SOME PHYSIOLOGICAL CORRELATES OF PINTAIL REPRODUCTIVE BEHAVIOR

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As a result of intensive field studies during the past two or three decades, knowledge of the general features of the ecology and reproductive behavior of most species of waterfowl is relatively complete. In contrast, information concerning physiological processes in these birds is almost nonexistent. Goodale (1916) showed that castration resulted in a loss of sexual behavior in domestic drakes, and the studies of Benoit and his co-workers (see Benoit and Assenmacher, 1955) have done much to elucidate the mechanisms of light stimulation of the pituitary-gonad axis in domestic ducks. The only studies directly pertaining to wild ducks are those of Seligmann and Shattock (1914) and of Höhn (1947, 1949, 1960). The latter studied histology and weights of gonads, thyroids, and adrenals of Mallards (*Anas platyrhynchos*) in an attempt to correlate variations in these organs with seasonal changes in behavior. In addition, Sowls (1955) included observations on the gross state of development of the gonads of a few ducks that he collected to determine the physiological states correlated with specific behavior patterns.

The present paper reports some of the data from six months of intensive field study and collecting of Pintails (*Anas acuta*) on the breeding grounds in southern Manitoba during the period from mid-April to mid-August, 1958, and supplementary observations made in 1960 and 1961. It is an attempt to determine some of the physiological mechanisms that underlie breeding behavior and ecology in this species.

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METHODS

The area around the Delta Waterfowl Research Station was searched repeatedly on foot and by car from St. Ambroise on the east to Langruth on the west and from the south shore of Lake Manitoba south for six to ten miles. Observations and collections also were made in the "pothole" country around Minnedosa. More than 6000 miles were covered by car in addition to many on foot, and 71 Pintails were collected. An attempt was made to take only those individuals that were engaged in particularly interesting activities. Special effort was made to collect birds (1) from migrating flocks and courting parties, (2) on "territory," (3) during incubation, and (4) in the so-called "renesting" flights. Organs were preserved in Bouin's solution immediately in the field, and gonads, oviducts, and thyroid and adrenal glands were weighed in the laboratory. Histological studies were made of thyroids and adrenals. Estimates of thyroid activity were made by measuring with an optical micrometer the heights of 100 epithelial cells picked by chance from several thyroid sections from each bird; the proportion of the adrenal cortex to the medulla was estimated by counting the cells of each type that fell under the intersections of an optical grid, located by chance on several sections of adrenals, until a total of 100 was reached for each bird.

RESULTS

Spring flocks.—Groups varying in size from a few pairs to several thousands of individuals are included here. Flocks appeared to consist primarily of pairs migrating through the area. Hochbaum (1944) and Sowls (1955) likewise noted that most Pin-

tails arrived paired at Delta. In 1958, many of the flocks contained numbers of apparently unpaired birds as well, and courting parties of several drakes and a duck were seen almost daily from mid-April to late May. In contrast, Sowls (1955:21) reported seeing courting parties only twice in five years of field studies at Delta, but Phillips again saw them there repeatedly in 1960 and 1961. It may be pertinent to note that water levels were low in 1958, 1960, and 1961, and that the usually abundant sheets and puddles of water were not present in the fields in these spring seasons.

To study the physiological condition of flocked individuals, collections were made of ducks that were found: (1) present in the flocks but whose pairing status was unknown; (2) paired and in the flocks; and (3) actively engaged in courting, either on the water or in the air. Weights and histological information are presented in table 1.

TABLE 1

MEASUREMENTS OF ORGANS OF FEMALE PINTAILS

	Flock		Dispersed pairs		Incubating		Renesting		Courting		Three-bird[1]
Ovary											
Weight (gm.)	4.31	(18)[1]	16.76	(17)	1.38	(11)	12.3	(7)	1.7	(4)	4.16
Largest follicle (mm.)	11.4	(18)	23.3	(17)	5.3	(10)	18.0	(7)	9.2	(4)	12.2
Oviduct											
Weight (gm.)	9.84	(18)	28.75	(17)	7.56	(11)	20.4	(7)	5.2	(4)	20.8
Thyroid											
Weight (mg.)	0.0504	(19)	0.0442	(16)	0.0505	(9)	0.0433	(5)	0.0537	(4)	0.047
Height epithelium (μ)	5.00	(17)	5.79	(14)	4.28	(8)	6.11	(5)	4.31	(4)	5.49
Adrenal											
Weight (mg.)	0.0760	(18)	0.0932	(14)	0.0632	(10)	0.1042	(5)	0.0504	(3)	0.091
Cortex (per cent)	61.81	(16)	67.20	(15)	67.10	(10)	71.43	(7)	62.33	(3)	60.20

