles, 1952). The winter birds are not normally territorial or aggressive towards one another. The authors do report non-functional "sexual chasing" occurring from January until the start of the breeding season but point out that pairing and territory establishment do not occur until the end of February and March.

My records show that for the years studied there was a gradual breakdown of winter flocking behaviour in the robin with a parallel increase in intraspecific aggressive territorial behaviour. This occurred from the beginning of February until early April, although few permanent territories were established before the latter half of March. During this period the hours of light per day increased from 10.6 to 14.5.

Once the territories are established the activities of the males and females in terms of defence, nest site locating, and nest construction are the same at the University of British Columbia as those described by others (Howe, 1898; Howell, 1942; Young, 1955). Howell (1942) did note a significant difference between the number of nests constructed in evergreen compared to deciduous trees at the beginning of the nesting period. My data did not show a difference between these two site types at any time of the breeding season but it did show that the robins preferred nest sites which offered some cover.

The roles of the males and females which I observed for egg-laying, incubation, care of nestlings and care of fledgings proceeded according to the pattern observed by others (Howe, 1898; Hamilton, 1935; Schantz, 1939; Howell, 1942; Young, 1955) with the exception that on two occasions I witnessed males (sexed on the basis of plumage colouration) incubating eggs. Howell (1942) quotes others as having recorded such behaviour although he did not observe it. Since I did not collect the birds in question I cannot be absolutely certain of their sex. In one of the two cases a much paler-coloured bird was nearby and took over the incubation. For this nest then either the male was assisting with the incubation or there were two females sharing the nest. This behaviour of the males may be more correctly called brooding rather than incubation as there is some question as to whether or not the male is capable of warming the eggs (Ryves, 1943).

Both the length of the incubation and nestling periods and the activities connected with them are much the same for the robins I observed as those observed by others (Howe, 1898; Hamilton, 1935; Howell, 1942; Young, 1955). Similarly the average clutch size does not vary significantly from the 3.04 ± 0.05 found by Young (1955) or the usual three or four eggs per clutch noted by Howell (1942) and Howard (1967). The latter investigator found a seasonal variation in clutch size, using data from nest record cards, which was significantly different for the periods of May and July. Similar changes in clutch size have been discovered by nest record card analysis for several British turdids (Snow, 1955a). No such significant variation with season is apparent in the birds which I studied but this could be due to the restricted number of nests observed.

The nesting success was the only other nesting parameter for which my results differed markedly from other published records. The overall success rate of 86.6 percent from eggs to fledgings in my study is much higher than the average 49 percent observed by Young (1955) or the 65.2 percent shown by Howell (1942). My results are also higher than the expected success figures for both open and hole nesting birds, 43 percent and 55 to 76 percent respectively, as calculated by Nice (1937). The incubation period had the greatest failure rate in all reports but this is also the period in which there is the most discrepancy between my results and the others. The robins I observed had a hatching success of 87.8 percent, whereas Young (1955) observed only 58 percent and Howell (1942) 73.9 percent. The rates for hatching to fledging success were 98.6 percent (my results) 88.2 percent (Howell, 1942) and 78 percent (Young, 1955). The high recruitment rate which I found for robins on the campus of the University of British Columbia could well be a local phenomenon and not representative of the robins of southwestern British Columbia as a whole.

In order to determine if this was so or not I checked my results with those of the British Columbia nest record card survey (Drent, pers. comm.). This data for robins in southern coastal gardens and parks indicates a 72 percent hatching success and 100 percent fledging success. The surveys of one person in the Vancouver area give an overall success figure of 75 percent for nests in 1969. The results for British Columbia as a whole, however, show a hatching success of 64.5 percent and a fledging success of 64 percent for an overall recruitment of 59 percent. These figures indicate that the southwestern corner of British Columbia, especially the area with gardens and parks, can expect a higher than average, for this species, success rate. The area of the campus which I studied is relatively free from cats, one of the main residential predators of robins, and from racoons, squirrels and birds of prey, important woodland predators. There is also little human interference or vandalism as there are few students and virtually no young children present on campus during most of the breeding season of the robin. This habitat would be comparable to that studied by Kendeigh (1942) for which he found an overall success rate of 71 percent with a hatching and fledging success rate of 86 percent and 83 percent respectively.

