BREEDING BIOLOGY AND BEHAVIOR OF THE OLDSQUAW (*CLANGULA HYEMALIS* L.)

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Special Associate Editor for this issue: Milton W. Weller
Author's address: Wildlife Branch, Ministry of Natural
Resources, Whitney Block, Queen's Park,
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INTRODUCTION

The Oldsquaw (*Clangula hyemalis*), or Long-tailed Duck, is probably more numerous and widespread than any other species of arctic waterfowl (Delacour 1959). It breeds across northern Eurasia and from Point Barrow, Alaska, along the Arctic coast of North America, including the western coasts of Hudson and James Bays and in northeast Labrador (Godfrey 1966). Breeding individuals have been found on almost all the Arctic islands of Canada to a latitude of 83° north, and the species reportedly breeds on Baffin and Southampton Islands (Phillips 1925). Although the Oldsquaw has bred along the east coast of Labrador and in the Gulf of St. Lawrence, there is no evidence that it breeds there now. The bird is circumpolar in distribution and commonly breeds in Greenland (to 83° 23′ N), Iceland, the Faroes, the north coasts of Norway, Sweden, Finland, Russia, on the New Siberian Islands and all along the coast of the Arctic Ocean to the Bering Sea (Millais 1913).

The winter range of the species is well known (Millais 1913, Bent 1925, Phillips 1925). However, wintering areas of specific northern populations are unknown, primarily because of the lack of banding data. A large proportion of the Iceland population apparently winters in southwest Greenland (Salomonsen 1950) while some individuals of certain Russian populations winter on the west coast of Europe (Boyd 1957).

The breeding biology of the Oldsquaw is poorly known. Drury (1961) mentioned certain displays that he saw on the breeding grounds. Millais (1913), Bent (1925), and Phillips (1925) described nest location, clutch size and aspects of adult behavior, but no studies of individually recognizable breeding Oldsquaws have been published.

The main objectives of my research reported in this paper were to determine:

(1) Oldsquaw population levels and breeding pair distribution,
(2) nest site tenacity and homing,
(3) nest distribution and location, nesting success, and the effect of weather upon nesting and renesting,
(4) territorial behavior, and
(5) to describe species-specific displays of this species in sufficient detail to permit comparison with those of other species.

MATERIALS AND METHODS

THE STUDY AREA

This paper contains the results of studies of Oldsquaws conducted in four consecutive breeding seasons, 1968 to 1971, at Churchill, Manitoba (58° 45′ N, 99° 5′ W). I observed Oldsquaws on a 4000 ha area about 5 km east

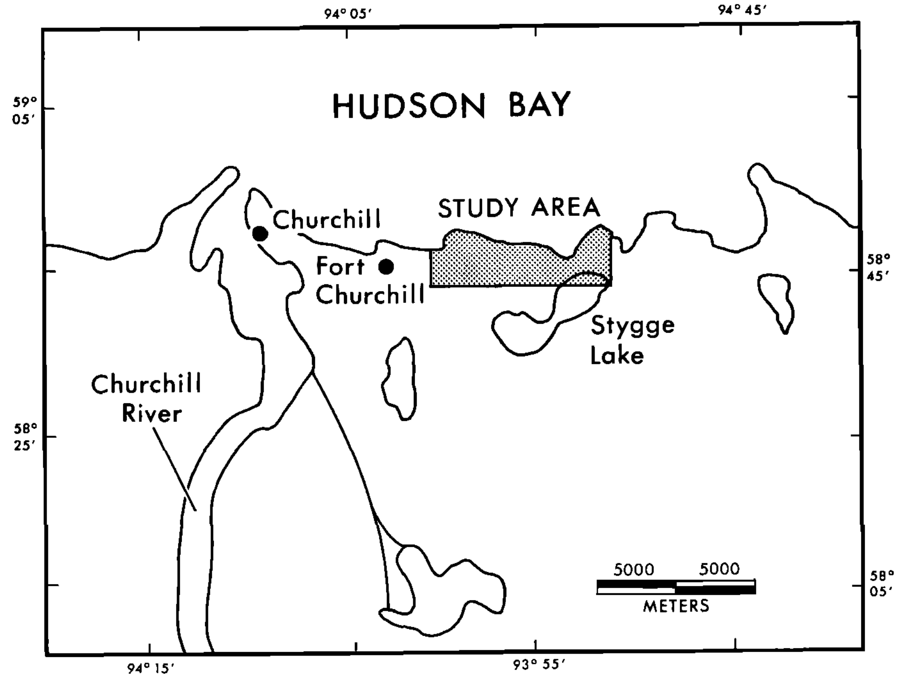

Figure 1. Map showing location of the study area.

of Churchill (Fig. 1). The Oldsquaw breeding population in this area averages 45 pairs, the majority arriving in the first week of June. Pairs are most commonly observed on small inland ponds but individuals and small groups may occasionally be seen among the chunks of pack ice in open water on Hudson Bay, especially at the mouths of rivers.

The study area is about 14 km east of the mouth of the Churchill River on the west coast of Hudson Bay and is contained within 58° 43′ N to 58° 46′ N and 93° 52′ W to 94° 01′ W (Fig. 2). The area includes sparsely forested tundra, dry upland, marshland and scrubland, and extends almost 10 km along the Hudson Bay coast. Jehl and Smith (1970) described the area in detail. There are 90 ponds and lakes ranging in area from 0.1 ha to about 20.3 ha and averaging 2.8 ha. None of these ponds and lakes was reduced to mud-flat conditions during the study. Most of the smaller ponds are ice-free by 10 June, and all the larger ponds and lakes (except Stygge Lake) are clear of ice by 20 June. Remnant ice may occur along the coast of Hudson Bay until late July.

Oldsquaws consistently outnumber all other species of waterfowl in the study area. However, the Common Eider (*Somateria mollissima*) and the Canada

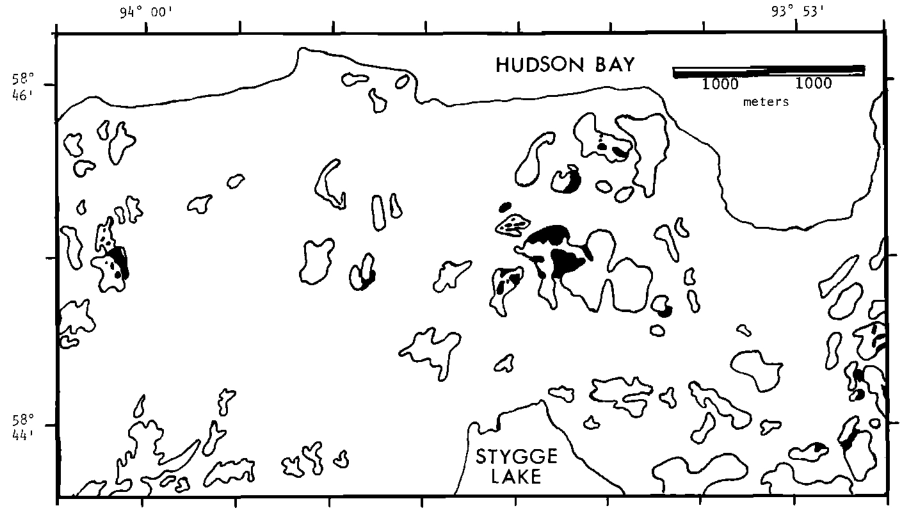

Figure 2. Map of the study area showing traditional nesting location. Minimum densities of one nest per 2.3 areas are shaded.

Goose (*Branta canadensis*) are quite common. The following species also occur more or less regularly: Greater Scaup (*Aythya marila*), Green-winged Teal (*Anas carolinensis*), Pintail (*Anas acuta*), American Widgeon (*Anas americana*), Red-breasted Merganser (*Mergus serrator*), Mallard (*Anas platyrhynchos*) and Common Scoter (*Melanitta nigra*).

In order that breeding ground data could be supplemented by observations of winter behavior, Oldsquaws were observed during the winters of 1967 to 1969 at Toronto Harbor, Ontario (43° 40′ N, 79° 30′ W). The average wintering population of this species at Toronto comprises about 7,000 individuals. In addition, observations of the behavior of six captive Oldsquaws supplemented field data.

WEATHER DURING THE STUDY PERIOD

In 1968, daily temperatures in the last 10 days of May were 3.5°C above normal (–2.1°C), whereas June temperatures were 5.1°C and 1.9°C, respectively, below normal (6.1°C). Most ponds were not clear of ice until 20 June that year. In 1970, temperatures in the final week of May averaged 2.2°C above normal, June temperatures averaged 3.0°C above normal, and ponds were clear of ice by 1 June.

June precipitation from 1968 through 1970 was below normal (51.4 mm), but in 1971, above normal rainfall was recorded for that month. Wind velocities throughout the study period averaged 21 kmph and the mean daily

Figure 3. Habitat typical of the study area showing Black Spruce and open tundra association.

maximum wind velocity was 38.8 kmph. In general, the 1968 breeding period at Churchill was dry and moderate, the 1969 season was dry and cold, the 1970 period was dry and warm, and the 1971 season was wet and cold.

VEGETATION IN THE STUDY AREA

Despite an overall impression of monotonous sameness (Fig. 3), the vegetation in the study area varied considerably locally. On the basis of component plant types, it was possible to subdivide the study area into the following categories: tundra, marsh, dry upland and scrubland.

(a) *Tundra.*—Tundra includes those typically grassy expanses lying beyond and occasionally within the limit of rank forest. The study area is mainly tundra and contains extensive lowland areas dominated by sedges, including Hudson Bay Sedge (*Carex amplyorhyncha*) and Northern Bog Sedge (*C. gynocrates*). Grasses (*Poa* spp.) and dwarf willows (*Salix* spp.) commonly occur. Frequently bryophytes and lichens predominate, the whole forming a continuous growth typically less than 35 cm in height. Isolated dwarf birches (*Betula* spp.) may occasionally occur.

(b) *Marsh.*—As a result of the relatively poor drainage large expanses of shallow surface water generally occur. In such marshland areas, the dominant vegetation includes hygrophytic sedges, such as Water Sedge (*Carex aquatilis*), grasses (*Arctagrostis* spp.) as well as hygrophilous willows (*Salix candida* and *S. myrtillifolia*) (Scoggan 1959). Occasionally "hummocks", averaging 25 to 50 cm high occur in marshland tracts, the resulting formation being termed "hillock tundra" (Polunin 1967). Conditions on hummocks are relatively dry, and lichens and ground-shrubs commonly grow. Depressions between adjacent hummocks form boglets.

(c) *Upland.*—Rocks commonly project above the surface contour. The vegetation in these tracts is usually less dense than in moist areas. Xerophilous sedges, grasses (*Hierochloe* spp.) and willows frequently occur. Although lichens and bryophytes are plentiful, and in most areas appear to dominate, the vegetation commonly barely covers the ground.

(d) *Scrubland.*—Frequently within the tundra proper, especially along watercourses and in damp areas, dense growths of dwarf willows and/or birches appear. In most instances, the overall growth does not exceed 0.9 m in height but rarely may attain heights of more than 1.8 m. Scrub areas are usually so dense and tangled that few other plants occur. However, where the dominant willows and birches are less tightly packed, a dense, rich underflora of lichens and/or mosses may develop.

Census Methods

I conducted total censuses of adult and subadult Oldsquaws throughout the study. The census route required about three hours to complete, and I always took censuses between 07:00 and 10:00 C.S.T. I made counts daily from 1 June to 30 June. By 1 July the entire breeding population had arrived and daily censuses were no longer necessary. In every instance age (adult or subadult) and sex of each individual were readily determined by plumage. Individual variation including variation in plumage (Fig. 4) and vocalization made recognition of most adults possible without marking (dyeing) and made it possible for me to trace the daily movements of individual pairs.

In order to examine nest site tenacity and homing in Oldsquaws, it was necessary to capture and band several adults. Although adult females were relatively easily captured with mist nets on their nests, adult drakes were more elusive. All females banded at the nest site subsequently returned and resumed incubation. In capturing other individuals, four-inch mesh mist nets were placed horizontally over holes in the ice on inland lakes and ponds. Oldsquaws attempting to dive into these holes were invariably caught in the nets. Whenever a female was captured in this manner, one or more drakes would fly from nearby open water and land near the entangled bird. Frequently these individuals became caught in the net as well. Pairs were often captured in this manner. By 1 July 1971, 45 Oldsquaws had been banded.

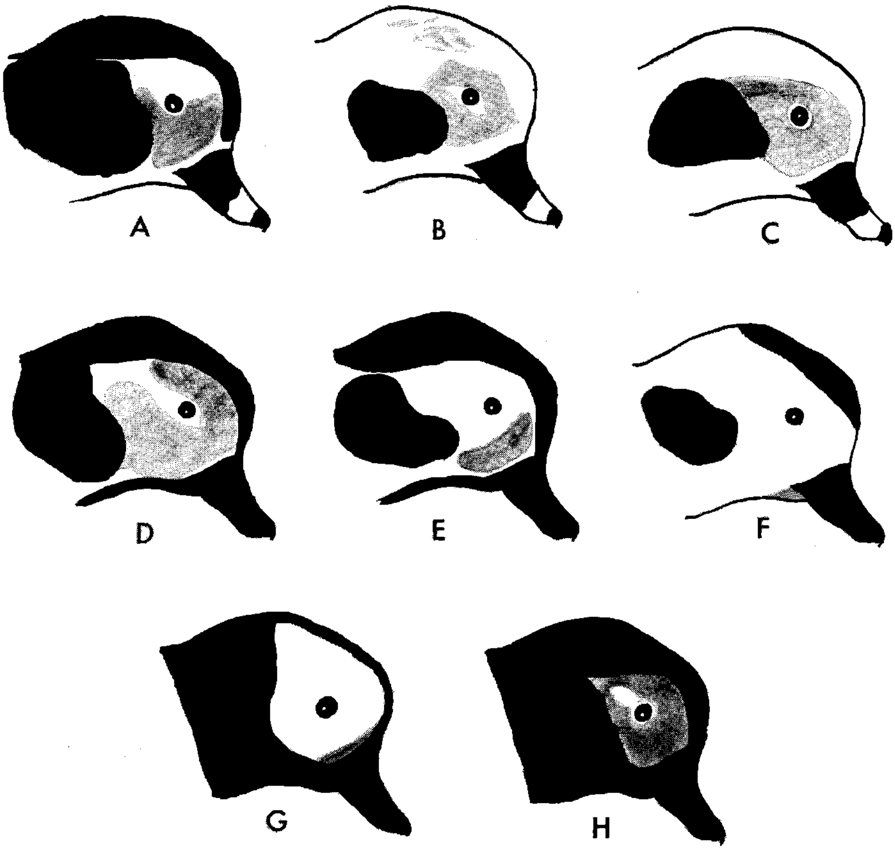

Figure 4. Head plumages of Oldsquaws. Male: A. Immature about 8 weeks old; B. Immature about 16 weeks old; C. Adult. Female: D. Immature about 8 weeks old; E. Immature about 16 weeks old; F. Adult. Head plumages of breeding adults. G. Male; H. Female.

Figure 5 shows typical nesting substrate in early June. Most active nests were found by careful censuses of traditional Oldsquaw nesting colonies. However, extensive searching was required before certain mainland and isolated island nests were located. As a result I did not discover several nests until the female had commenced egg laying, and these were not included in the data. The location of each nest was noted in relation to the nearest open water and the nearest active Oldsquaw nest. All active nests were photographed. Nest surveys frequently yielded not only active nests but also nest cups of previous years (during the study, I found 259 nest sites of previous years). All active nests were censused daily but if the female was present the nest contents were not examined.

Figure 5. "Hummock" habitat in early June suitable for Oldsquaw nesting.