[1] Sample size; in three-bird group, sample was 5 throughout.

The most noticeable feature about all these groups is that their reproductive organs were only partly developed, indicating that the ducks were still a week or more from active nesting (see following). All birds from flocks had heavy subcutaneous and abdominal fat. Four females collected from courting parties within the flocks appeared to be at an earlier reproductive state than flocked females generally (most of the latter were paired). This conclusion agrees with behavioral evidence indicating that pairing mostly takes place before migration.

Three-bird flights.—A conspicuous activity of Pintails on the nesting grounds is the three-bird flight or "territorial pursuit" described by Hochbaum (1944) and by Sowls (1955). These flights usually consist of: (1) a male that has flown up from his mate to pursue the (2) female of a passing pair, and (3) the mate of this second female lagging behind. Five females were collected from "three-bird flights," three from flights arising from flocks and two from flights arising from isolated pairs. The ovaries of the first three were small and only partly developed; those of the two isolated females were mature and both birds were ovulating. These measurements of reproductive tracts support behavioral evidence suggesting that flights arising from flocks are associated with

pair formation, whereas those arising from scattered pairs are more likely aspects of a nest dispersal mechanism. Often females were seen to initiate the former type of flight by making repeated short flights near males until two or more took flight after her. In the case of flights from scattered birds, our observations confirm those of Hochbaum (1944) and Sowls (1955) and indicate that males initiate these flights. For a more complete discussion of duck flights see Geyr (1961 and previous papers).

Laying and incubating.—Females were collected from pairs on the nesting areas. These pairs were isolated to a greater or lesser degree from flock activities, each showing a considerable attachment to the area in which it was found. Such pairs were much more easily approached than others and would fly "reluctantly" and alight or return quickly after being flushed. Of 17 females thus collected, 12 were laying and two more appeared to have laid but were no longer doing so. Three of the females had not laid, confirming Sowls' (1955) observation that pairs disperse from flocks before the females are ready to nest. He collected six females from pairs that he observed in "searching" flights and found that the maximum ovum in five was about pea-sized (that is, five to seven mm. in diameter). The rate of follicle development, discussed below, suggests that pairs leave the flock at least a week before the first egg is laid.

Laying.—The physiology of laying in Pintails has been discussed elsewhere (Phillips and van Tienhoven, 1960), but the data are summarized here in table 1 to allow comparison with the other stages under discussion. Briefly, ovaries and oviducts reach maximum development during laying, as do adrenal weights and thyroid activity. The pituitaries of layers contained less gonadotrophins than did those of non-laying, mostly

