Field studies on the Harlequin Duck in Iceland

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Summary

A five-year study of a breeding colony of about 50 pairs of Harlequin Ducks on the River Laxá near Mývatn, north-east Iceland, has added some numerical data on breeding behaviour, chronology and output to the meagre published information. The Harlequins return from the coats to the breeding river at the end of April and begin to lay from the middle of May. The interval between eggs is normally 2–4 days. Most eggs are laid in early June. The average clutch on the Laxá is 5.5 eggs. Many eggs are collected (quite legally) by man. The Mink is probably the next most important predator. In recent years the ducks have increasingly nested on the banks of small remote streams instead of on islands in the river. Duckling survival is relatively high, with losses of about a third in the first week but few later. The males desert the females early, moving away from the nesting area, and play no parental role. The social and sexual behaviour in May, June and July is described. Territorial behaviour is most apparent in areas where pairs are scarce. Visual displays are probably less important than vocalizations. Feeding activity, described in detail, shows a diurnal rhythm, with greatest activity around 8–9 p.m. and 5 a.m. Harlequins are far more efficient divers in a fast-flowing river than other ducks. On the coast in winter they are much more gregarious and active than in summer.

Introduction

Throughout its breeding range the Harlequin Duck *Histrionicus histrionicus* lives an inconspicuous life often in rough mountainous areas far from civilization. This is the main reason for our lack of detailed information on its breeding biology. A characteristic feature of the life of the Harlequin at its breeding grounds is its preference for turbulent streams and waterfalls. In this respect the Harlequin is unique among the ducks of Europe and North America but it shares this adaptation to fast running rivers with two genera of ducks in the southern hemisphere, *Merganetta* and *Hymenolaimus*.

The biology of the Harlequin in winter, when it is found at sea, is poorly known.

This paper is a preliminary report based on a series of field studies of Icelandic birds conducted during six expeditions during the five years 1960–64. Five of the expeditions, varying in length from two weeks to three months, fell between 10th May and 15th August while the sixth was carried out between 10th December 1964 and 10th January 1965. The members of the expeditions have changed and I have been accompanied by both English and Swedish ornithologists. The Harlequin has been observed in several parts of Iceland. The main study area has however been the River Laxá at the outlet of Mývatn, the well-known duck refuge in north-east Iceland. The area is one of the best for Harlequin in Iceland and has the advantage of being situated near colonization where the expedition could be based.

My inability to reach Mývatn before 10th May has resulted in a serious deficiency in my material concerning the first weeks of activity at the breeding ground. Nor, as my investigations have ended in mid-August or earlier, have I observations of the later stages in the growing-up of the young.

Each year immediately after my arrival at the study area in May I have tried to estimate the population size, with special reference to sex ratios, and to compare the progress of breeding activities with those of other years. The Harlequin is a rather late nester in Iceland and as a rule egg-laying is not completed until mid-June. Fresh clutches may be found as late as the first week of July.

Though the major part of pair-formation seems to be finished by the second week of May when my observations begin, until mid-June there are usually fairly good opportunities to watch displaying Harlequins as well as to make notes on general behaviour. During the last weeks of June the activity of the Harlequins decreases rapidly as the females begin to incubate and the males congregate and prepare for their departure from the breeding ground. The moult period has also started and some individuals have already lost their spectacular reddish and bluish nuptial plumages.

From mid-June onwards broods are regularly seen and parental care, growth of the young, etc. can be studied. I have made efforts to establish the nature and importance of different mortality factors affecting the Harlequin broods. In addition the behaviour of the downies has been compared with other species of ducks frequenting the same habitat.

The male Harlequins leave the breeding ground at the end of June and go to the sea. Little is known about this migratory movement.

In addition to the observations at the breeding grounds I spent some days in the fishing village of Grindavík south-west of Reykjavík in the south in December 1964 to study the winter ecology and

ethology of the Harlequin. The weather was very unfavourable and prevented any successful work.

Occurrence in Iceland

Icelandic Harlequins are highly sedentary and rarely leave the island. From September until early spring they are sea-dwellers and flocks are seen diving for food in the surf all around the coast. The rest of the year they spend at their breeding grounds up in the rivers, sometimes far into the interior (Hantzsch 1905, Timmermann 1937–49, Gudmundsson 1961). They are widely distributed all over Iceland and are to be met with in most streams in more or less abundance. Even in the isolated rivers in the central parts of the country one can expect to find Harlequins and in this respect they show similarities with the Long-tailed Duck *Clangula hyemalis*. I have seen Harlequins in rivers flowing through sterile 'lava-gravel-deserts' with a minimum of vegetation on the banks of the rivers.