The degree of concealment of each nest was subjectively rated as follows:

(1) Well concealed.—Incubating duck concealed from above and all sides.
(2) Open from above.—Duck concealed from all sides.
(3) Partially concealed.—Duck poorly concealed from sides and not at all from above, and
(4) Poorly concealed.—Duck not concealed from any side or from above.

Predator censuses were frequently conducted although no attempt was made to locate nests or burrows of predators.

TERRITORIAL BEHAVIOR

I examined the territorial behavior of 10 adult drake Oldsquaws. Five of these individuals were exposed to each of several combinations of decoys (one combination per bird for a period of 5 minutes every 2 days). Five others were exposed to the same combinations, but in each instance a 1-minute recorded sequence comprising 24 "ahr-ahr-ahroulit" vocalizations (Alison 1970) was played from a hidden cassette recorder capable of producing about 2 watts.

Oldsquaw decoys were prepared from skins taken from a series of specimens caught in fishermen's nets near Picton, Ontario, in May 1969. Each skin was filled with "Styrofoam" and subsequently shaped. Glass eyes were placed in each decoy and faded bills were painted appropriately.

The decoys were placed in each territory, 10 m offshore, while the defending drake was submerged (feeding) and thus presumably unaware of my presence. Each experiment required about 15 minutes to complete, and I remained hidden behind small spruce clumps during the period.

Aggressive behavior, including "ahr-ahr-ahroulit" vocalizations, bill toss, threat postures, or attack comprised a positive response. Any other behavior or no response at all within 5 minutes comprised a negative response.

WINTER BEHAVIOR

Although day-to-day recognition of an individual bird was difficult, it was nonetheless possible on a daily basis to identify in flocks certain individuals possessing unique plumage. As a result behavior of individual males or females was sampled at random on separate occasions. Initiation and development of epigamic behavior were observed in two marked adult males between October 1968 and May 1969.

RESULTS

POPULATION CHARACTERISTICS

Adult and subadult populations.—Oldsquaws generally arrived on the study area in June. Individuals were first noted on 3 June 1968, 3 June 1969, 4 June 1970, and 31 May 1971. I was able to study in detail the arrival of the breeding population each year. In 1968 there were 47 pairs of adults; 8 pairs of these arrived on 3 June, 4 on 6 June, 20 on 11 June and 15 on 16 June. In 1969, there were 43 pairs of breeding adults; 2 pairs arrived on 3 June, 3 on 4 June, 10 on 8 June, 4 on 11 June and 24 on 23 June. In 1970, 47 pairs were resident on the study area; 5 pairs arrived on 4 June, 4 on 5 June, 11 on 9 June, 11 on 11 June, 10 on 12 June and 6 on 20 June. In 1971, there were 44 pairs of adult breeders; 2 pairs arrived on 31 May, 2 on 1 June, 5 on 4 June, 21 on 10 June and 14 on 16 June. Thus, in the study period the entire breeding population invariably had arrived by 23 June. Of the non-breeding adult Oldsquaws that were occasionally observed on the study area, nine unpaired females remained throughout one breeding period.

From 1968 through 1971, 8 (all females), 9 (8 females), 11 (all females) and 5 (all females) subadults, respectively, remained in the study area. None of these birds could be identified as homing individuals, as immatures were not banded. Commonly subadults remained in small flocks aloof from breeding pairs.

Invariably the entire breeding population arrives paired and only a few surplus individuals, mostly females and subadults, are present throughout one breeding season. Bent (1925), Salomonsen (1950), Millais (1913) and others have reported in contrast that pairing usually does not occur in this species until the birds arrive at the breeding grounds. I am convinced that this conclusion was based upon a confused recognition of pair-forming and pair-maintaining displays (Alison 1972). It has been noted (Alison 1970) that pair-formation requires at least 30 days and that the maximum possible breeding period at Churchill would probably not be sufficiently long for pair-forming to occur on the breeding grounds. Drury (1961) reported that on Bylot Island Oldsquaws appeared to be paired on arrival and that there were only a few surplus drakes. Although it has generally been reported that subadult Oldsquaws summer on the Arctic coasts, this does not appear to be strictly true. Thirty-three subadults, mostly females, remained on the study area in June and July (varying numbers in each year). These birds may have been reared in the Churchill area or even in the study area in previous breeding seasons.

An apparent inconsistency recurs concerning the relative proportions of the sexes in migrating flocks of this species. Drury (1961) and Salomonsen (1950) reported a surplus of drakes on the breeding grounds. Ekblaw (in Bent 1925), stated that males outnumber females in the first flocks but later the females appear to be as numerous as the males. However, records of Females might have resulted from erroneous identification by previous authors of immature females and subadults as males. Migrating flocks of Oldsquaws generally comprise several hundred individuals (Bergman and Donner 1964). At Churchill the breeding population does not arrive en masse; rather, several pairs arrive at intervals of a few days. It is likely therefore that as a migrating flock passes a certain breeding locality, those females returning to natal ponds leave the flock taking their respective mates with them. Thus, homing females and pairs are encountered at the southern extremity of the breeding grounds. As more homing females and pairs leave a migrating flock, the relative proportion of adult drakes inevitably rises with increasing latitude. This would explain the notation in Bent (1925) that in the far north males outnumber females in the first flocks. There is also some evidence that the main body of subadults is about one week behind the adults in migrating north. The later arrival of the subadults in the far north would appear simply as an increased proportion of female-like individuals in observed flocks—an increase which may have been misinterpreted by authors cited by Bent (1925) and others as constituting the arrival of the as yet unpaired adult females.

Adult and subadult mortality.—Nest surveys, censuses and other activities associated with this study resulted in regular intensive coverage of the entire study area. The remains of dead Oldsquaws that appeared to have been killed and eaten by predators were occasionally found. An unknown number of these may have succumbed first to disease and subsequently been eaten by scavengers. The number of adult drakes in the study area in 1968 was 47 and of these two were killed (in June) by unknown avian predators. In 1969 and 1971, no adult drakes were found dead. In 1970, one adult drake (out of 47) was killed by a male Marsh Hawk (*Circus cyaneus*). In every year of the study female mortality was nil, and no subadults were found dead. On 12 June 1971, an apparently unhealthy adult female Oldsquaw (which could not fly) was repeatedly attacked and finally killed by an Arctic Loon (*Gavia arctica*) outside the study area.

Residence.—Adult populations generally increased in June and decreased in July and August. Although resident breeders had invariably arrived by 23 June, non-resident migrating individuals were occasionally found in the study area until 1 July. Each breeding pair occupied a small pond and sometimes two or three pairs occupied each of the larger lakes. Of the 90 ponds and lakes in the study area, only 27 were occupied annually whereas 49 were never occupied by breeding Oldsquaws. The attractiveness of certain ponds or lakes may have been a function of nesting cover (i.e. the presence of long-isolated peninsulas or islands).

Drakes were generally sedentary throughout June even after incubation had begun, but by 10 July several drakes had departed the study area and gathered in flocks on the Hudson Bay coast. By 30 July no adult drakes remained in the study area. Small flocks comprising adult drakes and subadults of both sexes occur along the coasts of Greenland in early August (Salomonsen 1950). Drury (1961) observed flocks of Oldsquaws, predominantly drakes, in the sea off Bylot Island in late July. The adult female population in my study remained constant throughout July, but by mid-August a slow but continuous decline was noted as females and broods deserted the inland ponds. By 31 August no adult females remained on the study area.

HOMING

Three ducks were each caught at their respective nest sites in two consecutive years and one other nested at the same lake in two consecutive years (Table 1). Adult females show a strong tendency to return to previous nest sites: 3 of 13 individuals returned to a specific site used previously; 8 females returned to the same pond as in a previous year; 2 ducks banded on nests moved to nearby ponds. Additional females may have moved to nearby ponds located outside the study area and remained there undetected. Two drakes were recaptured at the same lake in at least two consecutive years; the second drake was captured in four consecutive years at the same lake.

Of three ducks caught at the same nest site in two consecutive years, all had had successful nests in the previous year. Four females nested at the same pond in two or more consecutive years, and of these two had had successful nests in the previous years whereas two had not. Of the latter two, one nested on the

TABLE 1

HISTORIES OF BANDED OLDSQUAWS AT CHURCHILL, MANITOBA

Band Number	History of Individual
CPF 2635	Adult female, banded on nest 1969; rebanded 596-64602 on same nest 1970; at same lake 1971.
596-64605	Adult female, banded on nest 1970; on same nest 1971.
CPF 2605	Adult female, banded on nest 1969; at same lake 1971.
596-64606	Adult female, banded on nest 1970; at same lake 1971.
CPF 2625	Adult female, banded on nest 1969; rebanded 596-64608 on same nest 1970; at same lake 1971.
CPF 2629	Adult female, banded on nest 1969; at same lake 1971.
CPF 2608	Adult female, banded on nest 1969; at same lake 1970; rebanded 596-64674 at same lake 1971.
CPF 2618	Adult female, banded on nest 1969; rebanded 596-64675 at lake 100 m east 1971.
CPF 2628	Adult female, banded on nest 1969; rebanded 596-64676 at lake 75 m southwest 1971.
CPF 2638	Adult female, banded on nest 1969; rebanded 596-64677 at same lake 1971.
596-64601	Adult male, banded as adult 1970; at same lake 1971.
CPF 2640	Adult male, banded as adult 1968; at same lake 1969; rebanded 596-64609 at same lake 1970; at same lake 1971.

same island as in a previous year (when the nest had been destroyed); the other moved from an island nest site to the mainland.

NESTING

Nest location and distribution.—Phillips (1925) noted that although many nests of this species occurred singly, some females were found nesting in colonies. In this study many Oldsquaw nests tended to be clustered. Only one instance of parasitism of one female Oldsquaw on another was noted, and in that instance both females were seemingly unaware that the nest was being shared. One female subsequently incubated the clutch while the other permanently deserted the nest but remained nearby.

Excluding this instance of parasitism the minimum distance between any two active Oldsquaw nests was 7.5 cm. In 1971, three active nests were observed within the same area of 0.3 m^2. Invariably whenever more than one active nest occurred at a particular tundra pond, the nests tended to be clumped. Obviously whenever the chosen nest site was on an island, the maximum possible distance between any two active nests was determined by the size of the island. However, mainland nests were generally clustered as well. Around

TABLE 2

LOCATIONS OF OLDSQUAW NESTS IN THE STUDY AREA, 1968 TO 1971

	Number of Active Nests			
Nest Location	1968	1969	1970	1971
Mainland				
Tundra	3(12.7)*	5(19.1)	2(8.4)	2(6.9)
Spruce Forest	3(12.7)	2(9.5)	5(20.8)	2(6.9)
Dry Upland	0	0	0	2(6.9)
Marsh	3(12.7)	2(9.5)	1(4.1)	3(10.3)
Scrubland	1(4.8)	1(4.8)	0	2(6.9)
Islands	11(57.1)	11(57.1)	16(66.7)	18(62.1)
Total	21	21	24	29

* Figures in parentheses are percentages.

one three-hectare tundra lake, all four active nests occurred on one isolated peninsula, that measured about 12 × 3 m. Further investigation revealed 24 other nest cups of previous years on the same peninsula whereas no additional nest cups were found anywhere else around that lake. In one instance two mainland nests at a 0.4 ha pond were 1.8 m apart. The maximum distance between any two active mainland nests at the same pond or lake was 409.4 m. Nonetheless, 36 of 95 nests (37.9%) occurred singly (i.e. no other active nest was within 60 m).

Oldsquaw nests have been found on offshore islands, on mainland tundra, along the edges of freshwater ponds and on islands in these ponds (Millais 1913, Phillips 1925, Bent 1925, Salomonsen 1950). In the study area, 56 of 95 nests (58.9%) of known history were located on islands in freshwater ponds or lakes (Table 2). Twenty-four nests (25.3%) were on mainland tundra whereas nine (9.5%) were in marshy areas. Four (4.2%) nests were found in scrubland and only two (2.1%) were in dry upland. There was no significant difference between the number of individual nests on islands as compared with mainland nests ($P \leqslant 0.05$).

The study area contains 79 islands in freshwater ponds or lakes and of these seven had at least one active Oldsquaw nest in four consecutive years. Active nests were found on 16 islands (20.2%) whereas 45 islands showed no evidence of former nests. Those nesting places on islands or on the mainland in which nests were located in two or more consecutive years are referred to as traditional nesting areas in this paper. Few nests were found at ponds occupied by pairs of Herring Gulls (*Larus argentatus*) and only two nests were discovered in lakes frequented by Arctic Loons. Oldsquaws did not nest at ponds

TABLE 3

CONCEALMENT RANKING FOR OLDSQUAW NESTS IN THE STUDY AREA*

	Number of Nests			
	Active Nests		Previous Nests	
Concealment	Islands	Mainland	Islands	Mainland
Well concealed	10(17.9)	16(41.0)	18(17.2)	27(24.3)
Open from above	46(82.1)	15(38.5)	110(82.8)	61(54.9)
Partially concealed	0	6(15.4)	0	19(17.1)
Poorly concealed	0	2(5.1)	0	4(3.7)

* Data from nests of previous years is also present for comparison. Figures in parentheses are percentages.

or lakes at which Common Eider colonies were found. In addition breeding pairs always avoided certain ponds for no apparent reason. Thirty-six of 50 island nests were located on large islands (over 9.8×10^{-2} ha). The maximum number of active nests on any island was seven. Three active nests were found on one 0.7 sq. m. island in 1970. In 1970 and 1971, a single active nest was located on the same small (28 cm × 41 cm) island.

Ekblaw (in Bent 1925) noted each nest was a small cuplike depression lined with dry plants or leaves and covered with varying quantities of down. On the study area, nests were always lined with dried leaves of dwarf birch or dwarf willow to a depth of about 2.5 to 5.0 cm. The first egg was always buried in this plant material. In each instance, it was not until after the second egg had been deposited that down appeared on any nest. In 43 (45.3%) instances, no down was found until after the third egg had been laid. Subsequent to the deposition of the third egg, increasing quantities of down were observed on each nest and after the fifth egg, the down layer appeared complete. In no instance was the nest lined with down. Occasionally the down layer was covered with or mixed with plant debris, especially on mainland tundra nests.

Twenty-six (27.3%) of 95 nests were well concealed from above (Table 3) by Black Spruce (*Picea mariana*) boughs and from the sides by various grasses, dwarf willows (Fig. 6) or dwarf birches. Sixty-one (64.1%) nests were open from above but were concealed from all sides by 10 to 15 cm of plant growth. Only 6 (6.3%) nests were partially concealed from the sides and open from above while 2 (2.3%) were poorly concealed. Mainland nests were more completely concealed ($z = 2.14$, $P \leqslant 0.05$) than nests located on islands in freshwater ponds or lakes.

Oldsquaw nests are reportedly generally found close to water (Phillips 1925, Bent 1925). However, Bent (1925) noted a nest 7 m from the water's edge and Evans (1970) observed nests at least 200 m from the nearest open water.

Figure 6. Oldsquaw nest cup located beneath concealing dwarf willow.

In this study average distances between nests on islands and the nearest open water were minimal and were determined mostly by the limiting size of each island. Average distances and corresponding standard deviations between nests on islands and the nearest open water were 0.8 ± 3.4 m (n = 56), but mean distances were greater in tundra and marshland areas 10.4 ± 9.5 m (n = 12), and 9.5 ± 3.4 m (n = 9). Two nests on dry upland were 143 m and 52.5 m, respectively, from the nearest pond. Evans (1970) found average distances from the nearest water for nests on islands to be about 2.1 m whereas nests on mainland tundra and on mainland beach averaged about 28.6 m and 9.0 m, respectively. Table 4 shows that about 65% of all active nests were within 1.4 m of open water whereas only 10% were more than 14 m from the edge of a pond or lake.