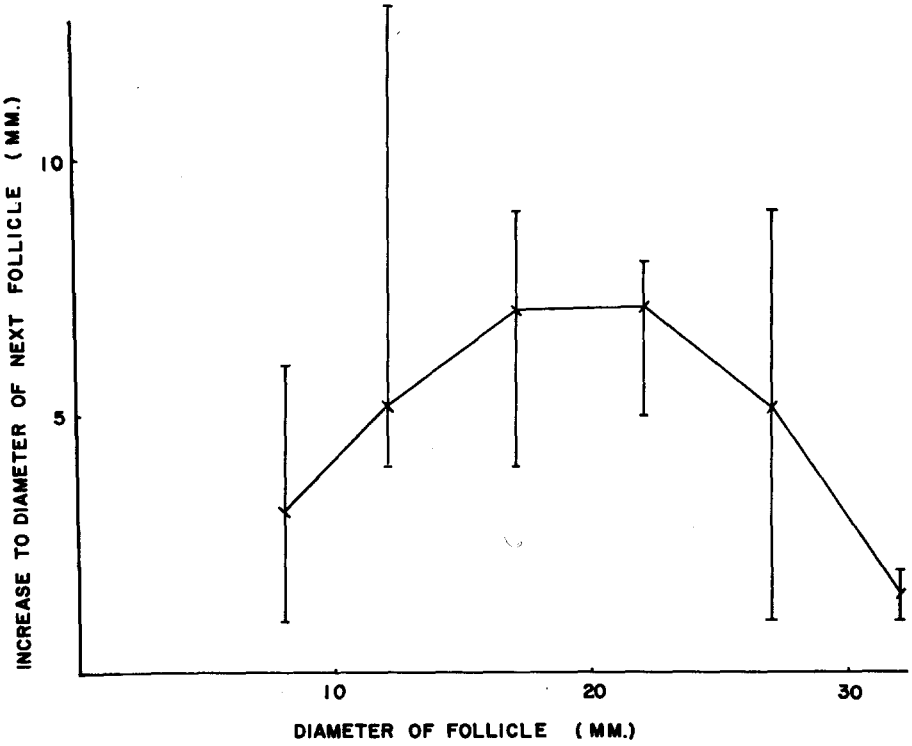

Fig. 1. Difference between diameters of adjacent-sized ovarian follicles plotted as a function of the diameter of the smaller one.

flocked, birds, a condition consistent with the situation found in chickens (Saeki *et al.*, 1956) and in Ring-necked Pheasants, *Phasianus colchicus* (Greeley and Meyer, 1953).

Measurements of the diameters of all the follicles containing yellow yolk in each ovary were made to estimate the rate of development during the period from the first appearance of yellow color (diameter about six mm.) to ovulable size (diameter about 30 mm.). Follicles of 15 to 24 mm. diameter showed the greatest rate of increase, whereas those larger and smaller both increase at a lesser rate (fig. 1). Counts were not made of follicles below 6 mm. in diameter because below this size growth appears to be very slow. Most ovaries show many follicles of all sizes below 6 mm., but only a few above it. Counts of follicles showed an average of six in the range from the largest down to the largest white-yolked ones. Assuming that the birds lay an egg daily (Sowls, 1955), this means that about seven days are required for a follicle to grow from six mm. (the usual maximum size of white-yolked follicles) to a diameter of 30 to 35 mm. at ovulation. This period is in general agreement with those cited by Benoit (1950) for chickens (5 to 13 days), pigeons (14 days), and ducks (10 to 13 days), and with growth estimates for ovaries of quail, pheasants, chickens, and ducks presented by Romanoff and Romanoff (1949:204).

Relation of ovary to oviduct.—The diameters of largest follicles and the weights of ovaries and oviducts were available for 72 Pintails examined in 1958. This figure in-