Breeding Season and Gonadal Condition

At the onset of the breeding season, as the previously described shift in social behaviour pattern is taking place, the photoperiod is increasing from 12 hours of light per day at the beginning of March to over 14 hours at the beginning of April when most territories are established. None of the ovaries collected at this time have follicles sufficiently developed to ovulate. The testes do not show any increase in size until the first of March and are at only half their potential weight by mid-April. The seminiferous tubules have, however, enlarged almost completely by mid-April, with some specimens possessing mature sperm. The difference in testes development between birds collected in Richmond, which were, at that time of year, generally found in groups, and those collected on campus, which were generally alone or in groups of only two or three, is marked. The Richmond robins could be males which had not, as yet, established territories or they could be migrants who would be moving further north before setting up territories. This would agree with Wolfson's (1942) findings on the Oregon Junco (Junco oreganus) that the testes of resident birds recrudesce earlier and at a faster rate than those of migrants. In either case the establishment of a territory and/or pairing with a female may be necessary to stimulate further gonadal development. Comparison of the testicular condition of each group of birds indicates that the onset of breeding behaviour in the American Robin can be correlated with detectable developmental changes in the histology of the testes.

The actual nesting period, as defined by the start of nest building until the last brood leaves the nest, runs from late March until August. Egg-laying occurs from early April until early July, with a peak in mid-April and a smaller one in early June (fig. 5). Howell (1942) working with a migrant population at Ithaca, New York, found that nesting territory establishment did not take place until the last week of March and that eggs were layed from early April until the first of August. Young (1955) discovered an egg-laying season of April 12th to July 20th at Madison, Wisconsin, based on the time of laying of the first egg of a clutch. He found a peak in nesting activity in the third week in April. Howe (1898) describes a nest construction period from early April until the third week of May in eastern Massachusettes. This, when compared to the results of a nest card survey of the same area (Howard, 1967) indicates that he may have succumbed to the well-noted human failing (Myres, 1955) to search less dilligently for nests in the latter part of the season.

The genus _Turdus_ in Great Britain has a breeding season lasting from March to July (Myres, 1955). The Blackbird may initiate nesting as much as two weeks later in woodland habitats than in gardens at the same latitude (Myres, 1955). Myres (1955) also demonstrated a delay in the start of the breeding season as one moves northward and a dependence on warm weather conditions before nesting will begin in March and early April. The thrushes of the Shetland Islands have a breeding season from April until early August (Venebles and Venebles, 1952) although the number of nests started after July 1st is much reduced. The season for the Blackbird in

New Zealand (Bull, 1946) runs from late August to early December, comparable to February through June in northern latitudes, with the majority of the activity occurring from mid-September to late October. The timing of the breeding season of various turdids at different latitudes is summarized in Figure 8.

It is clear, from this information, that the timing of the breeding season is related to latitude, and hence, to photoperiod, but not exclusively dependent upon it. Other factors such as temperature, habitat, and food availability may ameliorate the situation on a local basis.

The histology of the gonads of those male robins collected on the campus of the University of British Columbia reveal that some are in breeding condition by the end of March and all are spermatogenic by mid-April, the time at which the majority of first nests are begun. Spermatogenesis is maintained until the end of June, and then the testes begin to regress very rapidly. The same pattern is shown (Howell, 1942) for the male robin at Ithaca, New York. The development of the ovary is not as straightforward. Females in full reproductive condition with eggs ready to ovulate were found only in the May sample. It is, however, obvious (fig. 5) that females must have been laying eggs from April to July. The lack of ovarian specimens to substantiate the nesting cycle of the female is probably partially due to the rapid development and regression of follicles (Meyer <u>et al</u>, 1947; Davis,