Several species of waterfowl, including the Mallard, Pintail, Gadwall (*Anas strepera*), Lesser Scaup (*Aythya affinis*) and white-winged Scoter (*Melanitta deglandi*) are known to nest in high densities among larids (Vermeer 1958). Evans (1970) presented evidence suggesting that some Oldsquaws at Churchill nest in association with Arctic Terns (*Sterna paradisaea*). It has been suggested that species of waterfowl nesting among certain larids may derive protection from the well-organized defense tactics apparently effective against some predators. Fifty-nine Oldsquaw nests were found in association with at least one Arctic Tern nest (at the same lake or pond). Of these, 44 (46.3%)

TABLE 4

DISTANCES BETWEEN OLDSQUAW NESTS AND THE NEAREST OPEN WATER

Distance in meters	Number of Active Nests				Percentages				Cumulative Percentages			
	1968	1969	1970	1971	1968	1969	1970	1971	1968	1969	1970	1971
0.0– 0.7	11	11	12	15	57.1	52.8	50.0	51.7	57.1	52.8	50.0	51.7
0.8– 1.4	3	2	2	5	14.3	9.4	8.3	17.2	71.4	62.2	58.3	68.9
1.5– 2.1	2	2	0	3	9.4	9.4	0	10.3	80.8	71.6	58.3	79.2
2.2– 3.5	1	2	4	1	4.8	9.4	16.6	3.5	85.6	81.0	74.9	82.7
3.6– 7.0	0	1	1	1	0	4.8	4.2	3.5	85.6	85.8	79.1	86.2
7.1–14.0	1	0	3	1	4.8	0	12.5	3.5	90.4	85.8	91.6	89.7
14.1–28.0	1	1	1	1	4.8	4.8	4.2	3.5	95.2	90.6	96.8	93.2
28.1+	1	2	1	2	4.8	9.4	4.2	6.8	100.0	100.0	100.0	100.0
Total	20	21	24	29								

were located on islands (Table 5) whereas 15 (15.7%) were on the mainland. But 12 Oldsquaw nests (12.7%) on islands and 24 (25.3%) mainland nests were located at lakes or ponds not inhabited by terns. On islands in freshwater ponds there was a significant association between Oldsquaw nests and Arctic Tern nests ($\chi^2 = 12.6, P \leqslant 0.01$). On the mainland a significant disassociation of the nests of the two species was observed ($\chi^2 = 12.6, P \leqslant 0.01$). In 1968, 1970 and 1971, Oldsquaw nests were invariably initiated prior to the arrival of terns on the breeding grounds. In 1969, 12 female Oldsquaws failed to nest until after several pairs of terns had arrived in the study area.

TABLE 5

NEST ASSOCIATION BETWEEN OLDSQUAWS AND ARCTIC TERNS IN THE STUDY AREA*

	Number of Active Oldsquaw Nests			
	On Islands		On Mainland	
Year	Terns Resident	Terns not Resident	Terns Resident	Terns not Resident
1968	9	2	4	6
1969	9	2	4	6
1970	13	3	3	5
1971	13	5	4	7
Total	44	12	15	24

* Only nests of known history are included.

THE EGGS

Egg laying.—The nest site was always selected by the female. The male invariably followed the female to the shore of the pond or lake but none was observed to follow her as she walked about on islands or on the mainland searching for a desirable location. I found no evidence that females selected and prepared a nest site prior to laying the first egg. Females presumably about to lay the first egg were frequently observed flying from pond to pond apparently searching each for a suitable nest site. One female required over an hour to walk about the surface of a 0.39 ha peninsula, apparently checking under each Black Spruce for a possible site. Seemingly finding none, the bird then flew immediately to a nearby pond, climbed up onto a small island, and disappeared beneath a short spruce tree. Forty-eight minutes later she reappeared, entered the water, swam about 10 m away from the island, and then flew to a nearby pond to join her mate. Two hours prior to this incident, I had visited the same island and found only one nest cup (from a previous year). At that time it had contained a few wet leaves and several egg shells. When I returned to the island subsequent to the female's departure, the nest cup contained a single egg buried beneath about two inches of dry leaves. The wet leaves and egg shells had apparently been removed by the female. The following year I observed the same series of events involving another female. In neither instance had the females bred at that particular nest site in the previous breeding season.

In two instances females, having laid the first egg, deposited the second (and the subsequent clutch) at another site on the same small island. Usually one egg was deposited per day. The first egg was most often laid about 1630, the second egg about 1100 the following day, the third egg about 1300 C.S.T. the third day and each subsequent egg at intervals of about 26 hours until the clutch was completed. There were no instances of interrupted egg laying such as those mentioned by Cooch (1965) in Common Eiders. Incubation in Oldsquaws always began subsequent to clutch completion. During the laying period females did not return to their nests, except to deposit eggs, even if the temperature fell below 0°C. After the clutch was complete females generally left their nests unattended only twice daily to feed, preen, or undertake some other maintenance activity. Most females were absent from nests between 0900 and 1000 and again between 1400 and 1630 C.S.T.

Clutch size.—In this species clutch size has been variously recorded as from 5 or 6 to 9 or 10 (Millais 1913), 5 to 7 (Bent 1925) and 5 to 8 (Phillips 1925). Salomonsen (1950) recorded the average clutch size of Oldsquaws in Greenland as 5.7 eggs. Two nests containing 11 eggs (Salomonsen 1950) and 17 eggs (Phillips 1925) have been reported, although these may have been the combined clutches of two females.

Clutch sizes of nests located on islands did not differ significantly ($F = 2.00$, $\mathrm{df} = 7/87$. $P \leqslant 0.1$) from those of mainland nests (Table 6). In five in-

TABLE 6

CLUTCH SIZES OF OLDSQUAWS IN THE STUDY AREA, 1968 TO 1971*

Nest Location	Mean Clutch Size			
	1968	1969	1970	1971
Islands in Freshwater Ponds	6.8 ± 0.6	6.9 ± 0.7	6.7 ± 0.5	6.8 ± 0.4
Mainland	6.8 ± 0.5	6.8 ± 0.4	7.0 ± 0.8	6.8 ± 0.8

* Figures are mean clutch sizes and standard deviations.

stances nests of banded females were located in two consecutive years. The sample is small; nonetheless, four out of five females had clutches comprising the same number of eggs (7, 7, 7, and 6 eggs, respectively) in two consecutive years. The fifth individual also laid the same number of eggs in both years, but in the second year the first egg was abandoned and the remainder of the clutch was laid at a nearby nest site. In two of these instances the nest was located on an island in the first year and on the mainland in the second year.

In waterfowl clutch and egg sizes are usually inversely related (Lack 1966a). In certain species of waterfowl (i.e. Arctic species) larger eggs probably aid in thermoregulation, provide newly hatched young with large food reserves, and apparently offset the advantage of small egg size. The clutch size in a given species must evolve so that a particular pair can maximize its genetic impact on subsequent generations. This may result, especially in precocial species, in a clutch size equivalent to the largest number of eggs that a female can efficiently incubate, or the largest number of eggs which she can produce in a short period of time. In the study area Oldsquaw clutch size was significantly larger (6.8) than that reported for the same species in previous studies (Salomonsen 1950, and others) conducted elsewhere. This apparently inconsistent clutch size cannot however be examined until a detailed comparative study involving several breeding localities has been conducted.

Viability of eggs.—Non-viable eggs included those which failed to hatch in successful nests due to infertility or death of the embryo. In this study 75 of 383 eggs (19.3%) were non-viable. The rate of non-viability was constant from year to year. In some other species of waterfowl egg loss due to non-viability averages 7 to 9% (Earl 1950, Anderson 1956 and 1957, Steel *et al.* 1956, Keith 1961). Perhaps the low viability of Oldsquaw eggs is related to the extended exposure of incomplete clutches to severe weather.

THE NEST AND INCUBATION

Nest initiation.—In this study only nests of known history were included in the data (i.e. exact date of initiation of each clutch was known). Oldsquaws tended to breed at traditional locations. Consequently, by surveying each of these sites daily it was possible to discover the deposition date of the first and each subsequent egg in 95 clutches. In the study period the earliest active nest was found on 3 June and the latest nest (not a renest) on 28 June. The mean dates of clutch initiation were 12 June, 23 June, 11 June and 9 June in 1968 through 1971, respectively. In 1969, the observed delay in nest initiation was apparently due to ice conditions on the breeding ponds. Egg laying generally extended over a period of about 15 to 20 days.

In 1971, when nesting occurred earliest, the warmest May and the coldest June of the entire study period were recorded. When nesting occurred latest, in 1969, both May and June temperatures were below normal. Above average temperatures in both May and June of 1970 did not significantly advance nest initiation. June snowfall apparently did not affect nesting, probably because no accumulation resulted. The effect of heavy rainfall upon Oldsquaw nest initiation is unknown. Keith (1961) found no correlation between precipitation and mean date of clutch initiation in several species of prairie waterfowl.

The average date of clutch initiation in Oldsquaws was significantly delayed only by cold May temperatures ($b = -1.23, t = 4.69, df = 2, P \leqslant 0.05$). Thus, in years with below average May temperatures, snow and ice disappeared from the study area later than in years when May temperatures were average or above average. Nesting was consequently delayed because potential nesting locations were covered by snow. Furthermore otherwise isolated islands were still connected to the mainland by ice bridges. Ryder (1969) found that most nests of Ross' Goose (*Anser rossii*) and "Lesser" Snow Goose located on offshore islands that were joined to the mainland by ice bridges were destroyed by Arctic Foxes (*Alopex lagopus*). While remnant ice remained in breeding ponds, Oldsquaw nests might be similarly available to mainland predators (Alison 1970).

Effect of weather upon incubation.—Low temperatures, snow, and moderate rainfall do not seem to affect egg loss through desertion in this species. The mean dates for clutch initiation from 1968 through 1971 were previously given as 12, 12, 11 and 9 June, respectively. In 1968, from 8 to 16 June, the mean daily temperature was 5.3°C, overnight lows averaged -0.6°C and 20 cm of snow fell. In 1969, from 19 to 27 June, daily temperatures and overnight lows averaged 4.4°C and 1.1°C, respectively. In 1970, from 7 to 15 June, the mean daily temperature was 6.3°C and the average overnight lows were about 0.1°C. On 10 June 1971, 18.6 mm of rain fell and on 17 to 19 June of the same year, 19.6 mm of rain were recorded. Oldsquaws were never observed to desert nests under these conditions. No nests of this species were lost due to flooding.

Predation on nests.—Most recent waterfowl studies have shown that predation was the main cause of nest loss. In this study also a larger proportion of unsuccessful nests resulted from predation than from any other cause.

TABLE 7
AVIAN AND MAMMALIAN PREDATORS AND NEST DESTRUCTION IN THE STUDY AREA

Potential Nest Predator	Number of Predators			
	1968	1969	1970	1971
Parasitic Jaeger	2	2	4	4
Common Crow	2	2	2	2
Common Raven	1	1	1	1
Herring Gull	16	14	14	16
Long-tailed Jaeger	2	2	0	3
Arctic Fox	2	3	2	3
Red Fox	0	1	0	2
Total	25	25	23	31
% of Nests Destroyed by Avian Predators	16.7	16.7	20.0	34.6
% of Nests Destroyed by Mammalian Predators	11.1	11.1	5.0	3.9
Total % Destroyed	27.8	27.8	25.0	38.5

The potential avian nest predators in the study area included Parasitic Jaeger (*Stercorarius parasiticus*), Long-tailed Jaeger (*S. longicaudus*), Common Raven (*Corvus corax*), Common Crow (*C. brachyrhynchos*) and Herring Gull. Of these only the Parasitic Jaeger was a known predator of Oldsquaw nests. In 1968 and 1969, Parasitic Jaegers accounted for all avian-destroyed nests. Although Long-tailed Jaegers, Common Ravens, Common Crows and Herring Gulls were not observed destroying Oldsquaw nests in this study, they have reportedly taken a heavy toll of waterfowl eggs elsewhere (Kortright 1953, Sutton 1932, Lokemoen 1966, Larson 1960).

The Arctic Fox and Red Fox (*Vulpes fulva*) were the only two species of mammalian predators observed in the study area. Neither of these was actually observed destroying nests, but several Oldsquaw nests were apparently destroyed by foxes (a characteristic fox odor persisted at each destroyed nest).

Predator density was determined by direct count. Each number in Table 7 represents an individual predator which was observed at the same location in at least 10 different censuses. Thus the data probably represent a minimum number of predators as other individuals that infrequently entered the study area from other areas were not included. Furthermore, in each year the nests of all recorded Parasitic Jaegers, Herring Gulls, and Common Crows were located. At least one active fox den was found in each year (two in 1971). In 1971, predator density was greater than in any other year of the study and a

TABLE 8

OLDSQUAW NEST LOSSES DUE TO PREDATION IN THE STUDY AREA

Nest Location	Total Number of Nests	Total Number of Nests Destroyed	Percentage Destroyed
Mainland			
Open Tundra	12	2	16.7
Under Trees	12	4	33.3
Marshland	9	1	11.1
Dry Upland	2	1	50.0
Scrubland	4	0	0.0
Islands			
Open Tundra	42	10	23.8
Under Trees	14	7	50.0

larger proportion of Oldsquaw nests were destroyed in that year. There was a significant correlation ($r = 0.998$, $df = 2$, $P \leqslant 0.01$) between predator density and egg loss due to predation. In each year it was found that all mammalian-destroyed nests were located on the mainland and that all but two avian-destroyed nests were located on islands. Two islands, each measuring about 0.3 ha located in the same pond, were visited daily by two Parasitic Jaegers throughout June 1971. Every Oldsquaw nest located on these islands was destroyed by these birds. During the period of the study, 16 clutches (113 eggs) were destroyed on these two islands and in 1971, 34 eggs were destroyed there between 10 June and 13 June. Seemingly poorly concealed nests at nearby ponds were not destroyed.

Renesting did not occur. Whenever a partially complete clutch was destroyed the female generally returned to the destroyed nest and subsequently laid several more eggs. In some instances these were incubated but in other cases they were deserted. Thus several incubated nests contained only two or three eggs (these were not included in the clutch size calculations). Cooch (1965) reported that one eider nest was destroyed twice by avian predators but that the female eider returned to the same site and successfully hatched a third clutch. The rate of egg loss due to predation decreased as the breeding season progressed and there was no indication that egg predation increased in relation to the age of the developing embryos.

Table 8 shows nest losses due to predation at various locations. Predation was highest among nests (50.0%) in dry uplands (where nests were exposed) and among nests under spruce trees on islands. Nests located on islands in freshwater ponds were as frequently destroyed by predators as nests located on the mainland ($z = 0.869$, $P = 0.615$, normal deviate test). In the study

TABLE 9

SUMMARY OF THE FATE OF OLDSQUAW NESTS IN THE STUDY AREA, 1968 TO 1971

			Predation			Other		
Nest Location	Total	Successful	Parasitic Jaeger	Unknown Avian	Foxes	Communal Clutch	Desertion	Cause of Loss Unknown
Mainland Tundra	12	6		1	1	1	2	
Mainland Under Trees	12	7			4		1	
Marshland	9	6			1		2	
Dry Upland	2	1		1				
Scrubland	4	2					2	
Island Tundra	42	28	8	2			2	2
Island Under Trees	14	6	6	1			1	
Total	95	56	14	5	6	1	10	2
Percentage of Total Nests		58.9	14.8	5.3	6.3	1.4	10.5	2.8

area, 30.4% of all Oldsquaw nests located on islands were destroyed by predators whereas on the mainland 20.5% were predator-destroyed. The size of an island was apparently irrelevant to the occurrence of nest predation. Island location appeared important, however, as nests located on certain islands were destroyed by predators each year whereas nests on other islands were successful each year. Nest loss due to predation was not correlated with the distance of the nest from the water. Table 9 shows the fates of 95 Oldsquaw nests of known history observed during this study.

