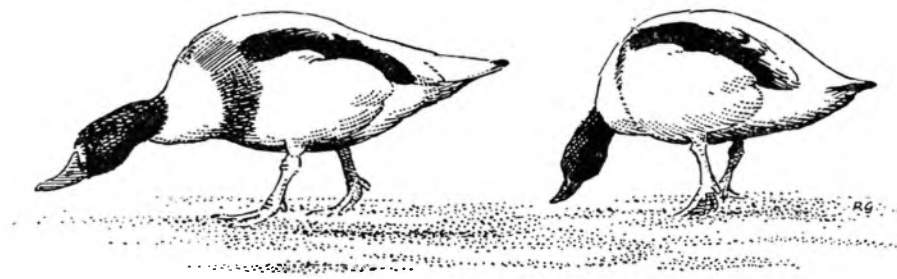

The moult migration

FINN SALOMONSEN

Introduction

The flight- and tail-feathers are shed simultaneously in wildfowl, auks, divers, rails and a number of other groups, thus rendering the birds flightless and rather helpless for a period each year. The birds withdraw at this critical time to special areas where they are safe, usually to secluded places in dense marshes, lakes, coastal waters or the open sea. The main requirements of such areas are sufficient food, safety from predation, and (in water birds) an adequate depth of water. If these conditions are not met on the breeding ground or its immediate vicinity, the birds make a pre-moult shift to areas further away. This has in some cases resulted in a mass transfer of individuals in a fixed direction towards localised moulting places. This so-called 'Moult Migration' is particularly highly developed in wildfowl.

A comparative analysis of our recent, and incomplete, knowledge of moult migration has hitherto not been attempted.

History

The existence of moult migration was unknown until 30-40 years ago, but in recent years many investigations have been carried out. The first to draw attention to this form of migratory movement was the Swedish zoologist Sven Ekman, who in 1922 described it in the Eider*, the Mute Swan and the Lesser White-fronted Goose (Ekman 1922). He called it *ruggnings-flyttning* in Swedish, and this term is now used in all languages (English: *moult migration*, French: *migration de mue*, German: *Mauserzug* Danish: *fældningstræk*). The importance of this phenomenon was not realised until 10-20 years later. In 1937-39 the Russians Vuczeticz and Tugarinov published the results of wildfowl ringing in the Soviet Union and demonstrated that enormous numbers of dabbling ducks originating from northern Europe and Asia, gathered in the Volga delta in order to moult their flight-feathers there. Subsequently, Stresemann (1940) described a similar phenomenon from a lake on the border between Tibet and Sikkim where, at an altitude of about 4,500 m., a number of dabbling ducks and Tufted Duck shed their flight-feathers after a migration of about 2,000 km. from their breeding places in northern Siberia.

Not until 1942, however, was the moult migration of a species in Europe described, i.e. that of the Shelduck (Hoogerheide and Kraak 1942). In North America no real movements to moulting areas were described until well after 1950.

General Remarks

In the best developed form, moult migration is from the breeding place to a special moulting area, common to a large number, in some cases hundreds of thousands, of birds. When the flightless stage is over the ordinary autumn migration to the winter quarters starts. This form of moult migration cannot be regarded as the first part of the autumn movement for three reasons. Firstly, the flight direction is often different, some-

* Scientific names will be found in the section dealing with individual species.

times the opposite of the autumn migration. Secondly, certain sections of the breeding population, usually the adult females, do not participate in the moult migration. Thirdly, the sharply circumscribed geographical situation and enormous population density in the moulting area are something quite unique. In the winter quarters the birds scatter over larger areas. In populations with typical moult migration the individuals adhere to a rigid schedule, which is followed regularly year after year. In other populations the system is less clear or only slightly developed.

The timing of the moult migration is dependent on that of breeding. When in late springs or unfavourable summers breeding is postponed, the moult migration falls correspondingly late, as demonstrated in various dabbling ducks and diving ducks in America (Hochbaum 1955) and in Europe (Bezzel 1964). The moult migration may in certain years be so delayed that the birds are forced to stop and shed their flight-feathers *en route*. This has been described in the Shelduck, which occasionally moults in Kent on its way to Germany (Eltringham and Boyd 1960), and in Steller's Eider, which sometimes moults in eastern Siberia on its way to Alaska (Jones 1965).

Some species (or populations) of ducks have no moult migration. The males remain in the breeding place and withdraw to a quiet, remote spot in a marsh or lake, sometimes within their own breeding territory. Here they carry out the wing-moult solitarily or in small groups, but never in large flocks. An example is the Pintail in Denmark, and, probably, in the whole of Scandinavia. At any rate I have observed solitary wing-moult in Swedish Lappland. This also illustrates the geographical variation in moulting behaviour, for this species performs extensive moult migrations in Russia and northern Asia and also in America.

Some species undergo wing-moult in the winter quarters and mass congregations may develop. In others, for example Brent Geese, immature birds may halt on the spring migration for this purpose.

It is possible therefore to distinguish between the following situations during the post-nuptial moult when an individual may shed the flight- and tail-feathers:

A. In the breeding territory or in the immediate surroundings.

B. During the ordinary autumn migration, or immature birds during spring migration.

C. In the winter quarters.

D. In a special area which is reached through a pre-moult migration starting in adult birds from the breeding range and in immature birds often directly from the winter quarters or from intermediate stations during spring migration.

It is clear that only in case D is it possible to speak about a genuine moult migration.

The size of the moulting flocks is another important character of the moult migration. Individuals may during the post-nuptial moult shed their flight- and tail-feathers:

I. On their own or in very small groups.

II. Assembled in comparatively small flocks, usually no more than a few hundred, occasionally up to a thousand birds.

III. Gathered in huge aggregates, in extreme cases numbering more than a hundred thousand birds.

All combinations of the classes A—D and I-III occur, except that the combination A III is found only in immature birds. If falling within class D, individuals belonging to all three groups I-III may be said to carry out a moult migration, but type D III represents moult migration as generally understood.

An obvious question is what purpose is served by concentrating in huge flocks in a special moulting area, sometimes situated more than 3,000 km. from the breeding area, when in other areas the same species can perform the moult on the breeding ground, solitarily or in small groups? It is evident that both forms of behaviour have certain advantages. In northern countries with short summers and early onset of cold the birds may run a considerable risk if they moult their flight-feathers on the breeding ground. Under such conditions selection for development of moult migration must be strong because it is, obviously, advantageous to transfer the time of wing-moult to areas with a milder climate situated nearer to the winter quarters, or even to postpone it until after the arrival in the winter quarters. There is also a high selective advantage when a part of the population (adult males and/or non-breeders) perform a moult migration, leaving the breeding areas and their food resources for the female and the ducklings. It is probable that in many (or most) species the ultimate cause of the development of moult migration has been a potential shortage of food on the breeding grounds.

It is possible that the enormous concentrations of individuals within a small moulting area may serve some social function (Wynne-Edwards 1962). Traditions, which play an important role in the ecology of wildfowl, may also be of significance in mass moult gatherings. Such traditions need not even be genetically fixed, although they evidently must be so in populations with a pronounced moult migration. In such populations the direction of the moult migration and the position of the moulting area are rigidly determined and the same area is used by the birds one year after another. The biological reason for choosing this particular area may date back to a distant past, the original migration pattern being maintained where it is still advantageous. In other species or populations the situation is more unstable. The populations then segregate in a number of moulting areas, each of which is frequented by a comparatively small number of birds, at most a few thousand individuals. Such minor concentrations may move, suddenly or gradually, to another place for no apparent reason.

A well-documented case of locality change has been demonstrated at the Ismaninger Reservoir in Bavaria. A small number of dabbling and diving ducks traditionally underwent wing-moult in this lake area, but when in 1955 the water surface was raised 2 m. artificially the number of moulting diving ducks increased considerably in the subsequent years. The Red-crested Pochard from 10-90 to over 300, the Tufted Duck from 100-200 to about 2,000, and the Pochard from 500-1,000 to no less than 9,000-11,000 individuals (Bezzel 1964).

In the majority of dabbling and diving ducks the post-nuptial (eclipse) moult in the males is initiated on the breeding ground. In the Mallard in Denmark the first body-feathers are shed as early as the middle of April. In species with moult migration the males leave the breeding place at a certain time, usually solitarily, but as a rule soon gather in small flocks. These gatherings increase gradually to some hundreds and occasionally to more than a thousand. At the same time the flocks move to intermediate resting places. During this movement the males perform the greater part of the eclipse moult, excepting the wing-moult which in the dabbling ducks constitutes the final stage. When this stage is imminent the birds leave for the moulting area together. The biggest moulting flight ever described was observed at Mud Lake, Idaho, where during one night (5th August) no less than 52,000 dabbling ducks, belonging to six species, arrived (Oring 1964). The postponement of the final flight until shortly before the wing-moult makes it possible to reduce the time spent in the moulting area to about three to four weeks. The moulting area is then abandoned, but new flocks are continuously pouring in and moulting males of a particular species are present for much longer, from two months in high arctic species (such as the King Eider) to four months in the Shelduck.

The final phase of the moult migration in ducks takes place rapidly and must be controlled by a very strong migratory urge. This is contrary to the usual more leisurely movements of ducks, interrupted by long pauses in resting places. The distance between the gathering place of the males (near the breeding place) and the moulting area is usually covered by a non-stop flight without deviations. The entire moult migration of the vast majority of the population is sometimes concentrated into a few days.

Many marine species, which during their usual migrations keep to coastal waters and avoid the interior, may cross large land-masses during the moult migration. The best known examples are the crossing of England by the Shelduck, the migration over the mountains of Baffin Island by the King Eider, and the crossing of Jutland by the Shelduck, Common Scoter and Eider (although the latter three species may occasionally cross the mainland during spring and autumn migration).

A review of the known moult migrations in the different groups of wildfowl is now given.

Swans and geese (Anserini)

The moult migrations of the swans and those of the geese have much in common. Moult migration is restricted to non-breeders, mostly to young, immature birds. Breeding birds remain with their young and indeed, in most swans and in many geese, the immature birds themselves undergo wing-moult in the vicinity of the breeding ground, usually gathered in small flocks (type A II), which means that such populations have no moult migration.