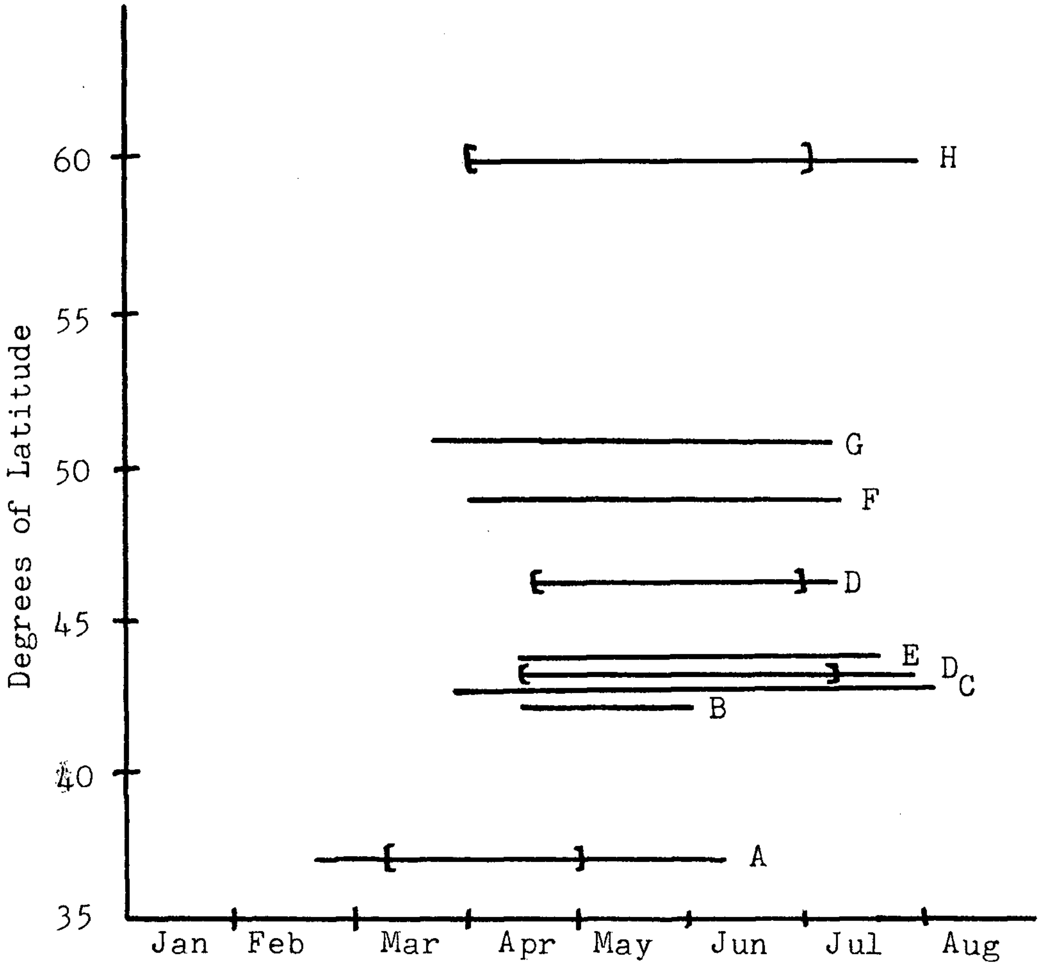

Figure 8. The relationship of breeding season to latitude. The area within brackets indicates the time span in which 90 percent of breeding occurs. The references are as follows:

A. Bull, 1946
B. Howe, 1898
C. Howell, 1942
D. Howard, 1967
E. Young, 1955
F. This study
G. Myres, 1955
H. Venables and Venables, 1952

1942b; Romanoff, 1943) and also to the dependence of the female on stimulation by some local condition that initiates ovarian development (Davis and Davis, 1954; Farner, 1964) rather than photoperiod (Wolfson, 1942). The precise factors that stimulate follicular enlargement are unknown but it is possible that the readiness of the female is a controlling factor in the timing of the breeding season.

Photoperiod Experiments

I conducted two sets of experiments to determine if increasing photoperiod would stimulate gonadal development in the American Robin, particularly testicular development, as was indicated by my field observations. A positive relationship between the two factors has already been established for several other species of birds including two junco species (*Junco hyemalis* and *J. oreganus*) (Rowan, 1929; Wolfson, 1959) and the White-crowned Sparrow (*Zonatrichia leucophrys gambelii*) (Farner and Mewaldt, 1952; Farner and Wilson, 1957; Farner, 1964; Farner *et al*, 1966). Both experiments which I conducted showed a positive correlation between the hours of light and recrudescence of gonads. In neither case, however, did the captive birds attain a gonadal condition equal to that of wild robins experiencing similar hours of daylight.

The birds which I maintained on short day length, eight hours of light per day, had average testicular weights that were greater than the average for the robins which I collected during the winter, even though the wild birds were experiencing photoperiods in excess of eight hours per day. The noise issued by robins which were experiencing longer photoperiods but which were housed beside the short day birds may have had an effect on the development of the latter. Also the intensity of the light used in the experiments, which I did not measure, may have been important in this regard (Burger, 1943; Bartholomew, 1949). The experimental robins on 12 hour days showed an average testicular weight that was similar to that of wild robins captured in early March, when the photoperiod is about 12 hours. The testes of both captive and wild birds at 12 hours of light showed only very slight development beyond the stage achieved by winter birds, indicating that the photoperiod must <u>exceed</u> 12 hours for any stimulatory effect to occur.