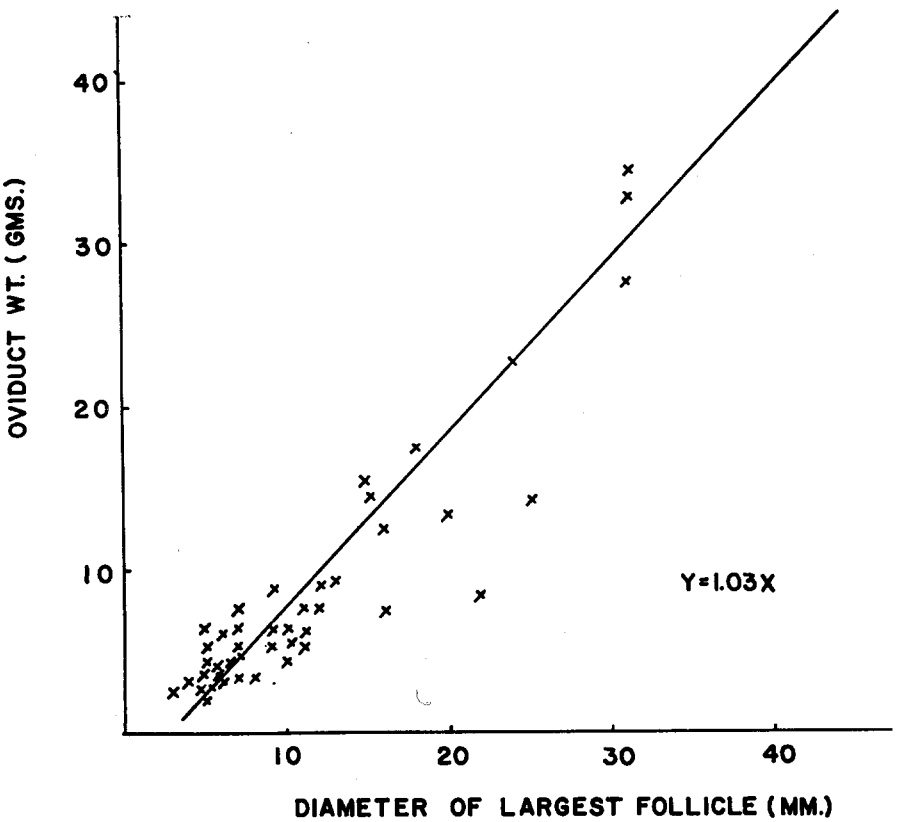

Fig. 2. Oviduct weight plotted against diameter of largest follicle to show the linear increase in oviduct weight with increasing follicle size.

cludes some from captives as well as those of birds shot in the wild. Only those birds that had not ovulated were used. A plot of oviduct weight on follicle diameter (fig. 2) yielded a straight line with a regression coefficient of 1.03 ($P < .001$), indicating a linear relationship between increase in diameter of the largest follicle and oviduct weight. The correlation coefficient is 0.95 which means that 90 per cent of the variation in oviduct weight can be predicted from the size of the largest ovarian follicle.

The specificity of the oviduct growth response to estrogen and the close correlation between follicle diameter and oviduct weight allow an estimation of the relative amount of estrogen secretion in living birds by simple laparotomy and measurement of the follicles in the ovary, giving the field worker a useful tool for determining the reproductive status of trapped birds.

Incubating.—After the female has finished laying, her behavior changes and she spends more time at the nest. Physiological changes also occur at this time to adapt her to incubation and to prepare her for rearing the brood. To study these changes, 11 females were collected from their nests, their organs were studied as described, and the length of incubation was estimated by candling the eggs. These data are presented in table 1. A comparison with the data for laying birds shows striking reduction in the sizes of ovaries and oviducts in incubating birds. Thyroid and adrenal measurements

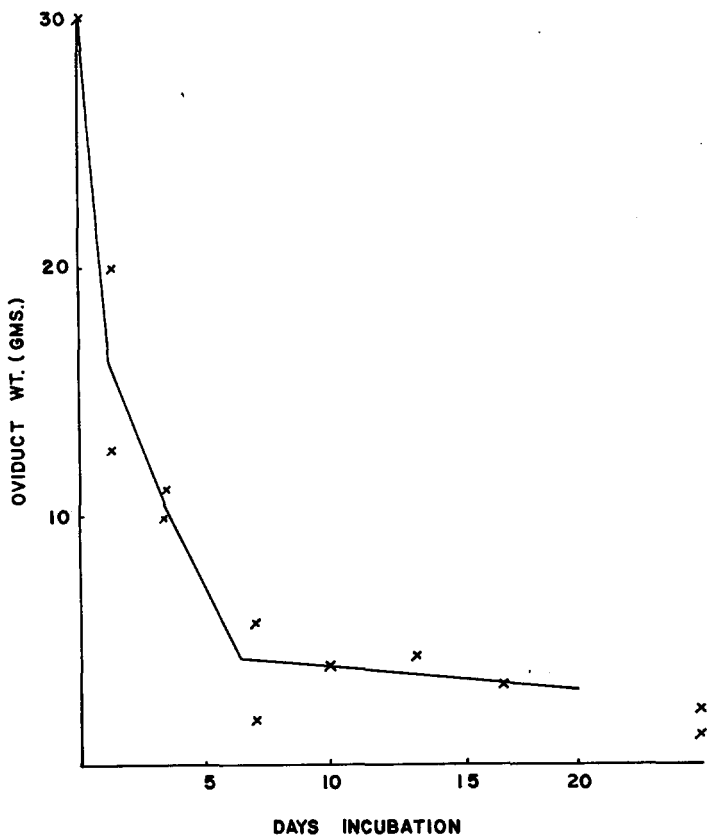

Fig. 3. Plot to show the rapid decrease in oviduct weight in the first few days of incubation.