Swans *Cygnus*

The adult birds perform the wing-moult in the breeding period, first the female and then the male. In this way there is always one of the parents to defend the nest or the young. The wing-

moult certainly takes place in this way in the Mute Swan *Cygnus olor* (Szijj 1965), the Whooper Swan *Cygnus cygnus* (Scott and Fisher 1953) and the Trumpeter Swan *Cygnus buccinator* (Banko 1960).

In the post-breeding period the swans roam about with the young, which still need parental care. The wing-moult cannot, therefore, be postponed until after the young are fledged because the flightless adult birds could not then follow their offspring.

From the point of view of moult migration the adult swans represent a primitive stage.

The non-breeding one year old and (usually) two year old swans gather in summer in flocks, numbering up to some hundreds of birds, occasionally many more. In most species the flocks remain in the vicinity of the breeding area (moulting type A II) and, evidently, do not carry out a real moult migration which is known only in the Mute Swan. The immature Mute Swans usually frequent shallow water along low and protected sea-coasts, performing the moult rather slowly, from the end of May to the end of August, the flight-feathers being shed in the latter half of July and the first days of August. In Denmark and southern Sweden smaller congregations of moulting birds are found in various places along sea-coasts with a water depth less than one metre. The southern Sound and adjacent areas off the island of Amager and in Køge Bay form a very important moulting area (type A III). This moulting area has been known for centuries because the shooting of the flightless birds was formerly a prerogative of the Danish kings and, the hunt being a spectacular performance, was often described, the first time being in 1557. The royal hunting stopped about 1750 but subsequently shooting of the flightless swans was for many years practised on the Swedish side of the Sound where it was a privilege of the prefect of Scania (Schiøler 1925, Weismann 1931). In the beginning of the 20th century the swans were virtually exterminated, particularly by excessive winter shooting. In 1926, however, full protection was given to the swans by the Danish and Swedish governments, and this resulted in an immense increase, which has continued to the present day. Probably climatic influences have also been involved in this population explosion.

In the 17th century moulting swans were numerous in late July from Gedser along the east coast of the islands of Falster, Møen and Zealand right to Amager and Saltholm in the southern part of the Sound, but in recent years the centre of the moulting area has shifted to the Swedish side of the Sound. According to Mathiasson (1964) more than 10,000 moulting birds were gathered in 1963 along the east coast of the southern Sound, and a further 200 in Skälderviken and 1,200 in Kungsbacka Fjord in Halland, further north (Figure 2). In another paper Mathiasson (1963) concludes that this enormous number of moulting swans comprises not only the entire population of non-breeding swans from Zealand and Scania, but also large numbers of birds from more remote breeding places. In this he is undoubtedly correct and the majority of the immature swans of southern Sweden, eastern Denmark and the northern coastland of East Germany probably gather there. Future ringing must decide whether this view is correct. Presumably, non-breeding Mute Swans comes from all directions to the moulting area in the Sound, the moult migration thus resembling that of the Shelduck, although on a smaller scale.

The flightless period in the swans lasts for about seven weeks. During the wing-moult the birds must have access to firm land or at least to very shallow water as they cannot preen while swimming.

Geese *Anser, Branta*

The adult breeding geese have no moult migration. Both sexes share the parental care, as in the swans, and both remain with the goslings on the breeding places, in late summer undergoing the wing-moult which, contrary to the ducks, begins the post-nuptial moult. Generally the moult of the female precedes that of its mate by about a week. The immature birds, joined (or led) by a small number of adult non-breeders, gather in flocks usually of some hundreds but occasionally amounting to several thousand individuals. They often remain within the breeding area of the population (type A II, A III) but in many species a real moult migration has developed of the type D II or even D III. It is noteworthy that this movement, at least in all known cases, invariably goes in a northerly direction, leading to areas situated beyond the boundary of the population's normal breeding range.

All known cases of moult migration in non-breeding geese are briefly outlined below and shown in Figure 1, represented by the numeral included in the description.

Pink-footed Goose *Anser fabalis brachyrhynchus*. Moves from Iceland to northeast Greenland, the migration involving more than 10,000 birds (1) (Taylor 1953, Christensen 1967).

Bean Goose *Anser fabalis*, various subspecies. Moves from northern Russia to southern Novaya Zemlya in great numbers (5) (Johansen 1945, Portenko 1959, Uspenski 1965a). Very important moulting places are found in northern Siberia on the tundra in central Yamal (6), western Taymyr (7) and the delta of Indigirka (11) (Uspenski 1965a). Portenko (1959) adds the Lena delta (8). All these places are situated in the northern part of the breeding range. Pleske (1928) states that moulting birds are found in small numbers on the New Siberian Islands (9), north of the regular breeding range of the Bean Goose.

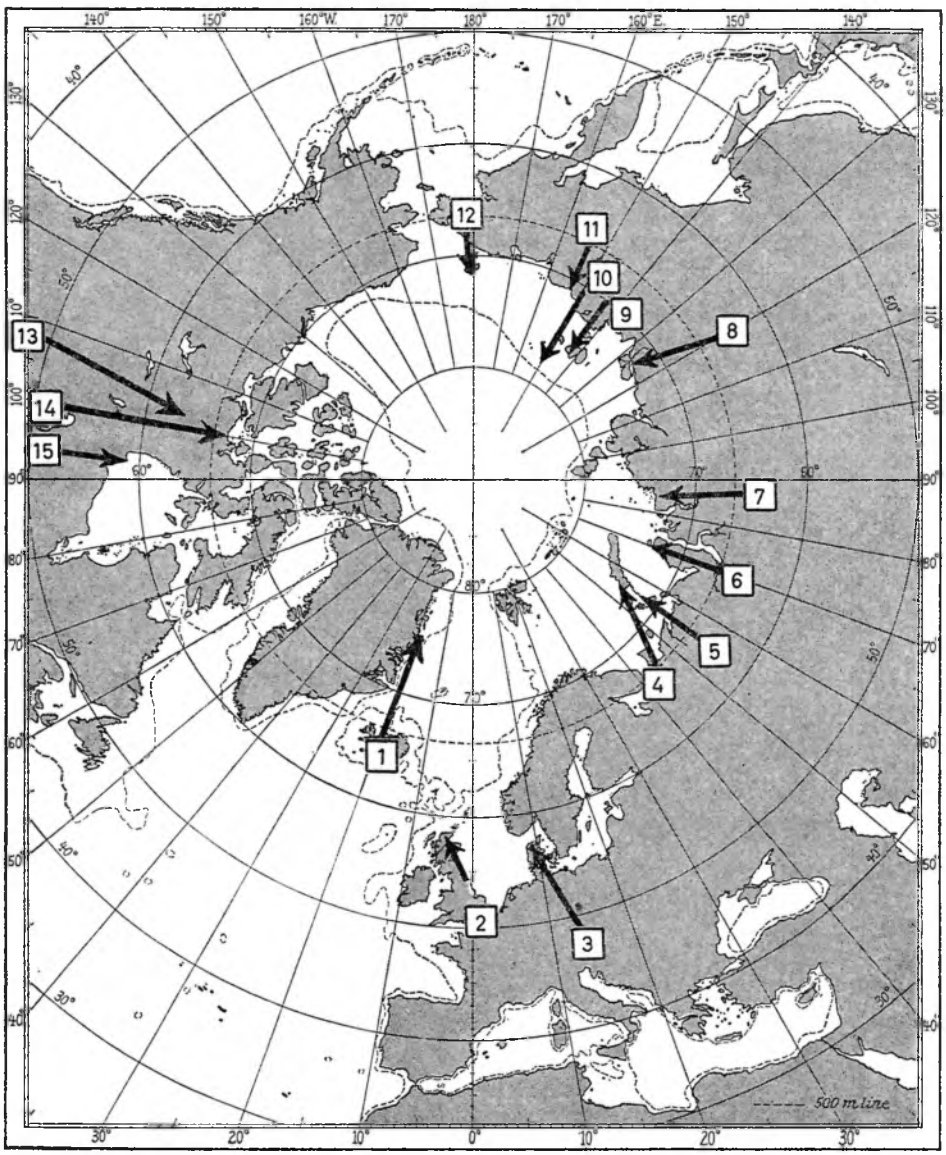

Figure 1. All known cases of moult migration in non-breeding geese. The arrows show direction and distance from origin to destination of the migration. The numerals refer to literature statements enumerated in the text pp. 8-10.

White-fronted Goose *Anser albifrons.* This makes similar movements in the Eurasian tundra to the Bean Goose, often mixing with that species in the moulting areas. Great moulting concentrations are found in Novaya Zemlya (5), central Yamal (6), western Taymyr (7), and the delta of Indigirka (11) (Uspenski 1965a) and moulting birds are also found in considerable numbers on the New Siberian Islands (9) (Pleske 1928), where the species breeds only rarely. Immature birds of the Greenland population *flavirostris* are strictly stationary, moulting in the breeding areas, assembling in small companies of at most a dozen individuals, probably the offspring of a few pairs. A similar situation is, apparently, present in North America.

Lesser White-fronted Goose *Anser erythropus.* According to Ekman (1922) the moulting birds of the alpine zone of Scandinavia withdraw to the uppermost parts of the mountains, where they gather in large flocks. No moult migration has been recorded from Siberia.

Greylag Goose *Anser anser.* The only known case of moult migration is found in the Danish population, of which the non-breeding birds moved to Vejlerne, an extensive marshland in northern Jutland. From ringing results it seems probable that many of these moulting birds originated from northern Germany, Poland and Austria (3) (Paludan 1965). The species did not breed in Vejlerne until about 1925 and individuals from other places did not use the area for moulting until the 1930s. In 1934-37 at most 200 non-breeding birds were moulting there, in 1934 500 (Salomonsen 1943) and in 1955 about 3,000 (Paludan 1965). The numbers began to decrease in 1959 and now only few are left. In 1959 summering Greylag Geese suddenly began to turn up in Holland, and in 1964 the number of moulting non-breeders at the lagoon Saltbækvig in Zealand (Denmark) increased considerably. It is probable, therefore, that these and other areas have now replaced Vejlerne as moulting areas (Paludan 1965).