Birds kept on 16 hours of light per day showed definite testicular enlargement and development although not to the same extent as wild birds collected when the photoperiod was about 16 hours. These latter birds had an average testicular weight twice that of the captive birds. The wild birds had mature sperm present in their seminiferous tubules whereas the captive robins had only developed to the spermatid stage. The testicular condition of the captive robins was closer to that of wild birds collected at about 15 hours of light per day photoperiod than to those collected at 16.

Retarded development of captive birds as compared to birds in natural conditions has been noted by others (Scott and Middleton, 1968 for the Brown-Headed Cowbird (Molothrus ater); Miller, 1960 for Zonotrichia leucophrys). This difference might be attributed to light intensity, type of food available, restricted activity, and social stimulus from conspecifics, especially birds of the opposite sex. The environmental stimulus of a suitable breeding territory may also be an important factor.

The effect of two of these factors, social interactions and light intensity, is further exemplified by the differing results of the two experiments. In the first set of experiments each cage held several birds, one of which appeared to be dominant. This bird would always eat first and often chased the other birds around the cage. The dominant robins, although not significantly different from others on the same treatment, weighed more and had the heaviest testes at the end of the experiment. Whether the social conditions served to stimulate the one bird or retard the others or both is not known. However, for the second set of experiments the robins were housed individually and these birds showed greater gonadal development on both light regimes than did the robins under the same light conditions in the previous experiment.

This difference was very noticable for the 16 hours of light per day birds which showed an average testicular weight of 200.5 mg. in the first experiment and 366.0 mg. in the second. For the second experiment not only were the birds caged separately but they were also exposed to natural rather than artificial light.

From these results it is clear that a photoperiod of greater than 12 hours per day over the period of my experiments, is necessary to initiate gonadal development. It is more difficult to determine if the light period must reach a certain amount before full spermatogenesis or ovarian development is reached. Certainly the collected birds did not reach such a state until there was 15 hours of light per day, but it is impossible to say whether or not they would have developed completely if kept at a ratio greater than 12 hours light : 12 hours dark but less than 15 hours light : 9 hours dark. This may depend on the genetic makeup of the species (Miller, 1960). Recent studies by Menaker (in press) indicate that it is not the length of the daily light phase that is important but the time of day at which light occurs. In other words, a brief flash of light repeated daily at a point in the circadian rhythm when the species is photoreceptive is all that is necessary to stimulate gonadal development. Wolfson's data (1953) will probably, on reanalysis, corroborate Menaker's hypothesis. If such a hypothesis is correct, then for the robins which I studied the photoreceptive period would have to be at some point in the circadian rhythm shortly after darkness would normally occur on a natural 12 hour light day. The effect of photostimulation at this time may then be cumulative until full breeding condition is attained.

It is also, however, evident from my results that factors other than photoperiod play a role in determining the precise timing of the breeding season. The relationship, if any, of photoperiod to the maintainence of reproductive gonadal condition throughout the breeding season and to the gonadal regression at the end of the season is untested for the robin.

During the second experiment I also measured *Zugunruhe* or night restlessness. This is an indication of migratory behaviour in species which migrate at night. I wanted to know if the relationship between increasing photoperiod, gonadal recrudescence and spring migration shown for other species (Rowan, 1926; Wolfson, 1942, 1959; Farner, 1955, Farner *et al*, 1960) would also occur in the robin. Since activity would be monitored from the onset of the experiment such a study would also indicate how rapidly the increased photoperiod would become effective. The results showed that a definite relationship between increased photoperiod and migratory behaviour exists. Virtually no night activity was demonstrated by robins on eight hour light photoperiods whereas those on long days showed *Zugunruhe* nightly beginning five days after the start of experimental conditions.

CONCLUSIONS

The breeding biology of the Amercian Robin of southwestern British Columbia, as observed in this study, is basically the same as that of this species studied elsewhere in North America. The facet of the breeding biology of the robin which is presented for the first time is the gradual nature of the onset of the breeding season as evidenced by the change in intraspecific territorial behaviour.

Field observations and laboratory experiments both indicate that photoperiod is a major factor controlling the onset of gonadal development and hence timing of the breeding season. Gonadal recrudescence will not occur until the photoperiod exceeds twelve hours per day. The laboratory experiments further demonstrate that long day lengths alone are not sufficient to stimulate full reproductive response. Other factors such as social stimulus from conspecifics of both sexes, and environmental stimuli may modify the rate of reproductive development. Much greater attention needs to be given to the role of the female as regards the timing of the breeding season.

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