Incubation period.—The exact incubation period for this species has not previously been determined accurately. Most suggestions are probably extrapolations from known incubation periods of other related sea ducks. I investigated incubation periods of 106 eggs and found that these required 26.03 (standard deviation = + 0.8) days to hatch (from the date of clutch completion). Non-incubated freshly-laid eggs placed in incubators generally required slightly longer. In two instances extreme incubation periods were recorded. Three eggs (comprising a partially destroyed clutch) required only 24 days whereas a single egg took 29 days.

The time required for each clutch to hatch (i.e. between the hatching of the first and last eggs) varied considerably. About 30% of all clutches required

TABLE 10

HATCHING DATES OF OLDSQUAWS IN THE STUDY AREA, 1968 TO 1971

	Number of Clutches Hatching			
	1968	1969	1970	1971
July 6				2
7			2	1
8	1			1
9	1			1
10	2			4
11			1	2
12	2		2	1
13	2		1	2
14			1	
15			2	1
16	2		1	1
17			1	
18	1			
19	1		3	
20	1			
21				
22			1	
23		2		
24				
25		2		
26		1		
27		2		
28		3		
29		2		
30		1		
Total	13	13	15	16

12 hours or less while 30% required over 48 hours. One clutch of seven eggs in 1969, required 52 hours to hatch completely. There was no correlation between clutch size and brood hatching time nor was there any annual difference in hatching times of individual broods. It is likely that the length of the interval between the hatching of the first and last eggs in a particular clutch depended partly upon the total incubation that each egg received. In some nests certain marked eggs were found towards the outside of the clutch whereas others were generally located centrally. The central eggs tended to hatch first. Unincubated incomplete clutches were frequently found to be warm although females had not yet commenced incubating. Thus, the warming effect of the Arctic sun in association with the partial insulating effect of an as yet incomplete down layer might have influenced clutch hatching time. Frequently the first egg laid was located centrally in the nest and was the first to hatch. More

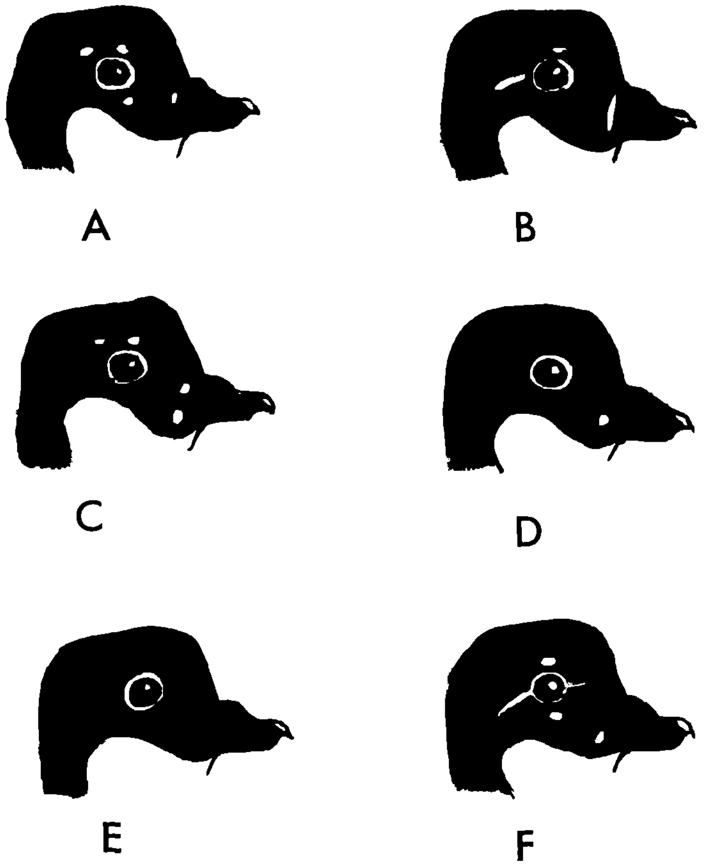

Figure 7. Variation in head plumages of downy young Oldsquaws about 24 hours old. A to D, females; E and F, males.

commonly the first two eggs laid hatched at about the same time. After a delay of about six or eight hours, the next two eggs laid hatched. In Common Eiders the first egg laid is invariably the first to hatch (Cooch 1965).

Hatching success.—In this study, 61.9, 61.9, 62.5 and 51.7% of Oldsquaw nests were successful, 1968 to 1971, respectively. Keith (1961) found that about 31% of "scaup" and Redhead (*Aythya americana*) nests in southern Alberta were successful and other authors have reported nesting success results of about 56% (Keith 1961).

THE YOUNG

Occurrence of broods.—Table 10 presents hatching data for successful clutches of Oldsquaws. In 1968 to 1971, the hatching periods comprised 12, 7, 14 and 10 days, respectively. Detailed studies of the activities of each brood in the study area were not conducted as it would have been necessary to mark (dye) each duckling individually. However, some general brood behavior was noted. Communal broods were common and certain females apparently abandoned the study area as soon as hatching was complete. The number of offspring adjusted for average clutch size was proportionately greater than the number of accompanying females in some instances. On one occasion an adult female and 32 young were observed. When the ducklings were dried (about 24 hours after hatching) they were conducted by the female to the nearest open water. At first the ducklings were not very proficient at diving. While diving among the young, the female caused material from the pond bottom to rise to the surface, and the ducklings examined and occasionally appeared to swallow some fragments. Considerable individual variation in plumage of ducklings was noted (Fig. 7) within and between broods.

Fledging.—Figures 8 and 9 show the development of plumage prior to fledging (which occurs at an age of about 35 to 40 days). Most other sea ducks have much longer fledging periods, including 63 to 77 days for the White-winged Scoter (Johnsgard 1968), and about 8 weeks for the Common Eider (Cooch 1965). Although Common Eiders reportedly leave their natal ponds for the sea before they can fly (Cooch 1965), Oldsquaws do not. Consequently, broods of the latter species must remain on the natal pond throughout the prefledging period. Hence, in certain ponds, especially ponds at which colonies of Oldsquaws have nested, large numbers of adults and immatures congregate. As the broods mature, food supplies in each pond are probably depleted. Broods leave the inland ponds and fly to the sea at an age of 35 to 40 days. There is evidence that many of these birds walk to nearby ponds at an earlier age (a flightless immature was known to have walked 1.2 km from one pond to another in a 5-day period). A shorter fledging period would allow a larger number of broods to be successfully reared at a given pond. In addition as Oldsquaws have a short available breeding period, the species would probably benefit from an unusually short fledging period. It was always possible to determine the age of individuals in the late summer and early fall by plumage (Fig. 10 and 11).

TERRITORIALITY

Bent (1925) and Phillips (1925: 347–366) described pursuit flights, generally involving a female and two drakes, that they erroneously assumed to be courtship behavior. On the study area all such behavior performed by

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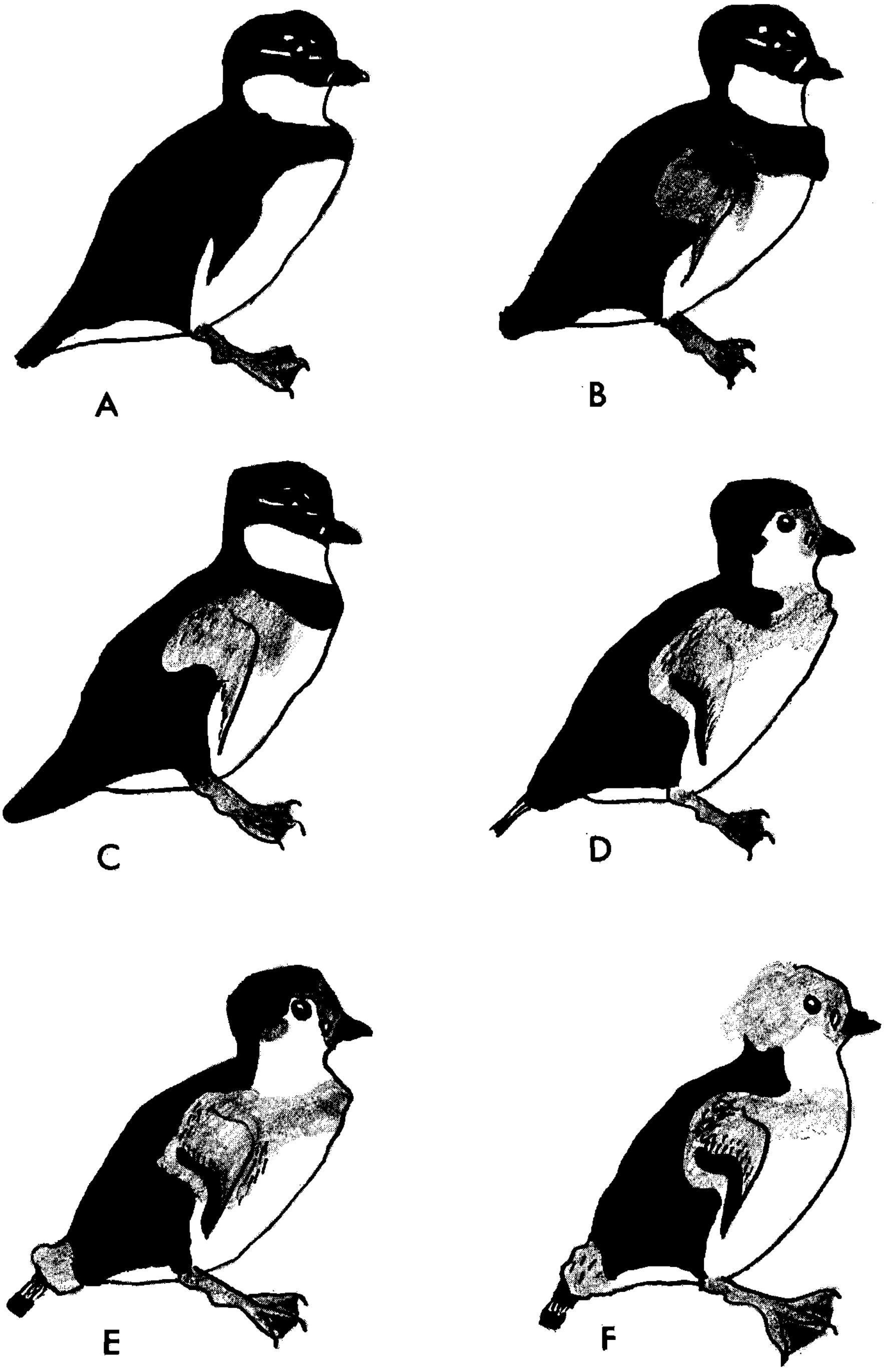
Figure 8. Plumage development in young Oldsquaws. A. one day old; B. 11 days; C. 13 days; D. 17 days; E. 18 days; F. 21 days. Colors: black, gray, and white.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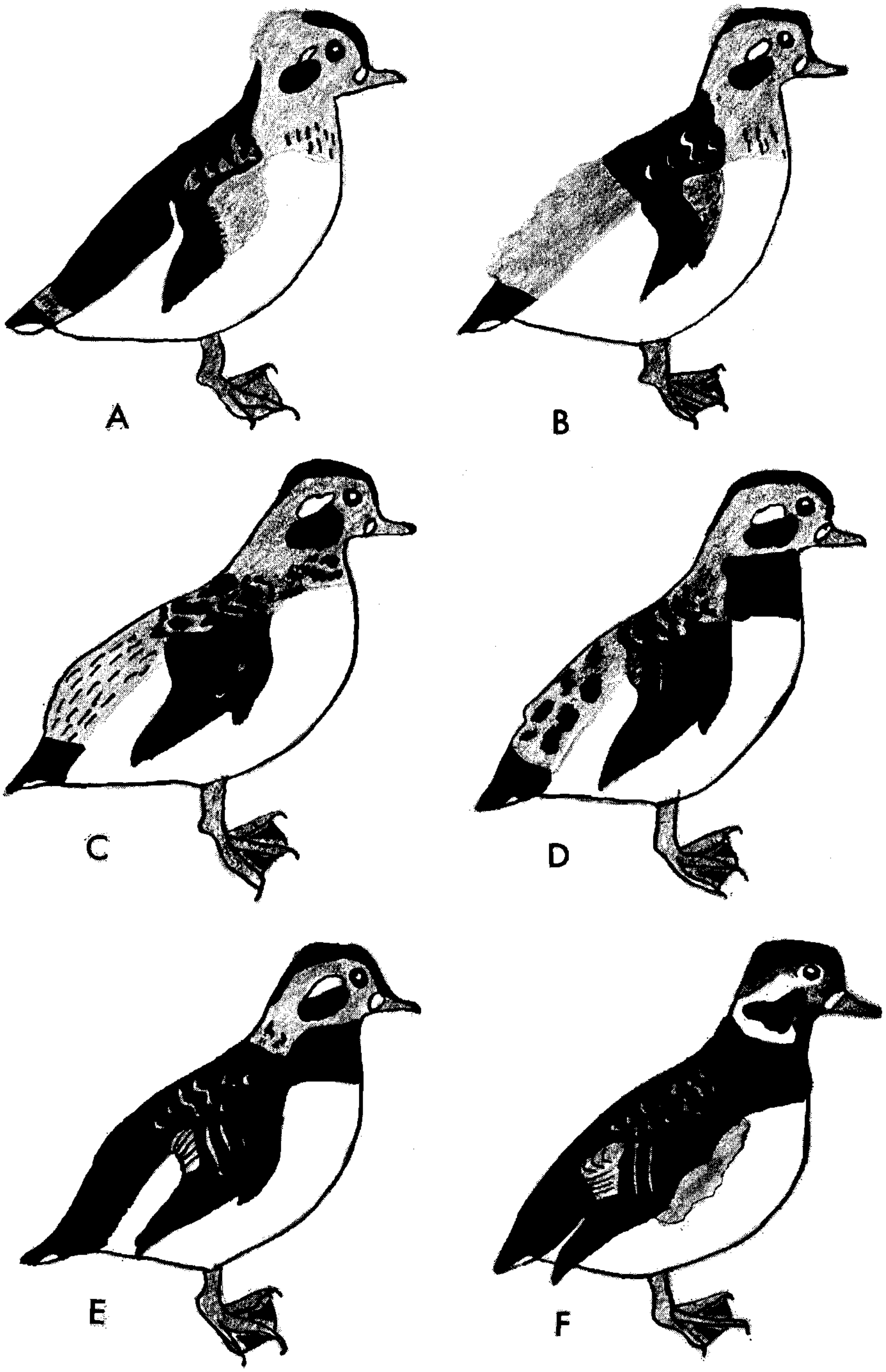
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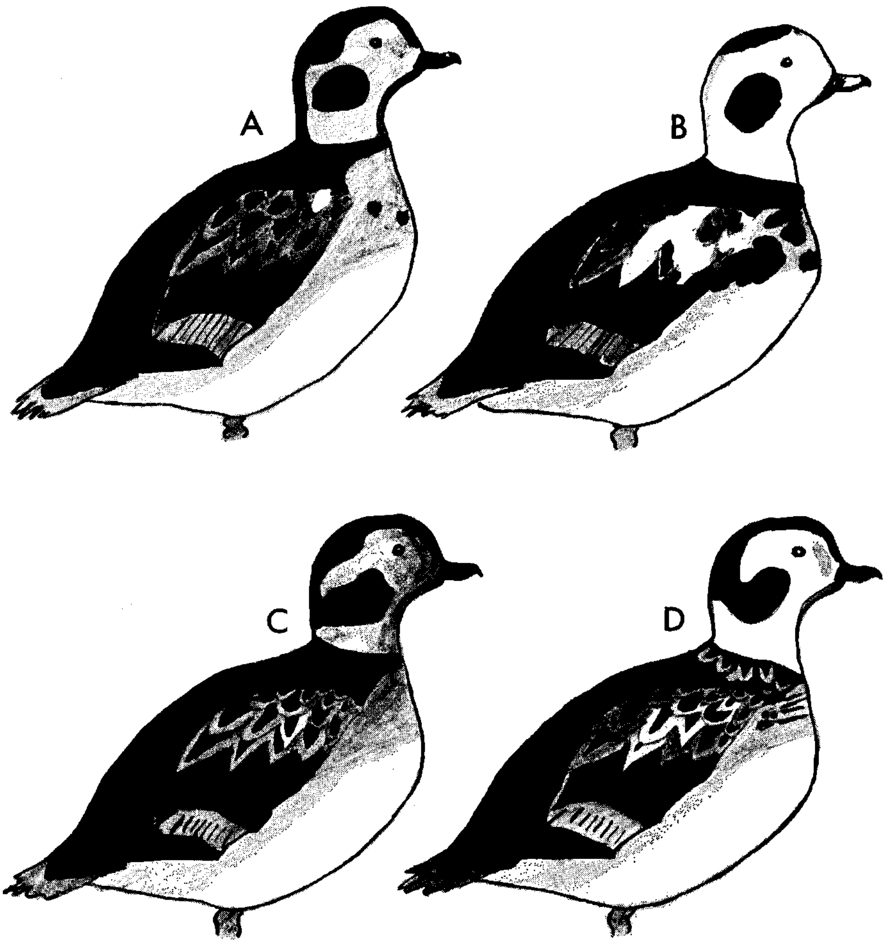

Figure 10. Immature male (upper) and female (lower) Oldsquaws. (A) and (C) mid-September to mid-October; (B) and (D) late October to mid-February.

marked birds comprised territorial pursuit flights. Invariably the female of a pair was pursued by the drake into whose territory (i.e. defended area) she had intruded. The intruding drake, paired with the female, always pursued and frequently fought with the defending drake, thus creating perhaps the appearance of two drakes fighting for possession of an unpaired duck. Ago-

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Figure 9. Plumage development in young Oldsquaws. A. 23 days old; B. 24 days; C. 25 days; D. 27 days; E. 28 days; F. 34 days.

