BURSAE, REPRODUCTIVE STRUCTURES, AND SCAPULAR COLOR IN WINTERING FEMALE OLDSQUAWS

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ABSTRACT.—Female Oldsquaws were collected on Lake Michigan between December and May 1951–55 and 1969–73. Measurements taken on bursae, ovaries, and oviducts were related to age class and scapular color. Bursae were significantly deeper in juveniles than in adults, and the adult females with gray scapulars had significantly deeper bursae than adult females with brown scapulars. Juvenile female ovaries were smaller than adult ovaries throughout the winter and spring and did not enlarge significantly in the spring as did the adult female ovaries. Oviduct weights were significantly different in immature females, gray-scapulared adult females, and brown-scapulared adult females. The data presented support behavioral evidence that Oldsquaws do not reach sexual maturity their first year. We hypothesize that gray scapulars in adults are indicative of a nonbreeding subadult cohort.—*Wildlife Resources, University of Idaho, Moscow, Idaho 83843,* and *Department of Wildlife Ecology, University of Wisconsin, Madison, Wisconsin 53706.* Accepted 2 August 1976.

IN birds with a protracted maturity, a yearling or subadult can often be distinguished from individuals less than 1 year old as well as from adults. Johnston (1956) described several age classes for the California Gull (*Larus californicus*) and related differences in plumage to changes in the bursa and gonads. Similar data have been collected for the Canada Goose (*Branta canadensis*, Hanson 1965) and for passerines including the Red-winged Blackbird (*Agelaius phoeniceus*, Wright and Wright 1944) and the Great-tailed Grackle (*Cassidix mexicanus*, Selander and Hauser 1965).

Oldsquaws (*Clangula hyemalis*) are one of several species of ducks that do not attain sexual maturity during their first year (Ellarson 1956, Alison 1970, 1975). Schiøler (1926) found adult females to be dichromatic in the winter plumage; some specimens had red-brown scapulars, while in others this tract was gray. Salomonsen (1941) described the sequence of molts and plumages of Oldsquaws from a large series of museum skins, and concluded yearling females had gray scapulars similar to those in females less than 1 year old, while breeding adults exhibited the red-brown scapulars. In addition, these yearling specimens lacked a bursa of Fabricius and the oviduct was thinner and straighter than in the adults.

Salomonsen's (1941) conclusion that Oldsquaws do not breed until they are 2 years old was based largely on plumage characters. Alison (1972, 1975) confirmed this hypothesis with captive birds and observations on the breeding grounds. The purpose of this report is to put that conclusion on a firmer basis by relating female scapular color to differences in bursae, ovaries, and oviducts. For ease in reporting the results, the authors assumed all female Oldsquaws less than 1 year old to be juveniles and all birds older than 1 year to be adults. Although age and reproductive data were also measured on male Oldsquaws, that material is not presented here.

METHODS

We obtained Oldsquaws from Lake Michigan commercial fishermen, who take the birds repeatedly in gill nets during the winter and spring. Collections were made between November and June 1951–55, and 1969–73. Specimens were either examined immediately after collection or frozen until they were dissected.

The sex and age of each specimen were determined by plumage characters, color of the bill, and a cloacal examination for presence of a penis or open oviduct (Ellarson 1956). The cold water prevented any

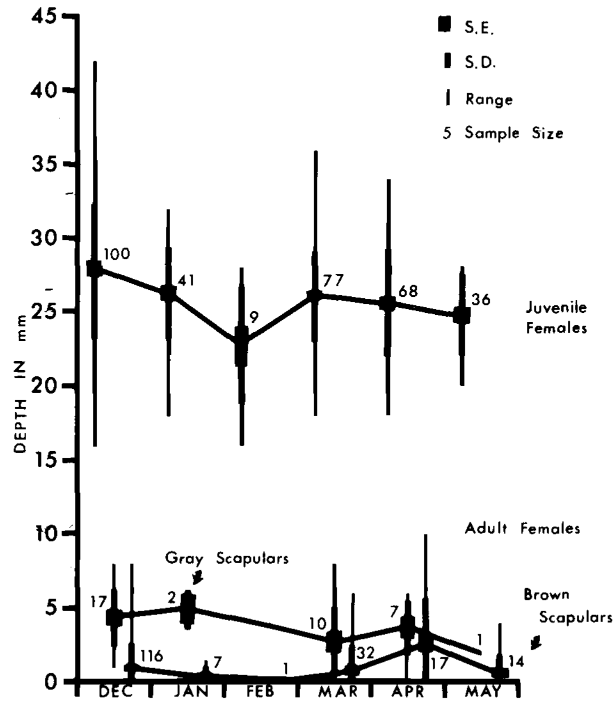

Fig. 1. Average bursal depths in juvenile and adult female Oldsquaws.