According to Gudmundsson (1961) the Harlequin has been observed on lakes only on a few occasions and I have myself only twice seen it in Mývatn (in June 1960 and July 1963).

Although Harlequins breed in most rivers their numbers cannot be compared to those of other ducks. There are not many places where the population exceeds 20 pairs in a limited area, as on the River Laxá. The Icelandic rivers are usually relatively poor in plants and animals and cannot support any greater number of waterfowl. It seems as if the rivers with concentrations of Harlequins of the order stated above offer the optimal requirements of food and possibly also of nest-sites. The Harlequin can hardly be regarded as a colonial nester anywhere in Iceland. Where sizeable populations occur they nest in clusters depending on the topography of the shores and islands in the river.

Winter habitat

No attempts have so far been made to estimate the total number of Harlequins in Iceland. A winter census along the coasts would probably give some idea of the size of the population. However, regular counts have been carried out only along the south-western coasts. From Grindavík to Staður (approximately 5 km.), Gudmundsson (1961 and personal communications) has counted up to 600 birds at the end of December. Along the same part of the coast I saw about 200 Harlequins for a week in December 1964. This part seems to be particularly favoured by the Harlequin in winter and it is the best place for field-observations. It is highly possible that there are more places in Iceland with as many or more wintering Harlequins still unknown because of their inaccessibility. Harlequins frequent all coastal waters of Iceland but in varying abundance. They are particularly fond of places where the surf breaks directly against the rocks. Consequently they seldom select deep bays or fjords but are seen around the outermost peninsulas. Their choice of winter habitat is determined by the bottom conditions and hence the availability of suitable food. The Harlequin is seldom seen feeding close to the shore but frequents a zone between approximately 100 and 300 m. from the shore. Apparently they prefer rather shallow waters with a depth not exceeding 3–4 m. At the winter quarters near Grindavík referred to above I usually saw them in flocks diving close to the low skerries which were exposed during tide. I never saw them use either the skerries or the shore as loafing spots.

No details as to the food consumed by the Harlequins when at sea were collected by me. They share the habitat with the Eider *Somateria mollissima* in particular. Probably the food of the Harlequin is very much the same as that of the Eider, i.e. molluscs and crustaceans. Stomach analyses of a small sample of Icelandic birds seem to confirm this (Gudmundsson 1961).

Behaviour in winter

Outside the breeding season the Harlequin is very sociable and is rarely seen solitary. While they are quite tame at the breeding grounds they are quite shy in winter and usually they took off when I was 500 m. away. The Eiders and Red-breasted Mergansers *Mergus serrator* let me approach to within 100 m. Although the Harlequins are in full brilliant breeding plumage, the males are not easy to spot in rough sea and poor light. The 'general appearance' is the best field-characteristic and dense flocks of Harlequins are unmistakable even at long range to the trained observer (cf. Bergman 1935).

Feeding was the predominating activity in December when I studied them on the south coast. The Harlequins were seen foraging from 10 a.m. until 3 p.m. No observations could be made during the rest of the day due to the lack of light. I am quite sure that they feed also in the dark to a large extent.

They feed in parties of 5–25 birds and usually dive simultaneously at the moment just before they reach the top of a wave, that is to say 'into' the wave. I believe this behaviour has something to do with the difficulties of maintaining position in

relation to the suitable places on the bottom in rough seas. It is also possible that food items are whirled up from the bottom by underwater currents caused by the conditions on the surface.

The length of the dives at sea in winter are about the same as in the rivers during the summer. I usually timed dives of 15–25 sec. and Alford (1920) found the same. I twice recorded dives of 45 sec.

I was able to collect some information on different sexual behaviour related to pair-formation but the end of December was obviously not the best time for that sort of study. Only a relatively small number of Harlequins were paired by that time. I found twelve pairs with apparently strong pair bonds out of some 200 birds. The paired Harlequins were usually seen well apart from the large flocks of unpaired birds. Some pairs fed together but the pairs always kept some distance between each other. No display activity was recorded except two cases of Inciting* behaviour by females when strange males came too close to the pair. The posture of an Inciting female will be described in another section of this paper.