Brent Goose *Branta bernicla.* During the spring migration of the nominate form from Europe towards the breeding range in northern Siberia, many immature birds remain to moult in eastern Kola Peninsula and northern Kanin Peninsula (type B II), while others divert from the eastward flight direction of the breeding birds and turn northwards to Novaya Zemlya, where they occur on both the southern and northern island (4). Many thousands moult in the New Siberian Islands (9), originating from the coast of NE. Siberia between Yana and Kolyma Rivers (Uspenski 1960). According to Uspenski there are many observations of birds flying north over the Polar Sea north of the New Siberian Islands and at Henrietta and Bennett Islands (10). It is very unlikely that they continue across the central parts of the Polar Sea to North Greenland or to some sterile ice-island. Uspenski's view that they turn eastwards to moulting areas in Alaska is borne out by recoveries in the New Siberian Islands, on Wrangel Island, and at the Kolyma Delta of birds ringed in previous years at moulting stations in western Alaska (Uspenski 1960, 1965b). Finally Wrangel Island (12) forms the moulting area of at least 10,000 non-breeding Brents, coming from the south, while only 1,000-2,000 pairs breed there (Uspenski 1965b).

No case of moult migration has been described in the North American populations. Apparently the immature birds moult in small flocks in the breeding areas of the adult birds (Scott 1951). Uspenski (1960, 1965a), however, reports that Brent Geese ringed during the moult in Alaska are recovered in subsequent moulting periods in eastern Siberia.

Canada Goose *Branta canadensis.* Moult migrations are known to go northwards to the Thelon River district (13), to Perry River (14) and to the western coastland of Hudson Bay (15) (Scott 1951, Hanson 1965, Sterling and Dzubin 1967). The last named authors have delineated the movements of the different races, and banding results (the earliest being those of Kuyt (1962)) have now indicated the movements of localised populations. The number of moulting birds is considerable, at Thelon River up to 16,000 individuals have been observed. In Great Britain numbers of moulting birds gather in Inverness-shire, Scotland, and ringing has demonstrated that at least some of them originate as far south as Yorkshire (2) (Dennis 1964).

The Canada Goose was introduced to Great Britain and the moult migration to Inverness, therefore, must be a comparatively recent phenomenon, certainly less than 300 years old, and probably of much more recent origin. It is reasonable to assume that it is a result of an ancient adaptation based on hereditary factors.

Very likely moult migration will be discovered in other species than those mentioned above, but it does not appear to be the case in those species which have been thoroughly studied. Uspenski (1965a), however, is of the opinion that

the non-breeding Snow Geese *Anser caerulescens* of Wrangel Island perform a moult migration.

The flightless period in geese covers about 35-40 days, but less than a month in the Snow Goose (Uspenski 1965a). The non-breeders begin the moult a fortnight earlier than the breeding birds, in most arctic species in the middle of July, compared with early August in the breeding birds, but according to Uspenski (1965a) the two groups moult simultaneously in the high-arctic Brent and Snow Goose. Cooch (1957), however, states that in the Snow Goose in Southampton Island the non-breeders moult much earlier than the breeding birds.

It is my belief that the ultimate cause of the moult migration of non-breeding geese is an endeavour to avoid heavy competition for food on the breeding places, but it is difficult to understand why the migration invariably moves in a northern direction while all other moult migrations in wildfowl lead to regions with a milder climate. There are three alternative explanations:

(1) It may have something to do with so-called 'prolongation of migration'. The immature birds are still in a migratory state when the time comes for them to leave the breeding grounds only a few weeks after arrival. Under such circumstances it is most likely that the choice of a flight direction will be the same as used during the spring migration, i.e. northerly. If the northern direction is genetically fixed it will be kept provided that selective forces do not favour any other direction.

(2) I was at first inclined to believe that the northerly direction of the moult migration in geese expressed a phenomenon similar to the so-called nonsense orientation in British and American Mallard, which demonstrates an instinctive selection of a northerly flight direction under certain circumstances. However, recent investigations by Matthews, Eygenraam and Hoffmann (1963) and Bellrose (1963) have shown that other species of wildfowl choose other directions during nonsense orientation, and that different populations of the same species may do likewise (Matthews 1963). I am now satisfied, therefore, that nonsense orientation is not involved in the northward moult migration in geese.

(3) The north direction may be the result of climatic influences. In arctic regions the length of time of snow-cover is of decisive significance for many ground-feeding birds and mammals. According to Uspenski (1965a) a snow-free period of three months is necessary for a successful accomplishment of the breeding cycle in most species of geese. Only the Snow Goose and the Brent Goose are able to manage the full breeding cycle in slightly over two months, owing to a particularly rapid development of the goslings and an accelerated wing-moult in the adults. Although the snow-free period in high-arctic areas is too short to permit breeding in most species of geese, the food resources can be utilised by non-breeding birds when the snow-melt in the latter part of June has made the food plants available to them. A high selective premium is paid to such populations in which the immature birds move north to the high-arctic region in June, leaving the food resources on the breeding places to the goslings and their parents, in this way enabling the breeding population to raise its productivity.

Shelduck (Tadornini)

The moult migration of the Shelduck *Tadorna tadorna* in northern Europe is of impressive dimensions. In this species both the immature non-breeding individuals as well as the adult breeding birds participate in the moult migration. Male and female share the parental care, but many leave the ducklings before they are fledged. Shelducks from the British Isles, the North Sea countries, Scandinavia and the Baltic countries move in the summer from all points of the compass to the German Waddensea coast in order to perform the wing-moult there (type D III). The biggest concentration of birds is found on the tidal flats Knechtsand, east of Cuxhaven, where at the peak about 100,000 gather. Smaller centres are found off the North Sea coast of Schleswig-Holstein, northward to the Ejdersted Peninsula. Before the migration the Shelduck collect in flocks and then leave at sunset, probably covering the whole distance in a single night. The migration usually follows a straight line, these normally coastal birds crossing the mainland of England and Jutland. The moult migration begins in Denmark in June (immature birds) and continues until September-October, but in England virtually the entire migration takes place in July. When the post-nuptial moult has finished, the autumn migration takes place more leisurely. It covers the period October - November and, paradoxically enough, transfers the British population back to its breeding range, while the Scandinavian and East European populations scatter, to winter in the coastal areas of the southern North Sea, France

and the British Isles (as shown by ringing of Danish birds; cf. Salomonsen 1967). Some flocks move northwards in the North Slesvig Waddensea or to the lagoons in western Jutland, but many thousands of birds winter within the moulting area proper.

The moult migration of the Shelduck, which in recent years has attracted much attention, has been studied particularly by Hoogerheide and Kraak (1942), Coombes (1950), Goethe (1957, 1961a, 1961b) and Lind (1957).

It is noteworthy that a moulting congregation of Shelduck, totalling more than 3,000 birds, was recently discovered in Bridgwater Bay, Somerset, in England, possibly being of Irish origin (Eltringham and Boyd 1960). Apart from this, apparently all European Shelduck west of the Soviet border perform the wing-moult in the German Waddensea. In Lake Rezaiyeh in Iranian Azerbaijan about 300 flightless Shelduck were observed in August by Savage (1964). This locality serves probably as a local moulting centre for Shelduck which assemble here from wide areas within Iran.

Dabbling ducks (Anatini)

The dabbling ducks breed when they are one year old (Wigeon often not until they are two years old) and it is, therefore, not necessary to distinguish between the moult migration of immature and adult birds. The males do not participate in brooding and parental care, but soon leave the female in order to perform the eclipse moult. Only the males perform a moult migration, whereas the females stay with the ducklings. A few females may join the males but only those which have given up breeding for the year.

The time for the males' desertion of the females varies somewhat. In the Mallard *Anas platyrhynchos* and Pintail *Anas acuta* the female is abandoned as soon as the clutch is complete, before incubation. In the Mallard in Europe this is in the second half of April. In most other species the males remain near the female until various stages of incubation. According to Hochbaum (1955) and Oring (1964) the Shoveler *Anas clypeata*, Blue-winged Teal *Anas discors* and Cinnamon Teal *Anas cyanoptera* sometimes remain even until hatching, in spite of well developed body-moult. The males of most holarctic species moult the wing-feathers in the period from the middle of June to the end of August. The Mallard is on average slightly but not significantly earlier than other species. The flightless period covers three to four weeks, and is shortest in the small species.

The females remain with the ducklings until they are more or less independent. They then withdraw to suitable areas in the same marsh or in its vicinity and perform the wing-moult, much later, of course, than the males. They may sometimes assemble in small parties, but never in big flocks, and usually they are solitary. The wing-moult in most species takes place from the middle of July to September or even October.

The females may in exceptional cases remain with the ducklings during the flightless stage, or they may occasionally commence the autumn migration before the moult, performing the wing-moult alone or in small groups during the migration (type B I) or in the winter quarters (C I). In the winter quarters of the Gadwall *Anas strepera* in Louisiana, Chabreck (1966) found two or three dozen females in the flightless stage in October. Lebret (1952) records a single flightless female of Gadwall in September and a number of flightless females of Wigeon *Anas penelope* in October, during their migration in Holland. However, no breeding females of any species of dabbling duck perform a real moult migration.

The extension and proportions of the moult migrations in the males is subject to considerable variation, both specifically, individually and geographically. In Denmark the greater number of males of all species moult on the breeding place proper, either solitarily or in very small groups (A I). Only the Mallard, and in some places also the Shoveler, has something approaching a moult migration. The males within an area collect in small flocks, usually less than two dozen birds, but occasionally up to about 200 (type A II). The same behaviour is displayed in most other European countries where the Mallard is non-migratory. It is even the case in Greenland, where the largest concentration of flightless males I ever saw amounted to only eleven birds. In western Europe also all other species of dabbling ducks evidently adhere to the moulting types A I or A II. In the flightless stage they prefer large marshes, also densely overgrown lakes, the Mallard even lagoons or quiet bays in fjords.

Populations breeding in regions with a continental or arctic climate carry out regular and often long migrations to winter quarters. In these populations the males have highly developed moult migrations, leading to large moulting centres where individuals coming from

very extensive areas collect in a restricted locality, usually 50,000 - 100,000 birds together, occasionally even more. These moulting areas, frequented year after year, are as a rule situated on the migration route (B III) or in the winter quarters (C III). True moult migrations of the type D III are hardly known within the dabbling ducks. A number of species assemble on these moulting places and form part of the huge congregations, but there are definite local and specific differences. Usually the Mallard and the Pintail predominate, but this is not always so.