substantial change in bill color. As juvenile Oldsquaws retain notched tail feathers until their second summer (Kortright 1942: 31), specimens were categorized as juveniles or adults by rectrix notching. Bursal depth was determined to $\pm$ 1.0 mm with a graduated probe. Ovaries were removed, cleaned of extraneous material, and weighed to $\pm$ 0.01 g. The largest follicle was measured to $\pm$ 0.1 mm with an ocular micrometer on a microscope. The oviduct was cut off at its junction with the cloaca, cleaned of the supporting tissues, and preserved. The 1969–73 samples were preserved in 10% formalin and later dried in an oven until the weight did not fluctuate more than $\pm$ 0.001 g, while those collected in 1951–55 were preserved in formalin acetaldehyde (FAA) solution, blotted to remove excess moisture, then weighed to $\pm$ 0.01 g. As we used two different methods to determine oviduct weights, the materials were analyzed separately; we then compared the two data sets for similar trends. Ellarson (1956) divided adults into gray-, intermediate-, and brown-scapulared birds. Because some subjectivity is involved in the intermediate category, we decided to separate adults in the 1969–73 sample into either gray- or brown-scapulared birds; those females with intermediate scapulars were pooled with the brown-scapulared birds.

RESULTS

Bursa of Fabricius.—We found the presence of the bursa of Fabricius to be a valid aging criterion for separating juvenile females from adult females throughout the winter and spring (Fig. 1). Little regression occurred in juvenile bursae while the birds were on Lake Michigan, and no overlap in measurements between juveniles and adults was noted. In adult females, gray-scapulared birds had deeper bursae, December through May, than brown-scapulared birds ($P < 0.001$; df = 213).

If we assume that once a bursa starts to regress it cannot enlarge at a later date, then it follows that the gray-scapulared adult females, with the significantly deeper bursae, are younger than the brown-scapulared birds. Other data we have collected indicates the size of the bursa is not related to the size of the bird as gray-scapulared adults are intermediate in weight between juveniles and brown-scapulared adults. If

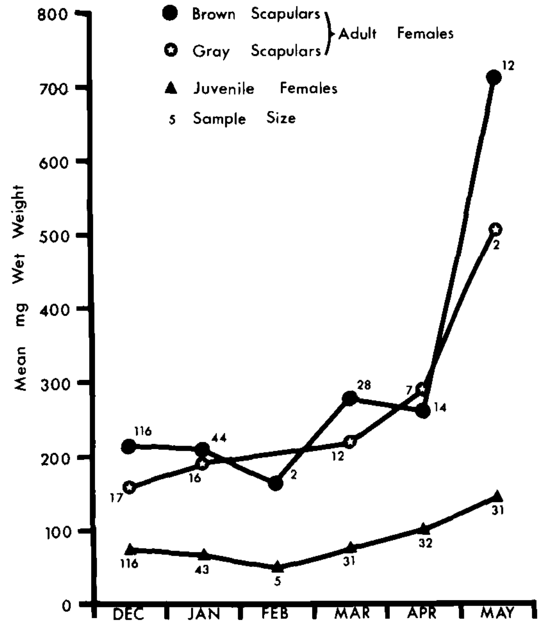

Fig. 2. Average ovary weights in juvenile and adult female Oldsquaws.

individuals of the gray- and brown-scapulared groups were the same age, we would expect the proportions of individuals having the bursa competely resorbed to be the same in the two groups. Such is not the case. In December and January, none of the 19 gray-scapulared adults had a completely resorbed bursa, but in 83 of 123 brown-scapulared adults (67%), no bursa was in evidence. Completely regressed bursae begin to appear during March in gray-scapulared adults. In addition, the regression line for the bursae of gray-scapulared adults collected between December and May is slightly negative ($P < 0.04$; df = 35) while the bursae of brown-scapulared adults do not exhibit a negative slope with time.

Ovaries.—Ovaries in juvenile females were much smaller than in either gray- or brown-scapulared adult females (Fig. 2). There was a gradual increase in ovary weight from February through April in both age classes, but then ovary weight increased markedly between April and May in adults. Juvenile female ovaries increased from an average of 74 mg in December to 147 mg in May, but at this time the weights of these ovaries were still less than the average weight recorded in either gray- or brown-scapulared adults in December.