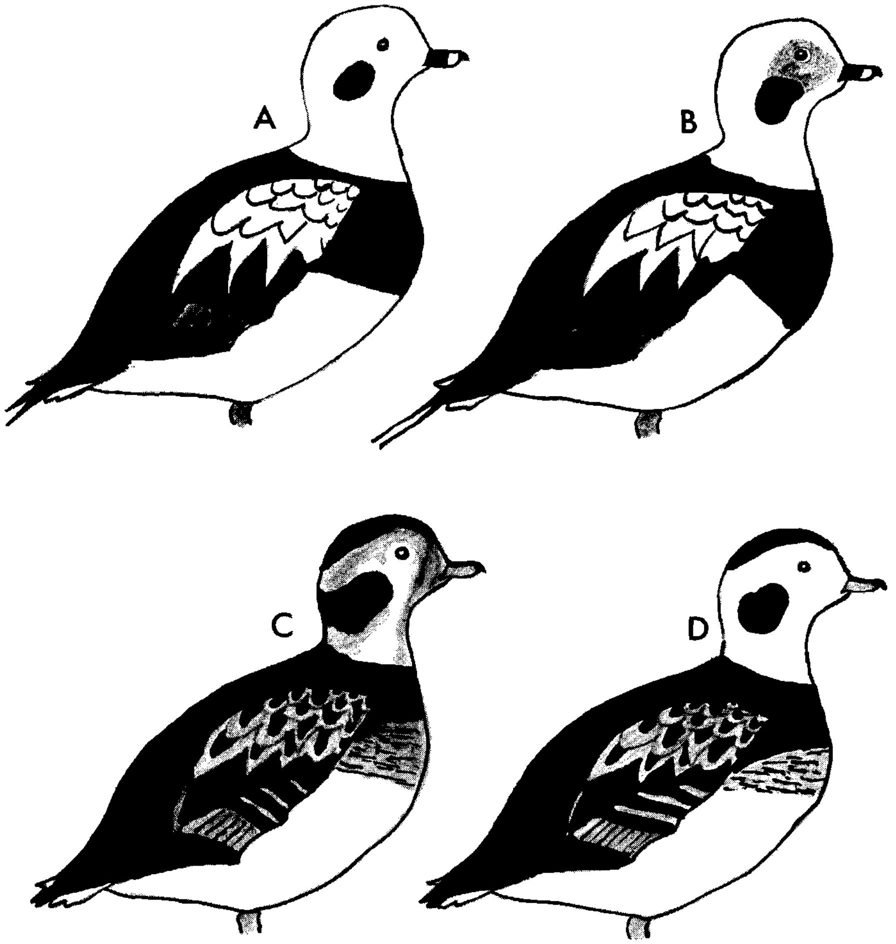

Figure 11. Adult male (upper) and female (lower) Oldsquaws. (A) and (C) early September to mid-October; (B) and (D) late October to late April.

nistic pursuit flights usually occurred when a pair landed within the territory of a second drake. The intruding female was always attacked and made to fly by the defending drake. The intruding drake then followed these individuals, apparently defending his mate from the attacks of the other male. As soon as the female left the territory the chase ended. Pursuit flights may also occur when a drake lands near a pair on their territory. In this instance, the new drake often makes the female fly by repeated threat gestures and attacks. Invariably her mate follows, seemingly trying to defend her.

In this study stuffed Oldsquaw decoys were placed within the territories of

TABLE 11

RESPONSES OF DRAKE OLDSQUAWS TO STUFFED DECOYS AND RECORDED VOCALIZATIONS

	Response									
	Decoys[2]					Decoys and Vocalizations[2]				
	Number of Drake									
Decoy Combinations[1]	1	2	3	4	5	6	7	8	9	10
Single drake (1)	+	+	+	+	+	+	+	+	+	+
Pair (5)	+	+	+	+	+	+	+	+	+	+
Single female (2)	+	+	+	+	+	+	+	+	+	+
Single subadult drake (3)	+	+	+	+	+	+	+	+	+	+
Single subadult female (4)	–	–	–	–	–	–	–	–	–	–
Flock of subadults (6)	+	–	–	–	–	+	+	+	–	–
Other species (7)	–	–	–	–	–	–	–	–	–	–

[1] The row sequence does not reflect the order in which the experiments were performed, hence habituation of drakes to decoys should not be inferred from this table. Figures in parentheses indicate the order in which the experiments were performed.

[2] Figures in columns one to five indicate responses to decoys without specific accompanying vocalizations. Responses in columns six to ten indicate results obtained when vocalizations and decoy combinations were tested together.

five drakes, each territory averaging about 0.5 ha. These decoys were investigated by the defending drake alone; the female never actively defended any territory. The following decoy combinations were tested: a single adult drake, an adult drake and adult female, a single adult female, and all drake-female combinations for flocks comprising three to five individuals (Table 11). The approaching defending drake always performed bill toss with the accompanying vocalization (Alison 1970). Single adult drakes were at first attacked and then seemingly ignored, as were single adult female decoys. When a pair was tested, the defending male always threatened the female of the pair and subsequently swam or flew back to his own mate. Subadult decoys were sometimes threatened but usually were ignored. Drake Oldsquaws never responded positively to stuffed Pintail, Mallard, or Greater Scaup decoys. Female Oldsquaws did not behave territorially.

Recorded Oldsquaw "ahr-ahr-ahroulit" (Alison 1970) vocalizations were then tested on five other drakes. The same decoy combinations as before produced the same results. Once again stuffed decoys of other species were not investigated by defending drakes. When the recorder was hidden 60 m from the decoy(s), the defending drake, before investigating them, usually flew or swam towards the source of the calls.

In four instances the female of a pair was captured, removed from her mate's territory, and released flightless (all primary feathers removed) at a lake 8 km east of the study area. On each occasion the drake abandoned the territory within 12 hours. When the drake of a pair was removed (captured and released flightless elsewhere), even before nesting was initiated, the female always remained (10 instances) on the previously defended territory. In each such instance a new pair arrived and began defending the same territory within 24 hours following the departure of the former defending drake, and in at least three instances the newcomers bred successfully. The female of the previous pair was pursued frequently by the new drake but never left her mate's former territory. In 1970, I was able to remove four successive defending drakes from the same pond. The fifth pair arrived subsequently and, although the drake of this pair attempted to drive them away, three of the four females from the previous pairs remained on the pond until late July.

Most species that are territorial during the breeding season are gregarious throughout the remainder of the year. Many geese are territorial, and the progeny of a particular family may return and nest near their own place of hatching. Colonial nesting behavior occurs in some eiders and, in instances where nesting conditions are suitable (e.g., on islands), in certain swans, geese, pochards, and dabblers (Johnsgard 1968). Specific nest site requirements of hole- or crevice-nesting waterfowl reduce nesting concentrations in these species. Although the physiological mechanism resulting in territorial behavior might be identical for most species of birds, selection for territoriality may depend upon different ultimate environmental factors.

In some species territorial behavior functions to regulate populations in a density dependent manner (Fretwell and Lucas 1969). When some birds are prevented by resident pairs, from establishing territories, populations decrease (Brown 1969). In those pairs that manage to establish territories by locating in less suitable habitat, reproductive success is low and the rate of population increase decreases (Birch 1960).

In this study adult drake Oldsquaws behaved territorially. Whenever a drake was removed from its territory, a new (paired) drake always arrived and began defending the same territory. At least 3 out of 10 replacement pairs bred successfully. Thus it can be demonstrated that removal of pairs of Oldsquaws can result in replacement of these birds by capable breeders. It is unknown whether replacement pairs would have nested elsewhere anyway.

It may appear inconsistent that defending drakes should attack the female of an invading pair rather than the male. As the pair bond in this species is strong (Alison 1970), the defeat of an invading drake by a defending territorial drake might not ensure the departure of the invaders unless the female was also induced to depart. As paired females are invariably followed about by their mates, territorial drakes might ensure the departure of invading pairs by attacking and driving off the female of the pair, because her mate would always follow her away.

Females took no active part in territorial defense and some females nested in loose colonies. In contrast to hole- or crevice-nesting waterfowl, ground-nesting sea ducks have less specific nest site requirements, and it is therefore possible for several individuals to nest at a particular location (Johnsgard 1968). The number of females nesting successfully at such locations might be governed by the available food supply as needed to satisfy the brood requirements of each female. Female Oldsquaws frequently nest within the defended territories of other drakes but always return to the territory defended by their mate to feed. Territories were no longer defended (the drakes had departed) after the broods hatched. It might therefore be concluded that the territories were not defended for their food value to the young. Whereas some territories contained three or four broods, about 70% contained no broods. As females are not territorial, it is possible that in a given year large numbers of homing females might attempt to nest at the same pond. Because female Oldsquaws do not conduct their broods from the natal lake to the sea for at least four weeks after hatching, possibly the food supply in such a pond, especially if the pond is small, might not be adequate to support so many adult females and maturing offspring. Consequently the number of females breeding at each potential colony would have to be limited.

In the study area each defended territory comprised the same pond(s) or lake(s) as in previous years, although a given territory may or may not have been defended by a particular drake in successive years. Hence the number of defended territories, and thus the number of breeding pairs, in each locality is fixed. Females commonly nest in a territory other than that defended by their mate, but in every instance the vocalizations of the female's mate when uttered from the defended territory were clearly audible to me at the nest site. It may be that the distance of the nest site from the defended territory is a function of the audible range of the drake's voice. Yet the maximum possible number of nests in a particular colony is probably limited by the number of immediately adjacent territories (a constant). In this way after the available territories are occupied the remainder of the homing population probably disperses and occupies nearby ponds or lakes, and these birds may have comprised the replacement pairs in removal experiments. Consequently local population density might be regulated.

While 36 nests occurred singly, 59 were clustered. In each instance the number of nests comprising a particular colony was approximately constant from year to year. As the number of occupied territories located immediately adjacent to these colonies was almost constant in each year, the size of each colony appeared to be regulated by the number of such occupied territories.

During the egg-laying period, females always returned to their mate's territories to feed. Apparently the potential food supply available to each female is limited by the size of her specific territory, but nothing suggests that female Oldsquaws nesting in colonies have smaller potential food supplies than females with isolated nests. Probably the only factor limiting food availability at a particular pond was the extent of ice cover. As long as any open water is available on a pond, Oldsquaws are capable of diving beneath the ice to obtain food. On 1 May 1968, I examined several individuals caught in gill nets placed 51 m beneath the surface of Lake Ontario near Picton. Schorger (1947) reported Oldsquaws caught in nets set up to 68 m deep. As a result of the bird's diving ability perhaps the total food supply of a pond is available to this species before a significant amount of the surface ice has melted.

In species of territorial birds behavior of this type is of obvious advantage to the territorial owners and their offspring. Each territory might provide a food supply, courtship area, nest site and in addition satisfy further requirements. Whether breeding pairs of birds defend territories of such dimension as to ensure adequate food for their young (Lack 1966b) is unknown. It is conceptually difficult to think of a territory in which drake courtship rarely occurs and wherein the female of a pair seldom nests. Oldsquaw territories are not lek areas and are apparently not defended for their food value. Indeed, Oldsquaw territorial behavior may be unique among nearctic waterfowl.

DISPLAYS

Descriptions of male displays.—Oldsquaws display (Fig. 12) in a variety of situations including drake-drake encounters, drake-duck encounters, before and after copulation, and in other less easily defined contexts. Although specific constellation (but not specific sequences) of displays may be performed in most of these situations, the frequency of occurrence varies.

(a) Lateral Head-shaking (LHs).—The most frequently performed display of courting males, this is accompanied by repetitive vocalizations that may be represented phonetically as "ahr-ahr-ahroulit" or "urk-urk- . . . urk." The head is rapidly shaken from side to side, suggesting the comfort movement of shaking water from the bill. This display is most striking in bright sunlight because the white back of the head flashes alternately with the dark face patch and is visible at a distance of 150 m.