In the Old World particularly large concentrations of moulting males are found in the West Siberian lakes, the Transuralian forested steppes, northern Kazakstan, Kuban flats, Rybinski Reservoir (north of Moscow), Volga delta, Russian - Finnish lakes, and Matsalu National Park in Estonia (Ottow 1956, Teplov and Kartashev 1958, Kumari 1962, Wolff 1966). In Matsalu Park there were formerly (until the 1930s) 'many hundreds of thousands' of birds, mostly Mallard and Teal, but also some Wigeon, Shoveler and Garganey *Anas querquedula*, but now, owing to human interference, only about 10,000 birds (Kumari 1962).

In North America great moulting centres are the Delta Marsh at Lake Manitoba (Hochbaum 1955) and the Camas Reserve in Idaho (Oring 1964), and probably many more. The main species moulting in Delta Marsh are Mallard, Pintail, American Wigeon *Anas americana*, and American Green-winged Teal *Anas crecca carolinensis*. In the Camas Reserve all these species moult, also Cinnamon Teal and Blue-winged Teal. Some of these may be local birds (probably only a small fraction) but certainly Pintail and Wigeon are not found breeding until many hundred kilometres further north. The greatest moulting concentrations are probably found in the American Green - winged Teal and American Wigeon, of which species Sowls (cited by Bezzel 1964) records congregations of 125,000 individuals in a particular locality.

Moulting congregations of this order of magnitude are not found in western Europe, as said already, but some localities approach them. In the Lake Tåkern in southern Sweden males of Mallard and Wigeon gathered in summer at least in hundreds (Lönnberg 1935) and the same is evidently the case with other lakes in south Sweden, such as Hornborgasjön. While Mallard, at least partially, may belong to local populations, Wigeon are uncommon breeders so far south in Sweden, and the greater part of them must obviously have originated from further north, now performing the wing-moult at a resting place situated on the ordinary autumn flyway (type B II).

The other known moulting areas in western Europe are principally of the same kind as Tåkern, holding some hundreds of moulting males, the majority of which having performed a B II migration, but a small fraction being local birds with an A II moult. A typical B II locality is Ijsselmeer in Holland, in which Mallard, Gadwall, Teal, Garganey, Pintail, Wigeon and Shoveler spend the flightless stage (Lebret 1950). In Lake Constance some hundred individuals of Mallard, Teal, Gadwall, Garganey and Shoveler moult the flight-feathers, but apparently no Pintail or Wigeon (Szijj 1965). The Ismaninger Reservoir in Bavaria is characterised by the large number of moulting Gadwall (about 400), but only a few of other species of dabbling ducks (Bezzel 1964). The Himalayan lake, described by Stresemann (1940), in which many dabbling ducks spent the flightless period is of a similar B II type as the above-mentioned European lakes. Even the locality in Scotland (Beauly River in Inverness-shire) described by Dennis (1964) as being full of moulting male Mallard may belong to this type, but it is more probable that the birds observed are of local origin (A II type). There are, of course, other localities of this kind in Europe than those mentioned, but the wildfowl ecology in these places has not yet been thoroughly studied.

I have selected three species for some special comments.

Pintail *Anas acuta*. Individual variation in moult migration comprises the types A I, A II, B II, B III. In Scandinavia and Denmark the males usually moult the wing-feathers in the breeding range, solitarily or in small parties. In other places they gather in large flocks in the breeding area, such as described by Scott (1951) from Perry River in arctic Canada. As a rule, however, arctic and sub-arctic Pintail make very extensive pre-moult migrations in a southerly direction, spending the flightless stage on intermediate resting stations, from which they continue the migration southwards when their wings can again carry them. These moult migrations are generally longer than in most other dabbling ducks. Sometimes the Pintail collect in hundreds in the moulting areas (type B II), as in Ijsselmeer in Holland, but in Soviet and U.S.A. the moulting congregations usually reach enormous dimensions (type B III).

In Bear River, Utah, 7,500 individuals have been recorded, in Camas Reserve, Idaho, 20,000 (Oring 1964), in lakes in Kazakstan 30,000 (Cuisin 1966). The autumn passage migrants of this species in Denmark, originating from Scandinavia, north Russia and some even from western Siberia (as demonstrated by recoveries of ringed birds; cf. Salomonsen 1967) belong to populations which perform the wing-moult in the breeding areas or in resting stations north of Denmark. The males pass through Denmark, all with new wing-feathers, from the end of August to the middle of September, well ahead of the adult females and juvenile birds; the rear party, passing after the middle of October, consists exclusively of juveniles (Schiøler 1925). The segregation on the migration of the two sexes reflects the different timing of the wing-moult, and is the rule also in Teal and Wigeon.

Teal *Anas crecca*. Like the males of the Pintail, those of the Teal moult either in the breeding area or on suitable resting places on the southward migration in autumn. The flight-feathers are shed within the period from the middle of June to the middle of August, usually in early August (Wolff 1966). There is a notable difference in the movements between Pintail and Teal, at any rate in the passage migrants passing Denmark. A substantial part of the males of northern Teal leave the breeding places soon after incubation has started and appear in Denmark, in small flocks, as early as the middle of June on their way to moulting areas further south or south-west (Palm 1950). Such an early passage has not been noticed in Denmark in any other dabbling duck. The Teal apparently do not spend the flightless period in Denmark, but are known to do so in some numbers in Holland and a flightless male ringed in Holland was recovered next autumn in Poland (Wolff 1966). Flightless males have often been obtained in Denmark in August but they may be local birds. During the ordinary autumn migration, starting in August, males (with new wings) arrive in advance of females, just as in the Pintail (Schiøler 1925). In Russia and U.S.A. huge concentrations of moulting males (type B III) have been recorded, as mentioned before.

Wigeon *Anas penelope*. This species differs from most other dabbling ducks by the postponement of breeding in most individuals until the second year. Many of the one year old non-breeding birds may spend the summer and moult the flight-feathers in areas south of the breeding range. The adult males moult the flight-feathers in June - July, the females in August-October. The majority of the males evidently leave the breeding range very soon after incubation, shedding the flight-feathers in areas further south, gathering in flocks (type B II). Lebret (1950) during a visit in August to the breeding places in Jämtland, in northern Sweden, observed hundreds of females with young, but virtually no males. The latter had already left and were moulting the wing-feathers in lakes situated further south or south-west on the flyways of the subsequent autumn migration. Flocks of moulting males are known in north-west Europe from the end of June onwards in Estonia (Matsalu), southern Sweden (Tåkern and Hornborgasjön), Denmark (Vejlerne, N. Jutland) and Holland (Ijsselmeer). The males leave the moulting areas and begin the genuine autumn migration as soon as the flightless period is over, usually in August. In Denmark as well as in Holland males (with new wings) predominate during the early stages of the autumn migration, while females and juveniles follow later.

The moulting areas of the dabbling ducks are wetlands with dense vegetation and very shallow water, usually open reed beds or other plant formations along the shore, furnishing cover and sufficient food. The really big moulting centres are extensive and secluded. The moulting birds must have access to firm land because they do not preen while swimming.

Diving ducks (Aythyini)

The diving ducks resemble the dabbling ducks in being able to breed at one year old and have, therefore, no distinct moult migration of immature birds. The general character of the moult migration is also very similar. The most striking difference is the participation of a certain number of adult females, but these are always much fewer than the males and they migrate considerably later. The moult migration of both sexes belongs to type B II, but moulting congregations of more than 10,000 individuals (type B III) are occasionally found. Probably a large number of individuals of both sexes remain in the breeding territory, spending the flightless period there (type A I or A II), but only scanty information is available. The performance of moult migration in females may have something to do with the fact that the females sometimes leave the brood before the young can fly. This has been observed in the

Redhead *Aythya americana*, and the Canvasback *A.valisneria*, whereas in the Lesser Scaup *A.affinis* the females remain with the young until they are fledged (Oring 1964).

These three American species, as well as a fourth, the Ring-necked Duck *A.collaris*, perform striking moult migrations, sometimes gathering in concentrations of more than 10,000 birds. Among the Palaearctic species the Tufted Duck *A.fuligula* and the Pochard *A.ferina* have moult migration, at least in some populations. Both species appear in large numbers on the Ijsselmeer in Holland in July-August but breed only sparsely in Holland (Lebret 1950). In Ismaninger Reservoir in Bavaria about 9,000-11,000 Pochard and more than 2,000 Tufted Duck spend the flightless period. The males arrive in June-July, the females (less than 10% of the numbers) not until August. Just as in Holland the two species are only scattered breeders in Bavaria, and the large flocks must have originated from rather remote breeding places (Bezzel 1964). The occurrence of these two species in central European moulting areas is probably the result of a pre-moult migration due east-west because northern birds apparently spend the flightless period in the breeding range, or at any rate on localities situated much further north. Extensive ringing in Denmark of Tufted Duck during autumn migration has demonstrated that these birds breed in Scandinavia, north Russia and NW. Siberia, and winter in Germany, France and England, occasionally in Italy (Salomonsen 1967). They do not arrive in Denmark until October, with new wings, and consequently must have spent the flightless period further north. Something similar can be said about the Pochard which appears as a passage migrant in Denmark in September - October. No moulting areas for these species are known in Scandinavia, but a great number of Tufted Duck and a smaller number of Pochard are known to moult their flight-feathers in Matsalu National Park in Estonia (Kumari 1962).

Possible the well-known strict sexual segregation in the winter quarters (allohiemy) in the Pochard and the Tufted Duck is a consequence of the difference in the moult migration in males and females. The males, having finished the wing-moult much in advance of the females, arrive earlier in the winter quarters where they apparently occupy all available space within the specific niches and pre-empt the food resources. The females, consequently, are forced to continue their migration to areas beyond, the two sexes performing a so-called leap-frog migration (Salomonsen 1955). Such a situation is unknown in dabbling ducks.