Not only were the ovaries of juvenile females smaller than adult ovaries, they differed grossly in appearance. Juvenile female ovaries had a smooth surface texture resulting from a lack of follicular development. In late March and April a few juvenile ovaries exhibited a slightly granular appearance from the development of pigmented bodies within the ovary. This stage appears to mark the onset of general follicle growth, while at the same time adult ovaries had relatively well-developed follicles that averaged 2.8 mm in diameter in March and 3.4 mm in May.

Differences in ovary size between gray- and brown-scapulared adult females were not so readily apparent as between juveniles and adults. Average sizes were significantly different only in December ($P < 0.01$) and March ($P < 0.05$). Ovaries in both

TABLE 1
MONTHLY VARIATIONS IN DIAMETER OF LARGEST FOLLICLE IN OLDSQUAW OVARIES

Month	Mean (mm)	SE	Sample size
December	1.8	±0.11	12
January	2.4	—	2
February	2.3	±0.05	104
March	2.9	±0.09	115
April	3.2	±0.12	38
May	3.8	±0.27	15

the gray- and brown-scapulared adults averaged about 275 mg in April, but 1 month later ovaries in brown-scapulared adults averaged 712 mg while those of gray-scapulared adults averaged 505 mg. An overall t-test comparing the ovaries of all gray- and brown-scapulared adults collected between December and May indicated no significant difference in weight.

To demonstrate the rate of development of the adult ovary with the onset of the breeding season, the diameter of the largest follicle was measured. Monthly means show a relatively constant rate of increase from December ($\bar{x}$ = 1.8 mm) to May ($\bar{x}$ = 3.8 mm, Table 1). A significant increase was found only between February and March ($P < 0.05$). The samples for these months were the largest for any of the months (104 and 115 respectively) and, in view of the relatively constant rate of increase shown by the monthly means, statistically significant monthly differences might have been demonstrated in other months had the sample sizes been larger.

Oviducts.—Dried juvenile oviducts remained at about 2 mg from December through April, but then increased markedly in May to an average of 34 mg (Table 2). Oviduct weights in gray- and brown-scapulared adults averaged higher than juveniles, and sharp increases between April and May also occurred in adult oviducts as in juveniles.

Where monthly oviduct weights are available for juveniles and adults, the following trend was observed: brown-scapulared females > gray-scapulared females > juvenile females. For example, in December, juvenile oviducts averaged

TABLE 2
MEAN OVIDUCT WEIGHTS FOR FEMALE OLDSQUAWS COLLECTED ON LAKE MICHIGAN

	Juveniles			Gray-scapulared adults			Brown-scapulared adults			t
Month	Mean[1] (mg)	SE	Sample size	Mean (mg)	SE	Sample size	Mean (mg)	SE	Sample size	Gray- vs. brown-scapulared adults
December	2	±0.2	4	63	±6	17	138	±5	100	6.044 $P < 0.001$
January	2	±0.2	2	28	±8	15	108	±11	45	4.062 $P < 0.001$
February	–	–	–	–	–	–	10	±4	2	–
March	–	–	–	46	±9	12	90	±13	28	2.113 $P < 0.05$
April	2	±0.6	24	53	±16	7	60	±17	11	0.281 N.S.
May	34	±8.0	22	192	–	1	288	±45	12	–
Total or mean	16	±4.0	52	50	±5	52	128	±6	198	–

[1] Excised oviducts were dried in an oven to constant weight.

TABLE 3

OVIDUCT WEIGHTS IN GRAY-, INTERMEDIATE-, AND BROWN-SCAPULARED ADULT FEMALE OLDSQUAWS[1]

Time period	Gray-scapulared			Intermediate-scapulared			Brown-scapulared		
	Mean[2] (g)	SE	Sample size	Mean (g)	SE	Sample size	Mean (g)	SE	Sample size
1 February 1954	0.40	±0.03	23	0.62	±0.03	22	0.68	±0.08	7
8–10 March 1955	0.30	±0.01	22	0.52	±0.03	42	0.65	±0.07	9
15 March 1955	0.53	±0.03	17	0.71	±0.02	31	0.89	±0.04	18
3–4 April 1955	0.36	±0.03	17	0.60	±0.05	24	0.71	±0.06	8

[1] Adapted from Ellarson 1956.
[2] Wet-weight basis.

2 mg, gray-scapulared adults averaged 63 mg, and brown-scapulared adults averaged 138 mg ($P < 0.001$). An overall F-test comparing average oviduct weights for the three groups of female Oldsquaws collected on Lake Michigan between December and May indicated a significant difference ($P < 0.001$).