(b) Bill-tossing (Bt).—This is a frequently described display. The head is lifted and immediately thrown back, remaining about half way down the back but not touching it. After a slight pause the head is returned to its original position. A modified form of Bill-tossing also occurs in flight, although typically performed by swimming birds. This display is accompanied by the

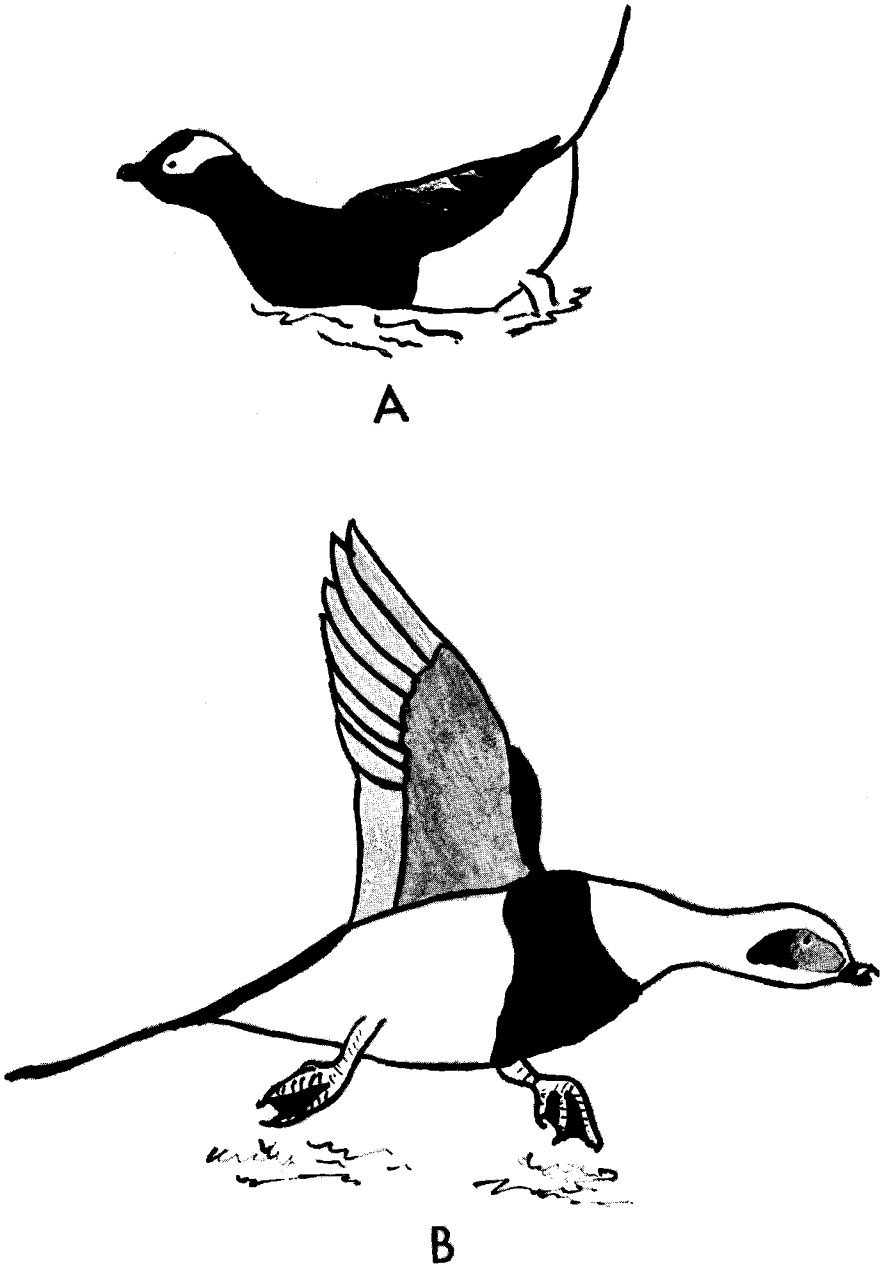

Figure 12. Characteristic postures of male Oldsquaws. A. Rear End Display; B. Pursuit posture.

"ahr-ahr-ahroulit" call, the first two syllables being uttered before the head is brought back, the "ahrou-" segment, as the neck is extended backward fully, and the last syllable, during the forward movement. The bill remains slightly open as its arcs forward and downward.

(c) Rear End Display (RE).—This is a rare display associated with the distinctive "a-oo, a-oo, a-oo-gah" call in which the movement commences with an alert posture, the head elevated high above the shoulders (Johnsgard 1965). Suddenly the hindparts are lifted out of the water so that the long tail feathers as well as the white feathers about the vent are clearly visible. The rear end of the drake is not consistently oriented so as to be visible to the female.

(d) Porpoising (P).—This is a quite commonly performed display that is not accompanied by any vocalization. Johnsgard (1965) has described certain comfort movements that constitute bathing. Porpoising differs from bathing only in that no flick of the wings occurs in the former. The display is so named because of its similarity in appearance to the undulating locomotion of porpoises. No appreciable distance is travelled during its performance. Porpoising is always followed by Lateral Head-shaking and either Wing-flapping or Body-shaking.

(e) Wing-flapping (Wf).—This display is seen frequently, especially following LHs. Drakes perform two distinct types of Wing-flapping, one of which is clearly a comfort movement and is given by both sexes. In the other type the drake assumes an almost vertical attitude in which the black breast band is fully displayed.

(f) Body-shaking (Bs).—A rare display, Body-shaking is not readily distinguishable from a similar comfort movement. It often occurs as part of a display sequence including Porpoising and Lateral Head Shaking in which case its seeming irrelevance would suggest that it probably constitutes a distinct display. As with Porpoising and Wing-flapping, no consistent mutual orientation between the sexes occurs, but a statistically significant preference ($P \leqslant 0.05$) for performing facing the sun, or, on cloudy days, facing into the wind, was noted for Body-shaking, Porpoising, and Wing-flapping.

(g) Parachute Display (PD).—This rarely seen display termed "Short Flight" by Drury (1961) may be accompanied by repetitive "ahr-ahr-ahroulit" vocalization. It involves a short upward flight terminated by a stiff-winged vertical drop of from 3 to 10 m to the surface of the water, which the bird hits with a heavy splash. The display is always performed so that the black breast band is oriented toward the female.

(h) Breast Display (BD).—This rare display (Fig. 13), which is probably the one that Drury (1961) refers to as "Swaggering," is not accompanied

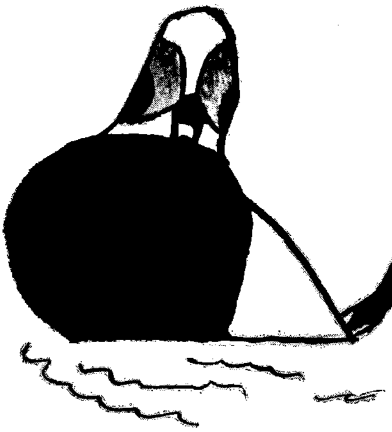

Figure 13. Adult male Oldsquaw performing Breast Display.

by any vocalization. It resembles Bridling (Johnsgard 1965) of certain pond ducks because the chest and upper breast arc upward. This posture is retained only momentarily.

(i) Turning-the-back-of-the-head (BH).—Rarely seen in Winter, this display is usually given by a paired drake. The back of the head is oriented toward the female. The display may be given in an alert posture (head elevated) but is more frequently given from the rest posture.

(j) Bill-dipping (Bd).—Bill-dipping is an important display of both males and females in flocks and is also performed by lone birds (Hull 1914). The bill is dipped toward the surface of the water, which it may or may not touch. If the bill does touch the surface, apparently no water is imbibed.

(k) Steaming (S).—This display occurs only when paired birds have become separated. It may last more than ten minutes and is always accompanied by the repetitive vocalizations "urk-ow-ow" or "ow-ow." In Steaming the head is elevated as in the alert posture, whereas the rump and tail are submerged.

(1) Chasing (C).—Males commonly swim or rush toward other males, females lunge toward both males and females, but males chase females only in certain courtship situations. Intensity of aggression ranges from pecking movements to vigorous chases over the surface and occasionally beneath the water. Although the pursuing bird seemingly chases only one individual, the entire flock usually scatters.

(m) Fighting (F).—Overt fighting is rare.

(n) Courtship Flights (CF).—Phillips (1925) described Courtship Flights. These are accompanied by repetitive "ahr-ahr-ahroulit" male vocalizations and "Kak-kak-kak-kak-" female vocalizations. Typically several drakes, usually three but sometimes as many as six, induce a female to fly. The female and pursuing males fly low over the water (1 to 3 m above the surface) in a zig-zag course. In most instances only one drake continues to follow until the female lands at which time he alights and continues courting on the water.

(o) Neck-stretching (Ns).—This display occurs rarely. The head is suddenly moved upward, as in alert posture, and slightly backward. Occasionally the movement is modified into a "Neck-jerk" (Johnsgard 1965).

Descriptions of female displays.—Females may frequently perform Bill Dipping, and occasionally Lateral Head Shaking and Porpoising. Other displays of the female include:

(a) Chin-lifting or Inciting (Cl).—Chin Lifting is the most common female display (Myres 1959). Two variations occur, both of which are accompanied by vocalizations "*rurk, urk, urk, urk, ong, ong, goo*" or "*gut-gut-goo'ah-goo'ah*" (see Drury 1961). The head is rapidly nodded through an angle of about 80 degrees. A modified form with more exaggerated nodding movements is also known.

(b) Steaming (S).—This display is similar to the Steaming of the drake and may be accompanied by Neck-stretching.

(c) Soliciting (So).—This display, which frequently precedes mounting, is described by Drury (1961), Millais (1913) and Bent (1925). A female usually faces a courting male and extends the neck and head flat upon the water while swimming toward him, turning when within a meter or two, and passing him. The male then turns and the performance is repeated.

(d) Hunch Display (Hu).—Drury (1961) has observed females hunched up, with the tail out of water and head drawn in tight to the shoulders, "as if cringing from the melee of rushing drakes around her." This display was observed only once, immediately succeeding copulation, at which time the male and female demonstrated no consistent mutual orientation.

Vocal displays given by both sexes.—Constant "gut" or "gut-gut" calls are emitted by males and females, particularly during feeding. They are so soft as to be scarcely audible except at close range. In the drake this call is of a lower pitch and considerable individual variation in duration and pitch occurs. The call is not associated with any special posture and differs distinctly from the only other monosyllabic vocalization, the alert call, "urk."

Sequence of displays in males.—As display sequences comprise individual displays, it is possible to recognize constellations of associated displays (Table 12). The commonest sequences are: Bt + Bt + Bt, LHs + LHs + LHs, P + LHs + Wf and LHs + Flying. Bt and LHs sometimes occur singly but are more commonly observed in mutually exclusive sequences.

RE is usually preceded by either Bt or LHs but not by both. Occasionally one or two RE's occur in series. Rarely, Bt, instead of LHs, precedes flying.

TABLE 12

THE ORDER OF DISPLAYS PERFORMED BY COURTING MALES (N = 60)*

		FOLLOWS											
		Bt	LHs	P	Wf	Bs	Bd	Fly	RE	PD	BH	Bd	Totals
PRECEDES	Bt	274	8	4	4	1	1	4	15	1	–	–	312
	LHs	9	355	4	51	2	3	26	10	8	–	–	468
	P	–	48	3	2	–	–	–	–	–	–	–	53
	Wf	–	1	–	–	–	–	–	–	–	–	–	1
	Bs	–	–	1	–	2	–	–	–	–	–	–	3
	Bd	–	–	–	–	–	–	–	–	–	–	–	0
	Fly	–	–	–	–	–	–	–	–	–	–	–	0
	RE	3	2	1	2	–	–	–	17	–	–	1	26
	PD	–	6	–	–	–	–	–	–	–	–	–	6
	BH	–	1	–	–	–	–	–	–	–	–	–	1
	Bd	–	–	–	–	–	–	–	–	–	–	–	0
Totals		286	421	13	59	5	4	30	42	9	–	1	870

* Figures indicate observed frequencies.

Males often perform Bt when engaging in Courtship Flights. In courtship situations in which more than one male is present Bt and LHs are mutually exclusive. That is, in any given interval, all males in the group perform Bt or all males perform LHs (T = 3.21, df = 5, $P \leqslant 0.05$).

Frequencies of displays in males.—Generally, displays observed in copulation sequences are also commonly performed by paired and unpaired males as courtship displays. The most commonly observed display is LHS, accounting for 45.7% (for paired males) to 50.0% (for unpaired males) of all displays, whereas Bt accounts for 9.9 to 31.5%, Bd for 3.7 to 15.5%, RE for 1.7 to 6.7% and P for 1.7 to 5.2% (Table 12).

Paired males display less frequently than unpaired males ($t = 1.3$, $n_1 = n_2 = 12$. $P \leqslant 0.05$—non-parametric Wilcoxon Rank Test analysis is used because the distribution of display frequencies is not normal). Paired males exhibit LHS more frequently than unpaired males ($F = 6.65$, df = 1/59. $P \leqslant 0.1$). BT is performed more often by paired than unpaired males ($F = 6.21$, df = 1/59. $P \leqslant 0.01$). Paired males perform Bd more frequently than unpaired males ($F = 7.80$, df = 1/59. $P \leqslant 0.01$). Thus, Bd may be an important display in maintenance of the pair bond. Similarly, the more common use of RE by unpaired males than by paired males ($F = 16.7$, df = 1/59. $P \leqslant 0.01$) perhaps shows that RE is important in pair-formation. The frequency of occurrence of P, Wf, Pd, BH and Bd does not differ significantly between paired and unpaired males.

Pair-forming displays.—Most drakes had found mates by mid-February but as late as 5 May some males were unpaired. It is possible that some of these apparently unpaired birds had at one time been paired but had become separated from their mates. Examination of several unpaired males in nuptial plumage revealed a higher incidence of broken wings or legs, or a larger number of endoparasites than in a random sample of paired males. These factors by increasing physiological stress may have affected the timing or occurrence of the spring molt as well as courtship.

Drakes may recognize available ducks by plumage or bill color that varies greatly with the age of the bird and also with the season. In July the bills of unpaired drakes invariably show the typical pink subterminal band whereas the bills of paired drakes are entirely black. Studies of captive birds indicate this phenomenon is not age-related. Similarly, unpaired and immature females have green-blue bills in June and July whereas bills of paired females are gray. Immature males sporadically perform Bt and LHs with accompanying vocalizations without evoking response from nearby females. Immature females are not courted by adult males and are never observed paired. Occasionally they perform modified Chin Lift movements that may also be performed by week-old downy young.

Adult males court at irregular intervals. Groups of courting males are encountered less frequently than single courting males. Courtship Flights involving one female and several males are commonly observed.

As the season progresses, an increase in male epigamic activities is seen. Bt and LHs occur more frequently in pair-formation than in pair-maintenance, as shown by a Tukey's Test of significance ($F = 4.20$, $\mathrm{df} = 5/54$. $P \leqslant 0.01$). The frequencies of all other displays remains relatively constant.

Courtship display intensity, 24 October to 20 January.—Males demonstrated low intensity courtship (0 to 8 displays per hour) toward any nearby female in early winter. All such attempts were met by female attacks. Drakes continued to display in groups throughout this period apparently displaying to each other. No pairs were observed during this period.

21 January to 1 February.—While the intensity of courtship did not increase markedly, drakes began to court individual females but usually were rebuffed by repeated attacks or female pecking movements. In spite of such response drakes repeatedly displayed only to one female. All males exhibited nuptial plumage and those females most often courted invariably had attained at least some patches of darker summer plumage on the head.

2 February to 5 February.—Display frequencies increased (16 to 24 displays per hour). Drakes courted one female solely and were no longer responded to aggressively, however the female gave no visible positive re-

sponse at this juncture. Females generally led males both on the water and in the air.

Frequently a second drake, demonstrating reduced courtship activity, would attempt to court such a female. If the interloper was not rebuffed by the female, he would follow and was always driven off by the male. Occasionally a third and fourth male appeared and the same response by the female again obtained. Finally the first drake would induce the female to fly by assuming a prolonged alert posture and performing numerous LHs. Usually the first drake and all the newcomers followed, and in the resulting Courtship Flight the female succeeded in eluding all but the original male.

6 February to 15 February.—The drake pursued the chosen duck relentlessly, in the air, over the water, and beneath its surface. Display frequencies increased (30 to 50 displays per hour) with the male assuming the alert posture and performing LHs almost continuously. Although the drakes fed occasionally, the females were seldom permitted to rest, preen, or feed.

The period in which constant chasing took place varied among drakes and occasionally lasted two or more days. Drakes attempting to display near the female were driven off by the male. Eventually the female no longer tried to escape the pursuing male but performed Cl repeatedly whenever confronted by the courting bird. This caused the drake to cease chasing. Courtship frequencies remained high during this period. These latter events signalled completion of pair-formation.

16 February to 1 March.—Courtship frequencies decreased slightly (25 to 35 displays per hour) but the proportion of mutually performed displays increased. Typically in response to a drake display, the female performed Cl repeatedly. Rotations would occur when two individuals circled toward each other on the water, while almost touching one another laterally and facing mutually opposite directions. Rotations were occasionally seen to accompany mutual displays, the most common of which included P and Ns. Courtship Flights were rarely performed, and any drake approaching the female too closely was immediately driven off by the male while the female made pecking movements toward the intruder.

2 March to 21 May.—Males performed 0 to 8 displays per hour. Those that did display directed them toward other nearby females rather than the chosen mate. Nonetheless mutual display between paired birds was noted often prior to and subsequent to copulation. The frequency of displaying was not observed to increase immediately prior to migration although the number of Pursuit Flights did increase slightly. Such an increase may be related to migratory unrest.