The Red-crested Pochard *Netta rufina* has a moult migration similar in many respects to that of the *Aythya* species. A comparatively large number spend the flightless period in various lakes in central Europe, about 300 individuals in the Ismaninger Reservoir, and about twice this number in Lake Constance. The males begin to arrive in the last part of June, the majority in July and early in August, the females not until August. The males moult the flight-feathers in July-August, the females in August and the first half of September (Bezzel 1964, Szijj 1965). In Ismaninger all birds leave in September for the autumn migration, while in Lake Constance, on the contrary, a new influx of birds which have finished the moult occurs in September-October, when about 4,000 birds can be present. In November they all leave again (Zink 1964). Ringing has definitely shown that the birds moulting in Lake Constance originate from the Camargue in southern France (Mayaud 1966). In certain years they do not move so far eastwards, but use lakes in Lorraine as a moulting area. The autumn migration, which takes place in September-November, goes the opposite way, towards the south-west, the main wintering places extending from the Camargue to Albufera de Valencia in eastern Spain. The ducklings from the Camargue move directly to Spain, naturally without performing any moult migration (Mayaud 1966). The eastward moult migration and subsequent westward return migration in the autumn strikingly resembles the situation in the British population of the Shelduck. The individuals which arrive in Lake Constance in September-October must originate from eastern breeding places (Balkans, S. Russia, SW. Siberia). Just as in the *Aythya* species mentioned above, these individuals perform a moult migration to Central Europe in a due western direction. Even so they winter probably somewhere in Spain. Ringing of Red-crested Pochard at breeding places in Denmark has demonstrated that the greater part of this population spend the winter in SE. France and NE. Spain (Preuss 1965) but apparently they perform the wing-moult in the breeding area.

The Scaup *Aythya marila*, although belonging to the same genus as the Pochard and its allies, is a marine species, which mainly frequents coastal waters.

Nothing is known about its moulting behaviour.

The moulting areas of the diving ducks are fresh-water lakes of varying size, though not very small ones. The moulting birds frequent the areas of open water off the riparian zone of vegetation (reed beds, etc.), usually in shallow water with a depth of less than 5 m., not too far outside the belt of vegetation. They do not need access to firm land, being able to preen while swimming. The Red-crested Pochard differs by preferring open reed beds, much like the dabbling ducks.

Eiders, scoters and sawbills (Somaterini and Mergini)

The moult migrations of the marine ducks are more diverse and better developed than in any other group of wildfowl. Those of the eiders and scoters are, however, similar. In the marine ducks, contrary to the situation in the dabbling ducks and the diving ducks, the one year old birds and in some species even the two year old birds do not breed but join the males in their comprehensive moult migration. The participation of the adult females in the moult migration varies considerably from one species to the other. They may spend the flightless period on the breeding places (type A I) or in the winter quarters (type C I), or they may participate in the moult migration together with the males, or more usually join them later in the autumn. Part of the female population at any rate must remain in the breeding places because the young are too small to be left alone. The departure of some of the females is compensated for by individuals which remain and are possessed of a strongly developed tendency to collect and keep large flocks of ducklings, as in the eiders. It is also developed in the Shelduck in which both sexes show 'crèching' behaviour.

The Common Scoter *Melanitta nigra* breeds in the arctic and northern high-boreal areas of the Old World. It has been known for a long time that summering and moulting individuals occurred in small flocks in the inner Danish waters and in the Limfjord, but only fairly recently was it pointed out that the actual moulting area was in the North Sea just off the west coast of Jutland (Salomonsen 1950a). Moulting birds occur in flocks of varying size right from the Danish-German boundary northward to the Skaw (Figure 2). The moult migration to this area, which is very spectacular and has been known for a long time, passes through the southern Baltic Sea, south of Denmark, and crosses Jutland along the fjord Slien (Jørgensen 1941), going westwards to the Waddensea of North Slesvig where the flocks gradually spread northward along the west coast of Jutland. The greatest concentrations of moulting birds are found, therefore, along the southern part of the west coast of Jutland; the flocks off Rømø Island amount to about 150,000 individuals, according to an aerial census made by Joensen (1964). A smaller proportion of the migrating birds pass somewhat further northward and have been recorded over southern Zealand (Sjaelland), in the Little Belt and at the town of Ribe, following the south-eastern fjords in Jutland westward (Flensburg Fjord, Åbenrå Fjord, Vejle Fjord) the most northerly observations being from Horsens Fjord (Schiøler 1926, Behrends 1955). Small flocks of some hundred birds, have been observed in early August to pass northwards through the Great Belt (Bruun and Schelde 1957), possibly heading towards moulting areas in the western Kattegat. By far the majority, however, spend the flightless period off the west coast of Jutland, and the densely packed flocks congregating there comprise undoubtedly the greater part of the Scandinavian and north Russian breeding population. It should be noted that the Common Scoter is the only species of wildfowl occurring off the sandy coast of West Jutland. The shedding of the flight-feathers takes place in August and early in September. The birds frequent the zone of shallow water over sand, with a water depth of less than 10 m., usually less than 5 m., often just off the heavy surf.

The moult migration across Jutland takes place at sunset or during the night and passes at a considerable height. It is initiated as early as the middle of May by the one year old birds which have curtailed their spring migration to the north-east before reaching the breeding range. Some individuals probably move directly from the winter quarters to the moulting area. The immature birds are joined by the adult males from the beginning of July until the middle of August. In the last part of this period some adult females probably participate in the migration, but this has not been observed with certainty. The greater part of the moulting birds disappear in September or October, spreading in the surrounding waters or continuing the autumn migration to the English Channel or the Bay of Biscay.

It is not known whether some individuals make a return flight across Jut-

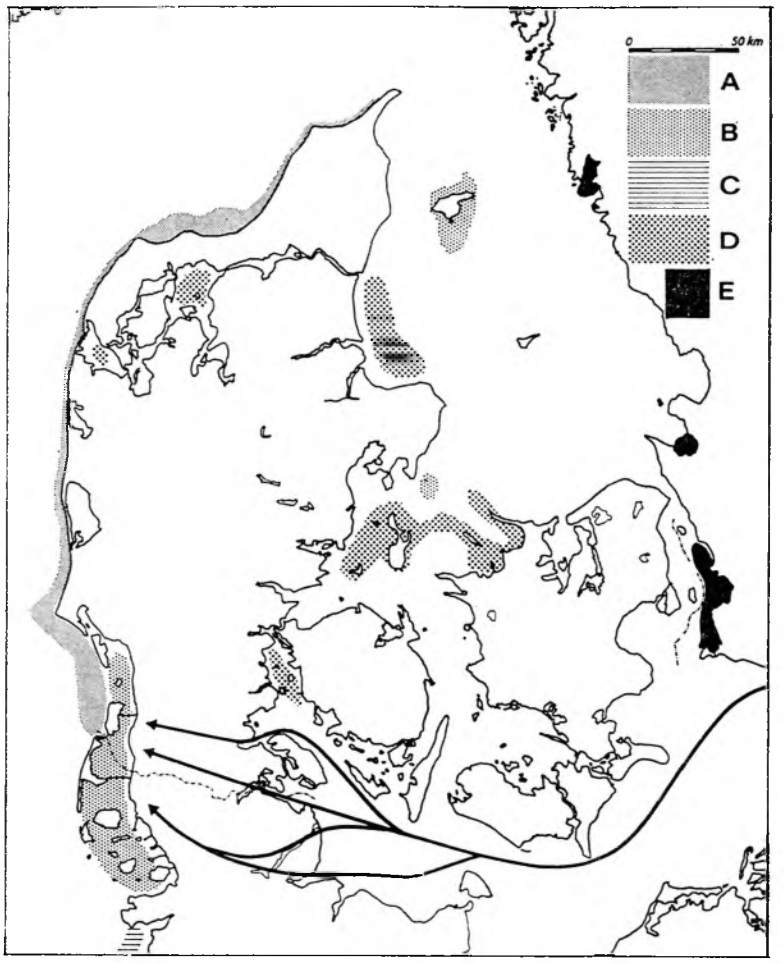

Figure 2. Moulting areas of northern wildfowl in Danish waters. A, Common Scoter *Melanitta nigra.* B, Eider *Somateria mollissima.* C, Shelduck *Tadorna tadorna.* D, Velvet Scoter *Melanitta fusca.* E, Mute Swan *Cygnus olor.* The solid lines (with arrow-heads) indicate the most important migration routes for the species A, B, and C.

land to winter quarters in the Kattegat, but it is unlikely. During spring migration part of the population may perhaps cross Jutland on their way to Scandinavian-Russian breeding places but there are no certain records. On the other hand, in the early part of April many thousands daily pass the Skaw on migration north-east (Hansen and Christensen 1954), and it is probable, therefore, that the main spring migration passes north of Jutland, not across the country.

No other moulting areas of the Common Scoter are known except in Great Britain. According to Atkinson-Willes (1963) large congregations of moulting males have been recorded off east Scotland in late summer 'and others may be found elsewhere'. These birds are either of Icelandic origin, or constitute flocks which have continued the pre-moult migration from Jutland across the North Sea.

Velvet Scoter *Melanitta fusca* also spend the flightless period in Danish waters. Flocks of immature birds occur commonly in the coastal waters. They are most numerous in the southern Kattegat, in the Little Belt and in the western Limfjord, where they are particularly common in Løgstør Bredning (Figure 2). A number of adult males join the immature birds in July and August, but quantitatively the moult migration of this

species in Danish waters is much less pronounced and much more scattered than that of the Common Scoter. The adult females do not arrive until much later. I have examined flightless females obtained in the Little Belt and in the southern Kattegat in October. Part of the population remains in Danish waters in winter but many continue the migration to western Europe in November-December. The Velvet Scoter occurs only exceptionally along the western coast of Jutland.

In the Eider *Somateria mollissima* the immature birds and males perform large-scale moult migrations to the Danish waters, where they collect in great numbers in a restricted area. The population of Bohuslän in western Sweden and, possibly, of southern Norway, gather in the Læsø area, particularly off the north-eastern coast of this island. Large flocks are seen also off Hjelm Island further south in the Kattegat. The large population of the Baltic segregates in various moulting areas, situated off Gotland and along the coast of Estonia and Latvia. The majority, however, perform a moult migration south-west through Kalmar Sound (Svärdson 1959), across the southern parts of the Danish islands or just south of them, and across southern Jutland to the North Sea coast. Tens of thousands of birds spend the flightless period in the North Slesvig Waddensea, from Fanø and Rømø Islands south along the German coast (Figure 2). The moult migration across Jutland takes place from the end of June until early August, usually following Flensburg Fjord westwards, i.e. somewhat further north than the main migration of the Common Scoter. However, flocks of Eider on moult migration have been met with frequently right from Eckernförde as far north as Åbenrå, incidentally the same area in which the Shelduck of the Baltic region move towards the moulting area in the Bay of Helgoland. Many ornithologists have observed the impressive east-to-west Eider migration across North Slesvig; I have personally once observed a single flock moving westward across southern Zealand.