showed a similar drop, the epithelial cell height of the thyroid being significantly lower in incubating birds than in any other group studied, including the flocked females that had not yet laid.

The changes in ovary and oviduct weight take place very rapidly, so that by the sixth or eighth day of incubation these organs are as small as they were in birds from migrating flocks prior to dispersal onto the nesting areas (table 1). Ovulated follicles regress and their lips fuse very quickly, making them indistinguishable from small atretic follicles. An attempt to relate the number of ovulated follicles that could be distinguished with the aid of a dissecting microscope in the ovaries of incubating birds to the number of eggs they were covering showed no close correspondence between the two. Some had more ruptured follicles than eggs, but others were incubating more eggs than there were ruptured follicles in the ovary.

Renesting flights.—When the female Pintail begins to incubate, her mate remains on the area for several days, joining her when she is off the nest. As incubation progresses, he eventually abandons her. If the nest should be destroyed, however, the duck will likely renest, and this requires a return to a physiological and behavioral state appropriate for egg production and laying. She also must find a new mate.

According to Sowls (1955), the new mate is found by the "renesting" or "teasing" flights which first appear late in the season. Sowls thought that the characteristic call was the inciting note of courtship, but more recent observations indicate that it is actually the harsher and more prolonged repulsion note (Weidmann, 1956), a call characteristic of incubating females. Sowls observed this "renesting" behavior in marked females when he disturbed them at the nest and after he had destroyed nests, but only after their mates had abandoned them. Weidmann (1956) reported that female Mallards gave the repulsion call even when they were alone, and he stated that this definitely

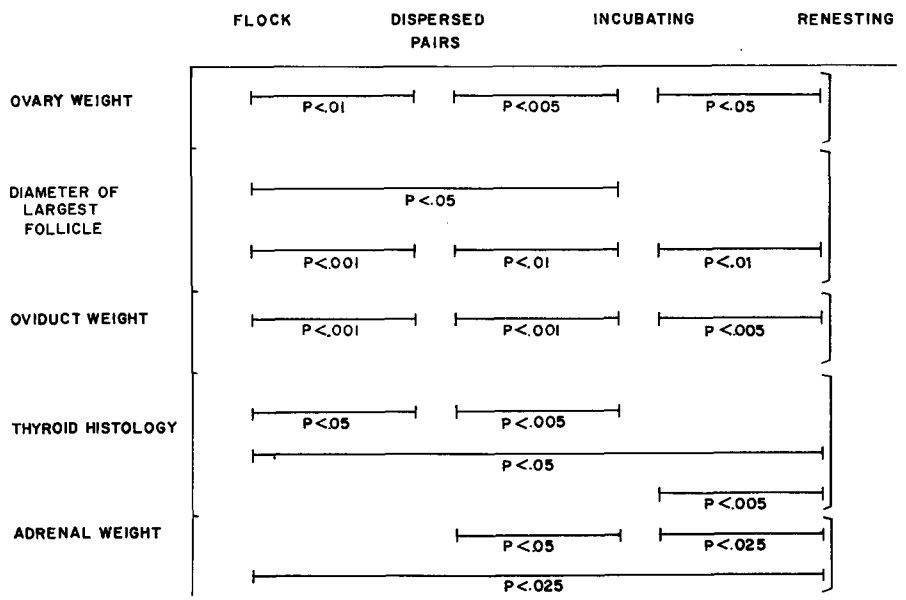

Fig. 4. Probabilities that the differences between groups shown in table 1 would occur by chance. The comparisons are shown by solid lines with probabilities below. Probabilities are given only for differences that tested significant at the five per cent level or better.

indicated an incubating bird. Our observations agree with those of Weidmann; Phillips has seen female Pintails exhibit repulsion behavior when he flushed them from their nests, and he also has seen several behave thus when alone.