Pair-maintaining displays.—The members of a pair spent much of their time in close proximity, moving apart slightly only when feeding; however in aggregations of birds members of pairs were not always those birds closest together. Both members of a pair attempted to drive away any intruding drake that approached too closely, but intruding ducks were generally ignored.

Paired birds rarely displayed to one another except in copulation situations. Whenever the birds become separated, the drake always searched out the duck. In such circumstances, the drake assumed S postures which were maintained until the female was located. The duration of the pair bond is unknown. While most birds were paired by the beginning of March, others were still courting vigorously in mid-April. Once formed, the pair-bond appeared quite strong in this species. Reportedly, if the drake is killed the duck will remain by his side for several minutes (MacKay 1892) and in my experience the converse is true for the drake. Such behavior has not been reported in other species of waterfowl.

Displays associated with copulation.—Copulation was observed on six occasions. These were on 7 April, 29 April and 6 May 1968, and on 12 and 13 February and 23 April 1969. Except for the first instance, both pre- and post-copulatory behavior was seen. Copulation or attempted copulation between immatures and adults or between immatures was not observed. No instances of attempted rape were noted.

The only previous reports of copulation in the Oldsquaw are three examples by Myres (1959) and one by Drury (1961). Myres reported that prior to copulation the duck invariably assumed a prone posture, but that no other particular pre- or post-copulatory displays were noted.

Copulation usually occurred after the pair moved away from the main flock. Copulation was neither confined to any particular time of day nor to any special circumstances. In most instances there was little indication that copulation was about to occur until the female began Soliciting.

Pre-copulatory behavior comprised courtship displays including Bt, LHs, P, BD and Ns and Bt and/or LHs were pre-copulatory displays in all instances of copulation noted. Ns was less common and occurred in three instances. The number of pre-copulatory displays performed by individual males on one occasion ranged from one to ten.

Female pre-copulatory displays included Cl, Hu, LHs, P, Ns and Soliciting. Of these, Ns (4 instances) and Cl (3 instances) were the most common. LHS, a common drake pre-copulatory display, was observed on only one occasion. The female of a pair never initiated the pre-copulatory activities but appeared to be responding to the drake's movements. In all five sequences observed, the female performed at least one pre-copulatory display and the maximum number of displays performed was 9.

Copulation occurred on water and in each instance the drake grasped the nape feathers of the female while mounting. As the drake mounted the female was invariably forced under, only the head remaining above water. On three occasions violent tail shaking accompanied the apparent intromission. Intromission is reportedly rather prolonged, occasionally lasting as long as one minute (Myres 1959).

No special male post-copulatory displays were recorded, but post-copulatory behavior always included courtship displays. BT was performed in two instances as were Ns and the sequence P + LHs + Wf. LHs (not as part of a sequence), S, and BH were each observed once only. Drakes performed from one to four post-copulatory displays.

P was the most common female post-copulatory display and was performed on two occasions whereas LHs was observed only once. Ducks performed from one to five post-copulatory displays in any given instance.

Discussion of displays.—Displays in waterfowl are derived from comfort movements and "intention" movements that have subsequently become ritualized (Johnsgard 1968). Many displays that are clearly derived from comfort movements seem irrelevant when performed as courtship. Porpoising is used by males in courtship and pre-copulatory display and by females in pre-copulatory and post-copulatory display. Body-shaking has become a male courtship display and occasionally occurs in male post-copulatory activity (following porpoising). Many avian displays apparently have evolved from behavior in conflict situations where a bird is simultaneously stimulated to behave in incompatible ways. Courting males sexually attracted by females may be driven simultaneously to attack or escape from other males or females. Females sexually attracted to males may be driven to attack or escape from males and females. In female Oldsquaws Chin-lifting (or Inciting) probably represents simultaneous aggression and appeasement toward the drake and occurs in pre-copulatory display and in response to male courtship. Similarly Hunch seemingly represents conflicting stimuli of aggression and appeasement. The back and scapular feathers are ruffled and the tail is elevated and slightly spread (aggression) while the head is withdrawn into the shoulders (appeasement gesture). This display is given by females in response to male courtship and as pre-copulatory and post-copulatory behavior. Bill-dipping is another display that could result from the simultaneous tendencies to attack and appease. Conceivably a paired bird could be simultaneously motivated to attack and appease a nearby mate. More likely though, an unpaired bird upon encountering another individual might be variously motivated to attack or escape or appease. Bill-dipping is more commonly performed by paired birds than by unpaired birds.

It is generally accepted that the perception of certain external stimuli presented by one animal can increase the probability that that animal will be attacked by another. These stimuli may include aggressive gestures, specific color patterns, and body markings (Tinbergen 1959). Thus hiding certain attack-eliciting patterns can lower the probability that an animal will sustain an attack. The black, pink-banded bill of the male Oldsquaw is similarly thrust forward in attack. Turning-the-back-of-the-head, a courtship pre- and post-copulatory display that hides the bill from another individual probably has appeasement function.

Visual alarm signals in most species of waterfowl include an alert posture with head held high. McKinney (1961) concludes that the Head-turn display of some eiders evolved from the habit of looking back alternately with one eye then the other toward some approaching threat source. Similar side-to-side head movements could result in Lateral Head-shaking, a common male Oldsquaw display. Alternatively, Lateral Head-shaking could be an apparently irrelevant displacement Flicking-water-off-the-bill resulting from simultaneous attack and escape stimuli. Lateral Head-shaking is performed by courting males and as pre- and post-copulatory behavior.

Rear End Display, unique among waterfowl, was probably derived from two separate movements. The bowing forward of the head may be a modified Bill-dipping motion. The subsequent lifting of the posterior part of the body vertically out of the water suggests movements performed by both sexes immediately prior to diving. The lifting of the tail may have evolved as a modification of the diving movement.

McKinney (1961) has concluded that several visible displays of eiders have apparently evolved to facilitate those vocalizations accomplished by a complex contortion of certain tracheal structures. During the Head-throw display of Common Golden-eyes (*Bucephala clangula*) the trachea is momentarily extended and then returns to normal position (Johnsgard 1968). This extension apparently aids the production of the most common vocalization of that species. Bill-tossing of adult male Oldsquaws, a display in which the trachea is similarly extended momentarily, may be related functionally to the complex "ahr-ahr-ahroulit" vocalization.

In the Oldsquaw, morphology and behavior ensure that immature birds do not pair. Adult plumage is not attained until the second winter (Phillips 1925). Immature males do not possess any of the distinctive plumage patterns of adult males. Whereas most immature males by 1 May are capable of performing all the visible displays of adult males, they do not produce the corresponding audible displays of adults. Bill-tossing performed by immature males is accompanied by distorted "ahr-ahr-ahroulit" vocalizations. Immature males performing Rear End Display do not produce any accompanying vocalization.

Sonograms of Oldsquaw vocalizations show that most calls range between

0.4 and 1.4 seconds in duration. Five renditions of the "ahroulit" portion of the "ahr-ahr-ahroulit" vocalization show a high degree of individual variation. A similar individual variation was visible in audiospectrograms of all other vocalizations. Marler (1960) has suggested that detailed changes in pitch can express individuality among several renditions of the same species-specific vocalization. Individual variation in bird song occurs in Chipping Sparrows (*Spizella passerina*) (Marler and Isaac 1960) that have only one song, as well as in Mistle Thrushes (*Turdus viscivorus*) (Isaac and Marler 1963) that have large repertoires of vocalizations. Borror (1961) has concluded that two individuals seldom produce identical songs. As Oldsquaws are nocturnal migrants voice communication between paired birds probably lowers the possibility of them becoming separated from each other during spring migration. Mutual vocal recognition was consistently demonstrated by a pair of captive adult Oldsquaws that constantly communicated with each other nightly throughout the spring of 1969. Yet nocturnal vocalizations emitted by another unpaired adult drake evoked no response from the paired duck.

OTHER ASPECTS OF REPRODUCTIVE BIOLOGY

Number of adults forming pairs.—Photographs of flocks of Oldsquaws taken twice weekly throughout the winter of 1968–69 facilitated determination of sex ratios. Adult males comprised 11.4% of all Oldsquaws counted in November and December whereas adult females represented 29.4%. In January the proportion of adult males increased significantly ($t = 4.23$, $df = 9$. $P \leqslant 0.01$) and comprised 31.4% of the winter population of the species, compared to the adult female proportion of 39.8%. The January population of adult females was not significantly greater ($t = 1.86$, $df = 9$. $P \leqslant 0.05$) than the December population. These data seemingly support the suggestion by Phillips (1925) that adult males migrate to the wintering grounds later than adult females and immatures of both sexes. No further change in the relative proportion of the sexes occurred.

By 15 February at least 22% of all Oldsquaws were paired, representing 35% and 29% of all adult males and females, respectively. By 16 March 34% of the population was paired (57% and 46% of the adult males and females, respectively). By 30 April 73% of the adult males were paired with 57% of the adult females (44% of the total population).

Endurance of pair bonds.—Unlike most other ducks Oldsquaws possibly pair for more than one breeding season (captive pairs reform each year). On the study area one pair of Oldsquaws was captured on the same lake in two consecutive years. There does not appear to be any reason why pairs could not reform in consecutive years, and other reformed pairs may have been present but remained undetected (i.e. the drakes had not been banded in previous years). In this species considerable flock shuffling probably occurs during the fall migration. Yet at least two adult Oldsquaws (one drake) captured and banded at Toronto, Ontario, were recaptured in a subsequent year at the same location (i.e. at the exact site as before) and both passed the entire winter of 1970–71 in the Toronto area. On the basis of feeding behavior, plumage characteristics, and vocalization peculiarities, I suspect that at least three additional drakes returned to the same site to feed daily throughout the winter of 1969–70 and 1970–71 (the feeding location made capture for banding impossible). It thus appears reasonable to assume that at least some Oldsquaws winter in the same general area, if not at the same loaction in consecutive years. If so it is highly likely that pairs could reform year after year even if the members of the potential pair migrate separately each fall, as long as both winter at the same location in consecutive years.

Only two of over 100 adult drake Oldsquaws banded in the study area were subsequently recaptured, although one of these was recovered in three consecutive years at the same pond. Very few adult drakes were banded, and it appears probable that had a detailed study of banded drakes been conducted, a larger number of banded individuals would have been recovered in subsequent years. If some adult drakes do home and if pair-formation does occur on the wintering grounds, then in every instance when a drake returns to a specific pond he must be paired with the same individual as in the previous year (assuming that drakes follow their mates from the wintering grounds to the breeding ponds). These circumstances would result in the emergence of a localized breeding population. At least some drakes do not always return in subsequent years to ponds used previously. Two drakes banded as adults at Yamal Peninsula in northern Siberia (72° N, 72° E) in August 1933 and 1934, respectively, were recovered, one in Norway in July 1938, and the other in Sweden in June 1935 (Boyd 1957).

Fidelity to nest site.—Some adult females return to the exact nest site occupied in a previous year. However, it must not be inferred that this phenomenon occurs only in those instances in which nests were successful. Hilden (1965) suggests that nest site fidelity occurs more likely in the absence of predation or other disturbance. The three females that returned to an exact nest site used previously had had successful nests in the previous year. One female nested on the same small island occupied the previous year even though the nest had been destroyed in the former year. Another female, whose unsuccessful nest was located on an island, nested on the mainland at the same pond in the next year. Success or failure of a previous nest clearly does not determine the nest site chosen in any given breeding season.

It is probably advantageous for birds to breed in localities with which they are familiar (Lack 1954).

Nest locations.—Evans (1970) noted nest associations between Oldsquaws and Arctic Terns at Churchill, but his sample of Oldsquaw nests was not random. In this study, among island-nesting Oldsquaws, a significant association between the two species was observed, but on the mainland a significant disassociation occurred. Koskimies (1957) suggested that Oldsquaws actively select tern colonies in which to nest as a result of imprinting (i.e. ducklings imprinted to nearby terns in the nest vicinity). Oldsquaws in my study have invariably completed or partially completed their clutches prior to the arrival of terns on the breeding grounds, and in most instances Oldsquaw clutches were complete before terns initiated nesting. Inasmuch as Oldsquaws nested prior to tern arrival in most instances, it is unlikely that they chose nest sites on the basis of visual or auditory recognition of terns.

Oldsquaw nests were frequently located at traditional locations. Only 7 of 79 islands located in the study area had Oldsquaw colonies in each year of the study; 11 had nests in at least one year, 16 had nest cups of previous years and 45 had no evidence of previous occupation by Oldsquaws. Evans (1970) noted concentrations of nest cups of this species on certain islands containing tern colonies and suggested that once a particular female Oldsquaw became established near a colony of terns, she might return in subsequent years regardless of the presence of terns. He noted many instances in which there were females nesting in tern colonies in one year, whereas in the next year these same individuals nested in locations with no terns nearby. Conversely some females that had nested at ponds where terns were not resident nested in subsequent years on islands containing tern nests. Hence it is doubtful that female Oldsquaws can become established, perpetual tern-colony nesters.

Oldsquaw nest loss by predation on islands with nesting Arctic Terns was not significantly greater than without the terns. The positive association between nesting Oldsquaws and nesting Arctic Terns is not a relationship significantly beneficial to Oldsquaws. In 1971, an entire island colony of Oldsquaw nests was destroyed by two Parasitic Jaegers, although two pairs of Arctic Terns nested on the same island (the tern nests were also destroyed). On two occasions I observed the jaegers walking about on this island, and although the terns swooped frequently toward the predators, the latter seemed undisturbed. Possibly some Oldsquaws might derive benefit from nesting in large colonies of Arctic Terns, but the observed positive nesting association between the two species is probably a result of similar habitat preferences, specifically overlapping nest site requirements.

MAJOR FACTORS INFLUENCING PRODUCTION

Weather.—Inclement weather and cool temperatures usually delay laying in waterfowl. Sowls (1955) observed that Mallards and Pintails delayed egg laying by as much as two weeks in years when 15 April to 30 May mean temperatures were below normal. Low (1945) noted that Redheads nested subsequent to the first warm weather in April or early May. At Churchill, 1969 May temperatures were unusually cold, and in that year Oldsquaws delayed nesting by about 10 days. Cooch (1965) reported that during inclement weather Common Eiders almost ceased egg laying. Interrupted egg laying also occurs in many other species of Arctic waterfowl, but it is not always regulated solely by inclement weather. No instances of interrupted egg laying were observed in Oldsquaws in this study.

I have suggested that a minimum possible breeding period is available to Oldsquaws at Churchill. In 1969 when nesting was delayed, breeding ponds remained unfrozen later than normal. Had these ponds frozen over earlier, late hatching Oldsquaws might not have survived. In most years it would be difficult for this species to delay laying and yet successfully rear a brood. Renesting does not occur in Oldsquaws. Yet in the one cold year of this study fewer eggs hatched from each clutch, and the resulting smaller broods seemed to be more efficiently brooded.

The effect of local weather conditions on incubated clutches in waterfowl is not well documented. Gollop (1954) reported that cold weather and snow in May did not adversely affect Mallard production in Saskatchewan, but Cooch (1965) found that adverse weather conditions could produce fluctuations in the magnitude of egg loss in Common Eiders. Miller and Collins (1954) observed that excessive rainfall was an important cause of egg loss in Redheads, but snow, heavy rainfall or low temperatures did not adversely affect nesting success in several species of prairie waterfowl (Keith 1961). In the present study it was similarly found that inclement weather did not significantly affect egg loss (although severely cold temperatures did not occur). This observation possibly correlates with the fact that Oldsquaws breeding at Churchill comprise a more or less isolated, stable population seemingly adapted to local conditions (including limited weather fluctuations).