The Eider migration across North Slesvig has been carefully followed and mapped by Behrends (1955, 1966). The movements take place predominantly in the evening hours, just as in the Shelduck and the Common Scoter, and are performed, primarily by immature birds and adult males, in June-July with a peak (3,300 observed in one evening) in early July. At the end of July the migration of the males ceases, and the immature birds decrease in number. The adult females then begin to arrive, reaching a peak (1,400 in one day) in early August, and the migration then soon comes to an end. Behrends made the interesting observation that a substantial part of the females remain in the western part of the Baltic and spend the flightless period there, i.e. they do not cross the peninsula of Jutland.

The more northern populations, which have undergone the wing-moult in the Baltic region proper, arrive in the south-western Baltic Sea and the eastern fjords of North Slesvig in September-October during their ordinary autumn migration but do not continue across Jutland to the North Sea. The three migration peaks (early July, early August, and September-October) correspond exactly with those which have been demonstrated for the migration along the coast of Kalmar Sound in southern Sweden (Svärdson 1959).

The moult migration of the Eider in Scotland, recently studied by Milne (1965), is much smaller than that in the Danish waters, but agrees with it on certain points. The migration passes southwards along the east coast, but only over short distances, at most 100 km., and quite slowly. The females follow one month after the males and go through the wing-moult more rapidly than the latter. The males move further generally than the females. Immature birds do not have such a well-defined moulting areas as the adult birds, but spread more evenly along the coast. The moult migration in Scotland is of the type B II, but the winter quarters are situated only about 50 km. further to the south. The condition in Great Britain is thus interesting in demonstrating the moult migration in an initial stage.

The Eider performs a moult migration, to a greater or lesser degree, in other areas, i.e. in Canada, the White Sea and the Baltic Sea (Milne 1965) and probably elsewhere. In Greenland and Norway the extensive areas of rocky skerries along the coast furnish, evidently, sufficient food and satisfactory protection to the moulting birds and, as far as is known, the flightless period is everywhere spent within the breeding range of the population (type A II).

The autumn migration of the population which spends the flightless period in the Waddensea off Slesvig, has not been investigated. A fair proportion of the birds remain in the area in winter but the greater part, undoubtedly, move gradu-

ally further south into the German and Dutch Waddensea. These two groups must, then, have performed a moult migration of type C III and B III, respectively. The birds do not winter off the open North Sea coast of Jutland north of Skallingen Peninsula and the moulting population of the Waddensea has never been observed to return across Jutland in an eastward direction in order to spend the winter in the Kattegat area, nor is this likely. The great number of Eider wintering in these waters do not arrive until October-November, having performed the wing-moult somewhere else. Ringing has demonstrated that these birds mainly belong to the breeding populations of Bornholm and south-eastern Sweden (Salomonsen 1967).

The spring migration of the Waddensea birds appears to pass across Jutland, judging from the fact that they do not then pass the Skaw. There are some observations on flocks of Eider passing eastwards across the eastern Danish islands.

It appears from Figure 2 that three species of ducks, differing considerably from each other in life habits and feeding biology, have divided the Danish North Sea coast between each other, using separate regions as moulting areas, the Shelduck in the Bay of Helgoland, the Eider in the Waddensea of Slesvig, and the Common Scoter off the west coast of Jutland. To these species should be added the other species which spend the flightless period in the eastern Danish waters, i.e. the Velvet Scoter and the Goldeneye (discussed below) in the Limfjord region and the southern Kattegat, the Mute Swan in the southern Sound and elsewhere, and the scattered flocks of Mallard in shallow water off the coasts of eastern Jutland, Zealand and other eastern islands as well as in freshwater lakes and marshes.

The King Eider *Somateria spectabilis*, which breeds in the high-arctic zone, performs a moult migration of an even more grandiose character (Figure 3). The entire population (i.e. the immature birds

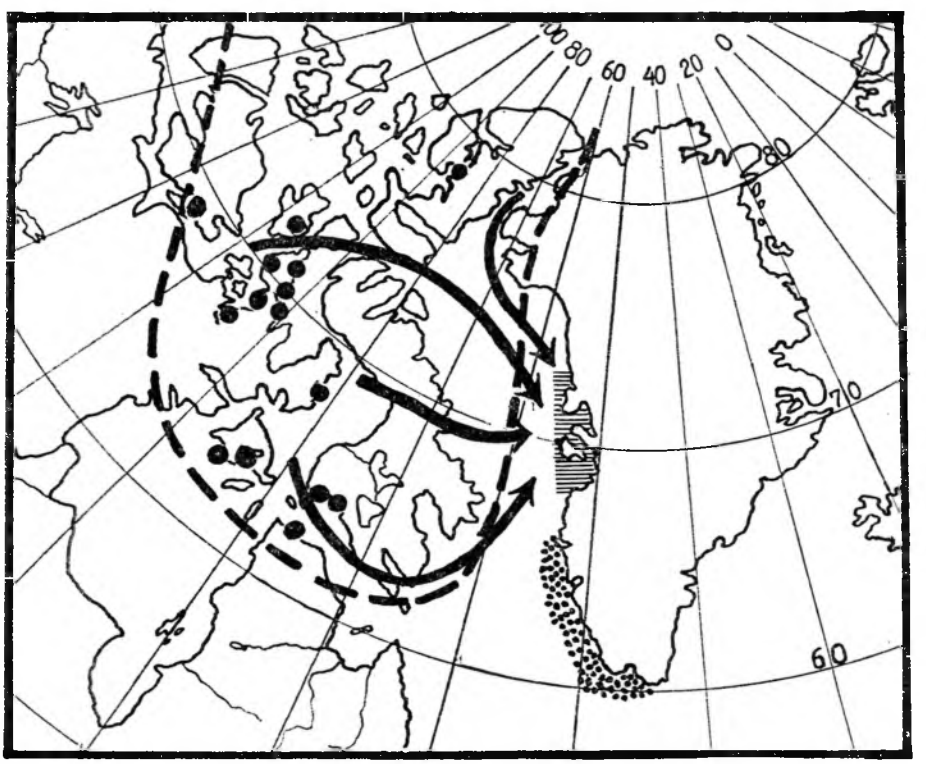

Figure 3. Moult migration of King Eider *Somateria spectabilis* **in Canada and Greenland.** From the breeding area within the dashed line males and non-breeders move along the routes indicated by solid lines (with arrow-heads) to moulting area (horizontally hatched). Solid circles give localities for recoveries in the breeding places (not in the winter quarters) of individuals ringed when flightless in the moulting area in West Greenland. The dotted area represents the winter quarters.

and the adult males) of the greater part of arctic Canada, the Canadian Archipelago and North Greenland congregate in a comparatively restricted area of western Greenland, extending from the southern Upernavik District southwards to Egedesminde District, with a maximum density in the Disko Bay. The males leave the brooding females early and by the first week of July the first have arrived in the moulting area. This is only about three weeks after the last breeding pairs passed on the northward spring migration. During the moult migration the males may move north or south of Baffin Island, but the majority cross through the mountain passes in the middle of the island, south of the ice-cap. In the latter half of July flock after flock numbering hundreds of birds, all adult males, flew in a north-eastern direction from Clyde Inlet, often at a height of 1,000-1,200 m. (Wynne-Edwards 1952). The number of King Eider in the moulting area reaches a peak in early August when some hundred thousand individuals are gathered there. This figure includes the immature birds, of which part move directly to the moulting area from the winter quarters. Others approach the breeding range, but interrupt the migration and return to the moulting area early in summer (June).

After the flightless period, in September-October, the King Eider begin the autumn migration which leads due south along the west coast of Greenland to the ice-free coasts of SW. Greenland, to Labrador and Newfoundland. This implies that the Canadian population changes the flight direction from east (during moult migration) to south (during autumn migration), demonstrating that the moult migration, at least that of the adult males, belongs to the type D III.

When previously describing the tremendous concentrations of King Eider in the moulting area in West Greenland (Salomonsen 1950b) I advanced the opinion, for several reasons, that the majority of these birds must originate in Canada. The correctness of my assumption has now been proved by the extensive ringing of flightless King Eider in West Greenland, carried out in recent years under my direction. The recoveries in the breeding places are shown in Figure 3. The birds breeding farthest to the west must migrate about 2,500 km. before reaching the moulting area in Greenland.

The adult females do not participate in the moult migration to West Greenland, where they occur in the area only exceptionally. Some of the females, however, perform a separate moult migration which takes place later than in the males and does not go so far. In the middle of August 1934 Dalgety (1936) observed thousands of females in Clyde Inlet where they probably intended to spend the flightless period. This resembles the situation in the Common Eider in Slesvig, where at least some of the females halted their moult migration on the east coast of Jutland.

The males of the King Eider must possess a strong urge to leave the high-arctic region before they lose the power of flight. Being marine birds they cannot fly southwards into the interior of America, but must choose to fly either eastwards or westwards from the Canadian breeding places to reach low-arctic regions where they do not risk being overtaken by the new ice in the flightless stage. The nearest low-arctic area is central West Greenland and the Bering Sea, respectively. The ringing recoveries have demonstrated that the migratory divide between the two diametrically opposite movements (to W. Greenland and the Bering Sea) is situated near Victoria Island, exactly the geographical centre between W. Greenland and the Bering Sea. This shows that selection for the most appropriate (i.e. the shortest) route of moult migration has operated very precisely. The moult migration of the western population, which moves to the Bering region, has long been known as a spectacular phenomenon at Point Barrow in Alaska, but the position of the moulting area is unknown. It is probable that it is situated on the Soviet side of the Bering Strait.

Evidently there is a similar migratory divide in Siberia, the immature birds in particular collecting in enormous numbers in easternmost Siberia and near Kolguyev in north Russia, respectively (Portenko 1959), but the phenomenon has not been closely studied.