During the period 1951–55, Ellarson (1956) calculated oviduct weights for three groups of adult females: gray-, intermediate-, and brown-scapulared (Table 3). Trends exhibited in Table 3 are similar to those shown in Table 2. Oviduct weights of gray-scapulared adult females were smaller than the oviduct weights of both intermediate- and brown-scapulared adult females ($P < 0.05$). Significant differences in oviduct weights between intermediate- and brown-scapulared adults occurred only in the 15 March sample ($P < 0.05$).

DISCUSSION

Our data on bursae, ovaries, and oviducts confirm the hypothesis that female Oldsquaws probably do not breed their first year. Hochbaum (1942) pointed out that the bursa is present only in juvenile waterfowl and degenerates to complete closure as the individual approaches maturity. The Mallard (*Anas platyrhynchos*) attains sexual maturity the first year (Höhn 1947), and the bursa is almost completely resorbed by the end of January (Johnson 1961); but in Canada Geese, sexual maturity is not reached the first year, and the bursa does not start to regress until the second year (Elder 1946, Hanson 1965). Similarly, the bursae in juvenile female Oldsquaws regress very little the first year but females older than one year, as evidenced by rectrix examination, have much reduced bursae in December. Apparently, regression of this structure proceeds quite rapidly during the second summer and fall. Alison (1970) pointed out that pairing is largely complete in this species by March. Our data indicate this is when completely regressed bursae begin to appear in gray-scapulared adult females.

Generally, it is difficult to distinguish avian age classes by ovarian examination. Johnston (1956) found some tendency for California Gulls in the first-year plumage to have smaller ovaries than those in older plumages, and the ovaries of adult female Great-tailed Grackles were at all times more advanced than the ovaries of first-year females (Selander and Hauser 1965). Juvenile female Oldsquaws are distinguishable not only by ovary weight but also by gross ovarian appearance throughout the winter and spring. In addition, ovarian recrudescence is not nearly so marked in juveniles as in adult Oldsquaws. Thus our data on ovarian development support the behavioral literature (Phillips 1925, Alison 1970) that juvenile female Oldsquaws do not breed.

Age-related differences in oviduct weights have been demonstrated in several species. In poultry, the oviduct in mature hens that have not laid is much smaller than in laying hens, and a partial atrophy of this organ occurs upon cessation of egg-laying (Buckner et al. 1925). Even though the breeding biology of the Mallard and Oldsquaw are considerably different, juvenile Mallard oviducts were found to be smaller than adult oviducts (Johnson 1961). In first- and second-year California Gulls, only a slight enlargement occurred whereas during the third year a further slight enlargement occurred during the April breeding season; breeding adults showed an abrupt enlargement of the oviduct following the inactive breeding condition, and the oviduct became more convoluted and twisted (Johnston 1956). Alison (1975) pointed out that morphology and behavior in the Oldsquaw ensure that juvenile birds do not pair. Our measurements on Oldsquaw oviducts agree with the above studies that nonbreeding juvenile females have smaller oviducts than adults and in the latter age class, gray-scapulared females have smaller oviducts than brown-scapulared females.

A primary question in this discussion of age-related breeding in female Oldsquaws is whether or not the delineated scapular colors accurately reflect the age, and hence the probable breeding status of individuals. If age is not related to scapular color, then the female population consists of two genetic variants: a brown phase and a gray phase. If this is true, then one would not expect to find the correlations observed between reproductive structures and scapular color in our 1951–55 and 1969–73 surveys nor in Salomonsen's (1941) treatise on the subject. However Alison (pers. comm.) has examined gray-scapulared breeding females aged 4 and 6 years.

The relationship of plumage characters to breeding condition is well known in many birds. During courtship, male Oldsquaws have long white scapulars, but after pair formation and generally prior to migration, these feathers are molted and replaced with brown scapulars. We did not measure scapular color or length in male Oldsquaws, but it is reasonable to expect such an obvious character to be important in courtship. Likewise we might expect scapular color to be important in indicating the breeding condition of female Oldsquaws with a protracted maturity. In light of the evidence presented, we suspect that variation in the scapular color of adult female Oldsquaws represents a continuum from gray in subadult female to brown in females several years old, depending on hormonal stimulation prior to molting these feathers. Presently, few data are available to substantiate further the hypotheses that plumage color, bursal depth, ovary size, and oviduct weight in Oldsquaws are age-related. However, since investigations in other species have not found the relation between bursal depth and age to be otherwise, the hypothesis offers a reasonable explanation.

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