Predation.—Most recent studies have demonstrated that nest predation is the chief cause of egg loss in waterfowl. Similarly in Oldsquaws of this study predation was the main factor contributing towards unsuccessful nests. Nests were frequently destroyed in traditional locations whereas nests located nearby were successful. In the study period one colony was completely destroyed annually, but another situated 5 km northeast of the first was never molested. Almost invariably colonial predation was caused by avian predators, and thus it might be concluded that certain avian predators hunted more intensively in traditional areas. It is not known whether individual avian predators returned to the study area annually.

Nest predation did not appear to be strictly regulated by the degree of nest concealment. Relatively exposed nests (in dry upland) were frequently destroyed and well concealed nests (in marshland) were rarely destroyed. An inconsistently large proportion of apparently totally concealed nests (those located beneath dwarf spruce trees) were lost to predators, specifically to Parasitic Jaegers. On two occasions I observed two Parasitic Jaegers land on large islands containing Oldsquaw nests, and in both instances the birds systematically approached every spruce tree growing on each island. In every case they walked around each tree several times and occasionally moved to lower boughs, apparently searching for nests. Frequently, especially on islands, nests located under spruce trees were destroyed before those located at other sites. Possibly jaegers not only search traditional areas but also examine, perhaps more carefully, certain potential nest sites (i.e. beneath the few spruce trees on islands). It would obviously be impractical for these birds to search beneath the thousands of small spruce trees on the mainland as only a slight proportion of these conceal nests. Hence, the disproportionately high rate of destruction of seemingly well concealed Oldsquaw nests (on islands) might result from specific feeding behavior of Parasitic Jaegers.

About 58.9% of all Oldsquaw nests were successful in this study. Keith (1961) summarized recent studies of hatching success in waterfowl (involving over 3,500 nests) and reported that 56% of "diver" (presumably *Aytha* spp.) nests were successful as compared to 39% for dabblers (*Anas* spp.). In his own study the same author reported that 31% of scaup nests hatched successfully. Lokemoen (1966) noted a hatching success of only 10.2% in Redhead eggs in Montana. The figure was further reduced (to 9.9%) when Redhead eggs laid in nests of other species were not included in the data. The most important cause of egg loss in Redheads was desertion (Lokemoen 1966) but predation also accounted for a large percentage. Although flooding may be an important cause of egg loss in certain species of diving waterfowl, no instances of flooded Oldsquaw nests were observed in this study. Egg loss due to predation appears to be greater for scaup and possibly Redheads than for Oldsquaws. The Striped Skunk (*Mephitis mephitis*) is an efficient destroyer of scaup and Redhead nests and accounts for the majority of eggs lost by those species (Keith 1961, Lokemoen 1966). The Parasitic Jaeger, the major destroyer of Oldsquaw eggs, may not be as proficient as the Striped Skunk in locating nests, especially mainland nests.

Cooch (1965) observed that only about 15% of Common Eider nests were destroyed by predators. In Oldsquaws about 27.8% of all nests were predator-destroyed. Although Common Eiders tend to remain at the nest more or less continuously (Cooch 1965), Oldsquaws frequently leave their nests, especially on warm days, for several hours. Assuming that a temporarily deserted nest is more susceptible to destruction by predators than a nest with the female present (given the predator is only an egg predator and will not kill the adult female), the differing egg losses due to predation might have resulted from female Oldsquaws' prolonged absences from their nests.

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SUMMARY

The breeding biology and behavior of the Oldsquaw were investigated at Churchill, Manitoba, from 1968, through 1971. The breeding population in the study area comprised about 45 pairs of Oldsquaws in each year and these always arrived between 1 June and 23 June. The birds invariably were paired on arrival. Several nonbreeding individuals, mostly subadults and adult females, were also resident in the study area until July of each year. Whereas adult drakes have always left the study area by 30 July, some ducks and broods remained until 31 August, in some instances. Mortality of adult drakes on the breeding grounds averaged 1.5% annually whereas the female mortality was nil.

In each year of the study, individuals were captured, banded, and released. Of these, 13 females and two males were recaptured in the study area in subsequent years. Several females nested at the same nest site as in a previous year. One drake was captured in four consecutive years on the same pond. Adult drakes were intraspecifically territorial, although ducks took no active part in territorial defense. I suggest that territoriality functions to limit local breeding population density in this species.

Courting males perform Lateral Head-shaking (LHs), Bill-tossing (Bt), Rear End Display (RE), Porpoising (P), Wing-flapping (Wf), Body-shaking (Bs), Parachute Display (PD), Breast Display (BD), Turning-the-back-of-the-head (BH), Bill-dipping (Bd), Steaming (S) and Neck-stretching (Ns). Of these, Bill-tossing, Rear End Display and Steaming are accompanied by unique vocalizations and Bill-tossing and Rear End Display are species-specific visible displays. The female performs Chin-lifting (Cl), Soliciting (So), Hunch (Hu) and Steaming (S).

Bill-tossing is the most common drake pre-copulatory display whereas females most frequently perform Chin-lifting. Lateral Head-shaking is the most common post-copulatory display of both sexes. Courtship behavior in paired males is limited to one or two displays per hour. By contrast non-paired males may perform 30 to 50 displays per hour. Bill-tossing and Lateral Head-shaking are the most frequently preformed individual displays. Occasionally, consistent sequences of two or three individual displays are performed.

The Oldsquaw is one of the first species of waterfowl to form pairs, and by mid-February about 40% of the adult drakes are paired. Early pair-formation is encouraged by the shortness of the Arctic breeding season and by the prolonged post-nuptial molt, which occurs subsequent to pair-formation.

The locations of 95 nests are described. In some instances, especially on islands, nests were clustered and other nests were isolated. One instance of intraspecific parasitism was recorded. There was no significant difference between the number of individual nests on islands as compared with mainland nests, and 58.9% of active nests were found on islands. The species tended to nest in traditional locations, especially on traditional islands. Nest site tenacity was apparently not related to previous success or failure at a specific site. Whereas certain islands had active Oldsquaw nests in each, 45 out of 79 islands showed no evidence of active or previous Oldsquaw nests. Mainland nests were significantly better concealed than island nests. Although some nests were situated close to water, over 80% were within 6.1 m of the edge of a pond or lake. On islands there was a positive association between Oldsquaw nests and Arctic Tern nests, whereas on the mainland a significant disassociation of the nests of these two species was observed. There was no significant difference between Oldsquaw nest loss by predation on islands with active Arctic Tern nests as compared to islands where terns were not resident, but this study alone is equivocal on this point. I suggest that the observed positive association of the two species probably results from similar nesting requirements and preferences on islands and isolated peninsulas.

The nest site was selected by the female and the nest was constructed immediately prior to the deposition of the first egg. Eggs were laid at intervals of about 26 hours until the clutch was complete. The average clutch size was 6.8 eggs. Nearly 20% of the eggs of this species were nonviable. From 1968 to 1971, the mean dates of clutch commencement were 12 June, 23 June, 11 June, and 9 June, respectively, and it was found that severe May temperatures could significantly delay nest initiation.

Egg loss apparently was not related to weather variations. Predation was the major cause of nest loss (26.4%), and the Oldsquaw nests located on islands were as frequently destroyed as mainland nests. Nests located on certain specific islands were destroyed each year and nests located on certain other islands were always successful.

The incubation period of Oldsquaw eggs was 26 ± 0.8 days and about 58.9% of all eggs hatched successfully. The time required for each clutch to hatch (between the hatching of the first and last eggs) varied considerably among clutches but about 30% of all clutches required 48 hours to hatch completely.

The territorial behavior of 10 adult male Oldsquaws was investigated. Although adult males were intraspecifically territorial, females took no active part in territorial defense and in most instances nested in loose colonies.

I suggest that a maximum number of suitable territories exists and that at male densities greater than this, some males are prevented from establishing territories by resident males, whereas others may defend less preferred territories, perhaps in less suitable habitat. As the suitability of the habitat declines, the potential for high productivity probably decreases. The highest reproductive success should occur in preferred habitats. Territorial behavior in this species seems to limit local breeding population size.

LITERATURE CITED

ALISON, R. M. 1970. The behavior of the Oldsquaw (*Clangula hyemalis* Linnaeus) Aves: Anatidae in winter. Unpublished M.S. thesis, Toronto Univ. Toronto.

ALISON, R. M. 1972. The breeding biology of the Oldsquaw (*Clangula hyemalis* Linnaeus) at Churchill, Manitoba. Unpublished Ph.D. dissertation, Toronto, Univ. Toronto.

ANDERSON, W. 1956. A waterfowl nesting study in the grassland, Merced County, California. California Fish and Game 42: 117–130.

ANDERSON, W. 1957. A waterfowl nesting study in the Sacramento Valley, California, 1955. California Fish and Game 43: 71–90.

BENT, A. C. 1925. Life histories of North American wildfowl, order Anseres, vol. 2. U.S. Natl. Mus. Bull. 130: 32–50.

BERGMAN, G., AND K. C. DONNER. 1964. An analysis of the spring migration of the Common Scoter and the Long-tailed Duck in southern Finland. Acta Zool., Fennica 105: 1–59.

BIRCH, L. C. 1960. The genetic factor in population ecology. Amer. Naturalist 94: 5–24.

BOYD, H. 1957. Movements of marked sea and diving ducks in Europe. Wildfowl Trust, Ann. Rept. 12.

BROWN, J. L. 1969. Territorial behavior and population regulation in birds. A review and re-evaluation. Wilson Bull. 100: 371–376.

COOCH, F. G. 1965. The breeding biology and management of the Northern Eider (*Somateria mollissima borealis*) in the Cape Dorset area, Northwest Territories. Wildl. Mgmt. Bull. Ser. 2(10).

COTTAM, C. 1939. Food habits of North American diving ducks. U.S. Dept. Agric., Tech. Bull. 643.

DELACOUR, J. 1959. The waterfowl of the world, vol. 3. London, Country Life Ltd.

DRURY, W. H. 1961. Observations on some breeding water birds on Bylot Island. Canadian Field-Naturalist 75: 84–108.

EARL, J. P. 1950. Production of Mallards on irrigated land in the Sacramento Valley, California. J. Wildl. Mgmt. 14: 332–342.

ERSKINE, A. J. 1961. Nest-site tenacity and homing in the Bufflehead. Auk: 389–396.

ERSKINE, A. J. 1966. Cape Breton Island waterfowl studies. Canadian Wildl. Serv. Spec. Rept. '66.

EVANS, R. M. 1970. Oldsquaw nesting in association with Arctic Terns at Churchill, Manitoba. Wilson Bull. 84: 383–390.

FOLEY, D. 1954. Survival and establishment of waterfowl released as ducklings. New York Fish and Game J. January 1954: 206–213.

FRETWELL, S. D., AND H. L. LUCAS. 1969. On territorial behavior and other factors affecting habitat distribution in birds. Theoretical development. Acta Biotheoret. 19: 16–36.

GODFREY, W. E. 1966. The birds of Canada. Natl. Mus. Canada Bull. No. 203.

GOLLOP, J. B. 1954. Waterfowl breeding ground survey in Saskatchewan 1953, special study area Kindersley-Eston. Waterfowl populations and breeding conditions–summer 1953. U.S. Fish Wildl. Serv. and Canadian Wildl. Serv., Spec. Ser. Rept.–Wildl. 25: 65–73.

HILDEN, O. 1965. Habitat selection in birds. Ann. Zool. Fennica 2: 53–75.

HULL, E. D. 1914. Habits of the Oldsquaw (*Harelda hyemalis*) in Jackson Park, Chicago. Wilson Bull. 26: 116–123.

ISAAC, D., AND P. MARLER. 1963. Ordering of sequences of singing behavior of Mistle Thrushes in relationship to timing. Anim. Behav. II: 179–188.

JEHL, J. R., JR., AND B. A. SMITH. 1970. Birds of the Churchill region, Manitoba. Manitoba Mus. of Man and Nature, Spec. Publ. No. 1.

JOHNSGARD, P. A. 1965. Handbook of waterfowl behavior. Ithaca, New York, Cornell Univ. Press.

JOHNSGARD, P. A. 1968. Waterfowl: their biology and natural history. Lincoln, Univ. Nebraska Press.

KEITH, L. B. 1961. A study of waterfowl ecology on small impoundments in southeastern Alberta. Wildl. Monogr. 6, October 1961.

KORTRIGHT, F. H. 1953. The ducks, geese and swans of North America. Harrisburg, Pennsylvania, Stackpole.

KOSKIMIES, J. 1957. Terns and gulls as features of habitat recognition for birds nesting in their colonies. Ornis Fennica 34: 1–6.

LACK, D. 1954. The natural regulation of animal numbers. Oxford, Clarendon Press.

LACK, D. 1966a. The significance of clutch-size in waterfowl. Wildfowl Trust Ann. Rept. 18.

LACK, D. 1966b. Population studies of birds. Oxford. Clarendon Press.

LARSON, S. 1960. On the influence of the arctic fox (*Alopex lagopus*) on the distribution of arctic birds. Oikos 11: 276–305.

LOKEMOEN, T. 1966. Breeding ecology of the Redhead duck in western Montana. J. Wildl. Mgmt. 30: 668–681.

LOW, J. B. 1945. Ecology and management of the Redhead, *Nyroca americana*, in Iowa. Ecol. Monogr. 15: 35–69.

MACKAY, G. H. 1892. *Clangula hyemalis* in New England. Auk 2: 330–337.

MARLER, P. 1960. Bird songs and mate selection. Pp. 348–367 *in* Animal sounds and communications (W. E. Lanyon and W. V. Tavolga, Eds.). Publ. No. 7, Washington, D.C., Amer. Inst. Biol. Sci.

MARLER, P. AND ISAAC, D. 1960. Physical analysis of a simple bird song as exemplified by the Chipping Sparrow. Condor 62: 124–135.

McKinney, F. 1961. An analysis of the displays of the European Eider (*Somateria mollissima mollissima* Linnaeus) and the Pacific Eider (*Somateria mollissima v. nigra.* Bonaparte). Behavior, Suppl. 7.

Millais, J. G. 1913. Brit. Diving Ducks. London, Longmans, Green.

Miller, A. W., and B. D. Collins. 1954. A nesting study of ducks and coots on Tule Lake and Lower Klamath National Wildlife Refuges. California Fish and Game, 40: 17–37.

Myres, M. T. 1959. The behavior of the sea ducks and its value in the systematics of the Tribes Mergini and Somateriini, of the Family Anatidae. Ph.D. dissertation, Univ. Vancouver, British Columbia.

Phillips, J. C. 1925. The natural history of the ducks, vol. 3. Boston, Houghton Mifflin Co.

Phillips, J. C. 1928. The crow in Alberta and the work of the American wild fowlers. Trans. North Amer. Game Conf. 15: 146–151.

Polunin, N. 1967. Introduction to plant geography. London, Longmans.

Ryder, J. P. 1969. Nesting colonies of Ross' Goose. Auk 86: 282–292.

Salomonsen, F. 1950. The birds of Greenland. Copenhagen, Ejnar Munksgaard.

Schorger, A. W. 1947. The deep diving of the loon and Oldsquaw and its mechanism. Wilson Bull., 59: 151–159.

Scoggan, H. J. 1959. The native flora of Churchill, Manitoba, with notes on the history, geology, and climate of the area. Guide book, Natl. Mus. Can.

Sowls, L. K. 1955. Prairie ducks. Washington, D.C., Wildl. Mgmt. Inst.

Steel, P. E., P. D. Dalke, and E. G. Bizeau. 1956. Duck production at Gray's Lake, Idaho, 1949–1951. J. Wildl. Mgmt. 20: 279–285.

Sutton, G. M. 1932. Notes on molts and sequence of plumages in Oldsquaws. Auk 49: 42–51.

Tinbergen, N. 1959. Comparative studies of the behavior of gulls (Laridae): a progress report. Behavior 15: 1–70.

Vermeer, K. 1968. Ecological aspects of ducks nesting in high densities among larids. Wilson Bull. 80: 78–83.

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