Steller's Eider *Polysticta stelleri*, breeding in high-arctic east Siberia and west Alaska, winters in a comparatively restricted area at the easternmost Aleutian Islands and the outer (western) part of Alaska Peninsula. It arrives there usually as early as August and immediately begins the wing-moult, i.e. it spends the flightless period in the winter quarters (type C III). It resembles the King Eider in congregating in enormous flocks, amounting to some hundred thousand individuals, within a restricted area. Ringing of flightless birds has been carried out also in this species (Jones 1965)

and recoveries have demonstrated that the majority of the birds originate from the east Siberian polar coast, westwards to the Lena delta which is situated 3,200 km. away. In unfavourable summers, when the breeding cycle is delayed, the moult migration is also postponed. The birds are then unable to reach the usual moulting area and are forced to perform the wing-moult at some (unknown) place *en route* (type B II or B III). In such years they do not arrive in the winter quarters until November (Jones 1965). A variation of this kind is not found in the King Eider in Greenland, and is altogether unknown in other species of ducks with large and compact aggregates of moulting birds. According to Jones both males and females participate in the moult migration and arrive simultaneously at the moulting area, although in separate flocks. The males, therefore, are probably not dependent on the females in their moult migration. It is incomprehensible to me, however, how the adult females can arrive in the moulting area as early as August. Jones does not mention the presence of immature birds and may probably have confused females with immature birds.

Evidently the Goldeneye *Bucephala clangula* has developed a moult migration but our knowledge about it is very fragmentary. Large flocks of males are known to gather and moult in the Matsalu National Park in Estonia (Kumari 1962) and a smaller number is known to spend the flightless period in Lake Tåkern in Sweden (Lönnberg 1935). In Denmark, which is situated much to the south of the Goldeneye's breeding range, one year old birds are commonly present from May to August in the Limfjord region in northern Jutland, frequenting the shallow brackish water of the coasts of the fjord as well as nearby fresh-water lakes. The Goldeneye is a numerous winter visitor in this area, and the young birds are probably remaining in the winter quarters through the subsequent summer, performing the wing-moult there without making any migrations. Certainly flightless specimens have been obtained in July and August. Adult females arrive in the Limfjord in September and a number of flightless individuals have been obtained there (Schiøler 1926). The scanty information available indicates that the moult migration of the males belongs to type B II, that of the females and immature birds to C I and C II. Apparently this species does not usually gather in large aggregates in the moulting areas.

The Long-tailed Duck *Clangula hyemalis* is a circumpolar species, breeding in the entire arctic zone. Everywhere in its breeding range this species is known to moult the flight-feathers in the breeding area proper, either solitarily (A I) or in small flocks (A II). Strangely enough the east Siberian population differs from this general pattern. Non-breeding birds, i.e. the males joined by the immature non-breeders, from Anadyr Land and the Tchuktch Peninsula perform an extensive northward moult migration across the Arctic Ocean to Wrangel Island where they gather in thousands although the species does not breed there (Portenko 1959). It has been mentioned already that this big island also forms an important moulting area for the Brent Goose.

Concluding Remarks

The description above has shown that the moult migration differs widely in the wildfowl. Within each tribe, however, the migration pattern is basically similar, at any rate as far as the participation of the sex and age groups is concerned. The migration pattern, therefore, can be used as an additional taxonomic character (Table I).

Table I. Participation in moult migration according to sex and age. xx : all individuals of group in question participate. x : only a small fraction of group in question participates.

	Adult males	*Adult females*	*Immature birds*
Anserini			xx
Tadornini	xx	xx	xx
Anatini[1]	xx		
Aythyini	xx	x	
Somateriini[2]	xx	x	xx
Mergini[2]	xx	x	xx

[1] Only the Wigeon has a tendency to moult migration in immature birds.

[2] These two tribes have been united in many recent studies, for example by Johnsgard (1960).

It is a common character in most species of ducks (not geese) with a separate moult migration that the individuals gather in moulting areas which have a milder climate than the breeding areas. In some cases they even perform the wing-moult in the winter quarters. It has been mentioned already that the high-arctic King Eider has a low-arctic moulting area, and the same holds good for the high-arctic Steller's Eider. The low-arctic and north-boreal species, such as Common Scoter, Velvet Scoter and

Eider, move to south-boreal (temperate) moulting areas, and the same holds good for various dabbling ducks. Only the Mute Swan, the Shelduck and the Red-crested Pochard, which as breeding birds belong mainly to the south-boreal zone, have their moulting areas in Europe situated in the same climatic zone. Apparently in these southern latitudes, with a milder climate, the necessity for moult migration is not so pronounced. Most species of wildfowl moult here in the breeding place proper or in its near vicinity. It also appears to be a general rule that stationary populations do not have any moult migration either. This may explain the fact that, so far as is known, no tropical species have developed a moult migration.

The moulting area is not always the first climatically suitable to be passed by the population during its post-nuptial migration. Traditions, historic factors or other circumstances may have caused it to be placed in areas which are further removed from the breeding area than appears to be necessary. The choice of moulting area is to a considerable degree dependent on the suitability of the locality and on biotic factors, primarily on peace from predators (foxes, man). The water depth is highly significant, for dabbling ducks as well as for diving ducks; the latter evidently has the capability of diving considerably reduced in the flightless stage. Extensive areas of shallow water, rich in food, and difficult of access or with good cover constitute the optimal conditions.

Some tendencies towards a development of moult migration are found also in other groups of birds made vulnerable by a simultaneous loss of flight-feathers. In all other groups than wildfowl it appears, however, to be developed only to a slight degree and in most species it awaits further study. The phenomenon is best known in the Coot, both the European species *Fulica atra* and the North American one *F. americana.* It has been noticed in many places (also in Denmark) that in certain suitable lakes the number of Coot increases in the summer time, and large flocks are known to congregate and spend the flightless period in places like Delta, Manitoba (Hochbaum 1955), and Ismaninger in Germany (Bezzel 1964). At the latter locality also the Water Rail *Rallus aquaticus* and probably even the Little Crake *Porzana parva* collect in order to perform the wing-moult. Apparently grebes *Podicipedes* sometimes have a moult migration, but only to a slight degree and not yet demonstrated with certainty. Savage (1964) observed that small flocks of Flamingo *Phoenicopterus ruber* spent the flightless period, in early September, in the salt Lake Rezaiyeh in north Iran, where they evidently did not breed. Elsewhere flamingos appear to moult the flight-feathers near the breeding place just before or after the breeding period. A most interesting case of moult migration in the Crane *Grus grus* has recently come to light. During a visit in May 1962 to the salt Lake Selety-Tengis, in Kazakstan, Gavrin observed a flock of about 3,500 flightless individuals, probably constituting birds which did not breed that year (Cuisin 1966, Stresemann 1967). Cranes apparently do not breed each year and perform a moult of the flight-feathers only in those years in which they do not breed. Gavrin's observation is the only known record of wing-moult in the Crane in the field (outside zoos) and this species must be extemely secretive during the flightless period.

Moult migration is definitely not developed in divers *Gaviae* and in auks *Alcae.* The latter may sometimes perform the autumn migration in the flightless stage, swimming very large distances, which in the case of Brünnich's Guillemot *Uria lomvia* off West Greenland may be more than 1,000 km. (Salomonsen 1967).

Birds with a gradual replacement of the flight-feathers do not perform moult migrations in the way that has been defined above. Nevertheless, some shore birds with extensive migrations divide the autumn migration into two parts separated by a resting period during which the wing-moult takes place in a definite moulting area. This parallels the situation in many species of wildfowl. Such a moult migration has been described only in one species, the Wood Sandpiper *Tringa glareola,* but it is undoubtedly developed similarly in some other related species, at least in the genus *Tringa.* The northern European breeding Wood Sandpipers leave the breeding area during high summer, usually in the latter part of July, and move in a non-stop flight southwards to southern Europe, for example the Camargue, where they temporarily interrupt the migration and, during a long resting period, perform the wing-moult before they start on the actual autumn migration to tropical Africa (Hoffmann 1957).

The moult migration is still imperfectly known and there is in most species much to be done before it is properly understood. The present review may, I hope, encourage further study of this interesting biological phenomenon.

References

ATKINSON-WILLES, G. L. (Ed.) 1963. *Wildfowl in Great Britain.* London: H.M.S.O.

BANKO, W. E. 1960. *The Trumpeter Swan. Its History, Habits and Population in the United States.* Washington, D.C.

BEHRENDS, O. 1955. Maritimt sommertræk over det østlige Sønderjylland. *Flora og Fauna* 61 : 1-16.

BEHRENDS, O. 1966. Om ederfuglenes (*Somateria mollissima* (L.)) sommertræk over Sønderjylland. *Flora og Fauna* 72 : 101-4.

BELLROSE, F. C. 1963. Orientation behavior of four species of wildfowl. *Auk* 80 : 257-89.

BEZZEL, E. 1964. Zur Okologie der Brutmauser bei Enten. *Anz. Ornith. Ges. Bayern* 7 : 43-79.

BRUUN, B. and O. SCHELDE. 1957. The autumn migration at Stigsnæs, S.W. Zealand. *Dansk Ornith. Foren. Tidsskr.* 51 : 149-67. (Danish, with English summary)

CHABRECK, R. H. 1966. Molting Gadwall (*Anas strepera*) in Louisiana. *Auk* 83 : 664.

CHRISTENSEN, N. H. 1967. Moult migration of Pink-footed Goose (*Anser fabalis brachyrhynchus* Baillon) from Iceland to Greenland. *Dansk Ornith. Foren. Tidsskr.* 61 : 56-66.

COOCH, G. 1957. Mass ringing of flightless Blue and Lesser Snow Geese in Canada's Eastern Arctic. *Wildfowl Trust Ann. Rep.* 8 : 58-67.

COOMBES, R. A. H. 1950. The moult-migration of the Sheld-duck. *Ibis* 92 : 405-18.

CUISIN, M. 1966. Les oiseaux-gibier du Kazakhstan (faunistique, écologie, valeur économique). (Review). *L'Oiseau* 36 : 292.

DALGETY, C. T. 1936. Notes on birds observed in Greenland and Baffin Land. *Ibis* 13(3) : 580-91.