Although this behavior is often a hostile response to intrusion at the nest, it has a very powerful attracting rather than repelling effect on drakes when the female is away from the nest. In many cases that Phillips observed, such a female apparently made no attempt to escape the drakes but rather seemed to entice or "tease" them by repeated short flights and runs or slow hovering flights that might tower hundreds of feet above the marsh, drawing males from a wide area. Some females seem utterly frantic about this behavior, running about, gobbling bites of food or guzzling water only to run or fly again almost before swallowing. Such action is similar to what one often sees in a female that has just come off her nest to feed.

Examination of the reproductive tracts of females shot during "renesting" behavior supports the idea that they were or had been incubating. Three of four such ducks collected by Sowls had ovulated and he could not be sure about the fourth; of seven "renesting" females that we examined, six had ovulated and the seventh probably had. Ovaries and oviducts varied from some that were similar to those of layers to some resembling those found in incubating birds; this variation would be expected of incubating birds or of those whose clutches had been interrupted. However, adrenal weights averaged higher than in incubating or laying birds and thyroid epithelial cell height was higher than that for any other group (table 1).

These high thyroid and adrenal activities are more similar to conditions in laying than in incubating birds. The interpretation that the birds are or have been incubating very recently and the observations that incubating birds often perform "renesting" activities on being flushed from their nests are hard to reconcile with this. If we assume, however, (1) that the nests of the birds Phillips collected had been destroyed an average of at least one day before the birds were shot, an assumption made plausible by the much larger ovaries (mean maximum follicle diameter 18.0 mm.) of "renesting" than of incubating females (mean maximum follicle diameter 5.3 mm.) and (2) that the thyroid and adrenal changes correlate with rather than cause renesting behavior, the following explanation seems plausible and is testable. Thyroid and adrenal activity increases during laying in Pintails (Phillips and van Tienhoven, 1960): if this is necessary for development of mature follicles (an idea supported both by the greater thyroid activity during laying than in other periods and by the much greater thyroid activity in wild-laying females than in nonlaying captives) it is to be expected that thyroid and adrenal activity must increase above levels found during incubation for a female to renest. If this is true, it follows that stimuli related to the loss of the nest cause increased thyroid and adrenal activity as well as trigger the behavior. Both behavioral and physiological changes then work together to prepare the bird to renest successfully.

Since the readiness to perform "teasing" develops with incubation whether the nest is destroyed or not, it may be brought on by high levels of prolactin, an anterior pituitary hormone that has been shown to be present in increased quantities in both chickens and pheasants during incubation (Saeki and Tanabe, 1955; Breitenbach and Meyer, 1959) and which induces broody behavior in chickens (Saeki and Tanabe, *op. cit.*). Another likely candidate would be progesterone; apparently it, not prolactin causes brooding in Ring Doves, *Streptopelia* (Lehrman, 1960). The hormonal basis of incubation has not been studied in ducks, however, so any such explanation is conjectural. Study of the mechanisms of these hormonal and behavioral changes in birds trapped at the nest would be an excellent means of leading to greater understanding of both the envi-

ronmental stimuli for and the hormonal mechanisms of control of the redevelopment of the ovary and renesting.

SUMMARY

Physiological correlates of several behavioral stages of the reproductive cycle of wild female Pintails (*Anas acuta*) were studied by intensive field observations and collecting in the area surrounding the Delta Waterfowl Research Station in southern Manitoba, Canada. Females from migrating flocks of mostly paired birds and from courting parties within the flocks had small ovaries and oviducts and moderate thyroid activity as measured by epithelial cell height. Birds dispersed and apparently nesting showed maximum reproductive development and high thyroid activity, as well as considerably increased adrenal weight. During incubation all these measures fell off rapidly to levels below that found in birds from spring flocks, but those females collected while showing "renesting" behavior showed moderate reproductive development and the maximum thyroid and adrenal measures found in any group.

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