DENNIS, R. H. 1964. Capture of moulting Canada Geese in the Beauly Firth. *Wildfowl Trust Ann. Rep.* 15 : 71-74.

ELTRINGHAM, S. K. and H. BOYD. 1960. The Shelduck population in the Bridgwater Bay moulting area. *Wildfowl Trust Ann. Rep.* 11 : 107-17.

EKMAN, S. 1922. *Djurvärldens utbredningshistoria på skandinaviska halvön.* Stockholm.

GOETHE, F. 1957. Uber den Mauserzug der Brandenten (*Tadorna tadorna* L.) zum Grossen Knechtsand. In MEISE, W. (Ed.), *Fünfzig Jahre Seevogelschutz* (pp. 96-106). Hamburg.

GOETHE, F. 1961a. A survey of moulting Shelduck on Knechtsand. *Brit. Birds* 54 : 106-15.

GOETHE, F. 1961b. The moult gatherings and moult migrations of Shelduck in north-west Germany. *Brit. Birds* 54 : 145-61.

HANSEN, E. and N. H. CHRISTENSEN. 1954. The spring-migration at the Skaw. *Dansk Ornith. Foren. Tidsskr.* 48 : 156-72. (Danish, with English summary)

HANSON, H. C. 1965. *The Giant Canada Goose.* Carbondale, Illinois.

HOCHBAUM, H. A. 1955. *Travels and Traditions of Waterfowl.* Minneapolis.

HOFFMANN, L. 1957. Le passage d'automne du Chevalier sylvain (*Tringa glareola*) en France méditerranéenne. *Alauda* 25 : 30-42.

HOOGERHEIDE, J. and W. K. KRAAK. 1942. Voorkomen en trek von de Bergeend, *Tadorna tadorna* (L.), naar aanleiding van veldobservaties aan de Gooije kust. *Ardea* 31 : 1-19.

JOENSEN, A. H. 1964. An investigation of the moulting areas of the Common Scoter (*Melanitta nigra*) at the south-west coast of Jutland, Denmark, 1963. *Dansk Ornith. Foren. Tidsskr.* 58 : 127-36. (Danish, with English summary)

JOHANSEN, H. 1945. Races of Bean-Geese. *Dansk Ornith. Foren. Tidsskr.* 39 : 106-27. (Danish, with English summary)

JOHNSGARD, P. A. 1960. Classification and evolutionary relationships of the sea ducks. *Condor* 62 : 426-33.

JONES, R. D. JR. 1965. Returns from Steller's Eiders banded in Izembek Bay. *Wildfowl Trust Ann. Rep.* 16 : 83-85.

JØRGENSEN, J. 1941. Sortandens (*Melanitta nigra*) Juli-Augusttræk. *Dansk Ornith. Foren. Tidsskr.* 35 : 137-43.

KUMARI, E. 1962. The wildfowl in the Matsalu National Park. *Wildfowl Trust Ann. Rep.* 13 : 109-16.

KUYT, E. 1962. Northward dispersion of banded Canada Geese. *Canad. Field Nat.* 76 : 180-1.

LEBRET, T. 1950. The sex-ratios and the proportion of adult drakes of Teal, Pintail, Shoveler and Wigeon in the Netherlands, based on field counts made during autumn, winter and spring. *Ardea* 38 : 1-18.

LEBRET, T. 1952. Pre-moult migration of a female Gadwall, *Anas strepera* L., and two female Wigeon, *Anas penelope* L. *Ardea* 40 : 75-6.

LIND, H. 1957. A study of the movements of the Sheld-Duck (*Tadorna tadorna* (L.)). *Dansk Ornith. Foren. Tidsskr.* 51 : 85-114. (Danish, with English summary)

LØNNBERG, E. 1935. *Svenska jåglars flyttning.* Stockholm.

MATHIASSON, S. 1963. Untersuchungen über jährliche Fluktuationen nichtbrütender Höckerschwäne, *Cygnus olor* (Gm.) in Schonen, Südschweden. *Lunds Univ. Årsskr.* N.F. Avd. 2. 58. Nr. 13.

MATHIASSON, S. 1964. Ett bidrag till kännedomen om knölsvanens, *Cygnus olor*, ruggningsansamlingar i Sverige. *Göteborgs Naturhist. Mus. Årstryck* 1964 : 15-19.

MATTHEWS, G. V. T. 1963. 'Nonsense' orientation as a population variant. *Ibis* 105 : 185-97.

MATTHEWS, G. V. T., J. A. EYGENRAAM and L. HOFFMANN. 1963. Initial direction tendencies in the European Green-winged Teal. *Wildfowl Trust Ann. Rep.* 14 : 120-3.
MAYAUD, N. 1966. Contribution a l'histoire de *Netta rufina* (Pallas), La Nette a Huppe rousse en Europe occidentale. *Alauda* 34 : 191-9.
MILNE, H. 1965. Seasonal movements and distribution of Eiders in northeast Scotland. *Bird Study* 12 : 170-80.
ORING, L. W. 1964. Behavior and ecology of certain ducks during the post-breeding period. *J. Wildl. Mgmt.* 28 : 223-33.
OTTOW, B. 1956. Ergebnisse der Vogelberingung in Sowjetrussland. (Review). *Vogelwarte* 18 : 226-30.
PALM, B. 1950. The migration of Teal (*Anas crecca* L.) in Denmark. *Dansk Ornith. Foren. Tidsskr.* 44 : 147-50. (Danish, with English summary)
PALUDAN, K. 1965. Migration and moult-migration of *Anser anser*. *Danske Vildtundersøgelser* 12 : 1-54. (Danish, with English summary)
PLESKE, T. 1928. Birds of the Eurasian Tundra. *Mem. Boston Soc. Nat. Hist.* 6 : 111-485.
PORTENKO, L. A. 1959. Peculiarities of bird-migration in the Arctic. *Aquila* 66 : 119-34. (Hungarian, with English summary)
PREUSS, N. O. 1965. The migration of Danish Red-crested Pochards (*Netta rufina* (Pallas)). *Dansk Ornith Foren. Tidsskr.* 59 : 38-40. (Danish with English summary)
SALOMONSEN, F. 1943. Grågæssene (*Anser anser* (L.)) på Vejlerne. *Dansk Ornith. Foren. Tidsskr.* 37 : 188-9.
SALOMONSEN, F. 1950a. Common Scoters (*Melanitta nigra* (L.)) summering off the west-coast of Jutland. *Dansk Ornith. Foren. Tidsskr.* 44 : 171-2. (Danish, with English summary)
SALOMONSEN, F. 1950b. *The Birds of Greenland.* Copenhagen: Ejnar Munksgaard.
SALOMONSEN, F. 1955. The evolutionary significance of bird-migration. *Dan. Biol. Medd.* 22, No. 6 : 1-62.
SALOMONSEN, F. 1967. *Fugletrækket og dets gåder.* 2nd ed. Copenhagen.
SAVAGE, C. 1964. Lake Rezaiyeh: a specialised summer habitat for Shelduck and Flamingos. *Wildfowl Trust Ann. Rep.* 15 : 108-13.
SCHIØLER, E. L. 1925. *Danmarks Fugle.* Vol. 1. Indledning og Andefugle (*Anseriformes*). Copenhagen.
SCHIØLER, E. L. 1926. *Danmarks Fugle.* Vol. 2. Oversigt over Grønlands Fugle og Andefugle (*Anseriformes*) II, Dykænder (*Fuligulinae*). Copenhagen.
SCOTT, P. 1951. The Perry River Expedition, 1949. *Wildfowl Trust Ann. Rep.* 3 : 56-64.
SCOTT, P. and J. FISHER. 1953. *A Thousand Geese.* London.
STIRLING, T. and A. DZUBIN. 1967. Canada Goose molt migrations to the North-west Territories. *Trans. N. Amer. Wildlife & Nat. Res. Conf.* 31 : 355-73.
STRESEMANN, E. 1940. Zeitpunkt und Verlauf der Mauser bei einigen Entenarten. *Journ. Ornith.* 88 : 288-333.
STRESEMANN, E. 1967. Ein sammelplatz mausernder Kraniche (*Grus grus*). *Journ. Ornith.* 108 : 81-82.
SVARDSON, G. 1959. Sjöfågelsträcket i Kalmarsund 1958. *Svensk Jakt.* 97 : 128-30.
SZIJJ, J. 1965. Okologische Untersuchungen an Entenvögeln (Anatidae) des Ermatinger Beckens (Bodensee). *Vogelwarte* 23 : 24-71.
TAYLOR, J. 1953. A possible moult-migration of Pink-footed Geese. *Ibis* 95 : 638-42.
TEPLOV, V. F. and N. N. KARTASHEV. 1958. Wildfowl research in Russia. Biological Foundations for the regulation of wildfowling in the central districts of the European part of the U.S.S.R. *Wildfowl Trust Ann. Rep.* 9 : 157-69.
USPENSKI, S. M. 1960. The Brent Goose (*Branta bernicla* L.) in the Soviet Union. *Wildfowl Trust Ann. Rep.* 11 : 80-93.
USPENSKI, S. M. 1965a. *Die Wildgänse Nordeurasiens.* Wittenberg Lutherstadt.
USPENSKI, S. M. 1965b. The geese of Wrangel Island. *Wildfowl Trust Ann. Rep.* 16 : 126-9.
VUCZETICS, V. and A. TUGARINOV. 1937-39. *Seasonal distribution and migration of ducks (subfam. Anatinae) on the base of bird ringing in the U.S.S.R.* Moscow. (Quoted after STRESEMANN, E. 1940)
WEISMANN, C. 1931. *Vildtets og Jagtens Historie i Danmark.* Copenhagen.
WOLFF, W. J. 1966. Migration of Teal ringed in the Netherlands. *Ardea* 54 : 230-70.
WYNNE-EDWARDS, V. C. 1952. Zoology of the Baird Expedition (1950). I. The birds observed in Central and South-East Baffin Island. *Auk* 69 : 353-91.
WYNNE-EDWARDS, V. C. 1962. *Animal Dispersion in relation to Social Behaviour.* Edinburgh and London.
ZINK, G. 1964. Ein ungelöstes Rätsel: Der Herbstzug der Kolbenente. *Kosmos* 1964 : 134-6.

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