In the flocks of 10 to 30 unpaired Harlequins 'courting-parties' were frequently seen, with a female followed by 3–8 males. The males displayed elaborately with their necks stretched and tails erected. They were seen to perform head movements (named Head-nodding by Myres (1959a)) with short intervals. Every now and then a male was seen to rush after the female and chase her for some 10 m. until she escaped by diving. The other males of the 'courting-party' then intensified their display; stretched their necks and performed Head-nodding but did not rush after the other male. No fighting was ever recorded. Occasionally a male chased another male for a few meters. Several ritualized movements of the type Body-up-with-wing-flap were seen to be performed by the males. The difficult conditions however made it impossible to get a clear picture of what happened. For the same reason no vocal activity could be heard. However, I am almost sure that they were quite noisy at times as the males were seen with open bills. No female displays were recorded.

Most displays were recorded about 2 p.m. The rest of the hours of daylight the ducks spent feeding and preening. Several different comfort movements could be seen such as 'preening-behind-wing', 'preening-dorsally' and 'abdominal preening'. It is possible that some of these activities are involved in some of the sexual displays but none of them were clearly ritualized.

Migratory movements

According to Gudmundsson (1961) the whole Icelandic population spends the winter in the sea around the coast of Iceland. Not a single record from freshwaters in winter is known. A few individuals have occasionally been recorded in other parts of Europe but not all of these are satisfactorily documented.

At the end of April or beginning of May the Harlequins start their 'spring migration' from the sea to the breeding grounds. Before that they have moved up the fjords to the river-mouths. The migration up into the river probably takes some time as they are said to swim most of the way. The sexes migrate together in the spring while there is a marked sex-difference in the 'autumn migration'.

At the end of June and beginning of July the males abandon their mates and leave the breeding ground in flocks heading for the sea. This time they move faster and fly most of the way if they are not too heavily moulted. The details are still somewhat obscure and contradictory hypotheses exist (Gudmundsson 1961, Sellick 1960).

The females usually remain at the breeding ground with the young until these are fledged, though sometimes when they are a few weeks old the female may start to move slowly downstream with the brood.

In the other breeding areas of the species (North America, Greenland and eastern Siberia) the migratory movements of the Harlequin appear identical in major patterns with those in Iceland (Gabrielson and Lincoln 1959, Salomonsen 1962, Bergman 1935), being confined to movements between the breeding grounds and the sea, with possibly some movements up and down the coasts in winter.

Habitat selection

No other European or North American duck is so strictly bound to fast running streams during the breeding season as is the Harlequin, though other species may secondarily occupy the same ecological niche (e.g. Barrow's Goldeneye *Bucephala islandica*).

In some American literature the Harlequin has been included in the list of 'hole-breeding' ducks or at least mentioned as a species laying in crevices (Kortright 1953, Johnsgard 1962). The Harlequin has also been reported to breed in hollow trees in the forested regions of its North American

* Here and elsewhere in this paper I have followed the convention of capitalizing the names of ritualized movements, introduced by Moynihan (1955).

range. In Greenland and Iceland no trees of sufficient size are to be found and the Harlequin is restricted to holes and crevices in the lava or in the banks of the rivers.

In Greenland Salomonsen (1950-1) states that the Harlequin breeds in two distinctly different habitats; (*a*) turbulent streams, and (*b*) along the coast on the outermost skerries. The latter category is not known from Iceland.

In Iceland the Harlequin frequents all rivers that can provide enough food and suitable nest-sites. Looked upon as a whole the biota of the Icelandic rivers is rather poor qualitatively as well as quantitatively. However, in some places where sizeable populations of Harlequins can be found both vegetation and aquatic fauna is unusually rich, for instance in the River Laxá close to Mývatn. There the small islands in the river on which the ducks breed are densely covered by low scrub mostly birch (*Betula* spp.) and willow (*Salix* spp.) and the herbage is rich in June–August. Mývatn is well-known as a 'good' area for flies (often called mosquitoes) and as a matter of fact the lake has got its name because of this (Midge Lake). Several species occur of which *Simulium vittatum* predominates around the River Laxá. *Chironomida* spp. are also very abundant.

Of the factors controlling distribution and breeding frequency of the Harlequin in Iceland the availability of suitable food seems to play the most important role. Gudmundsson (1961) found in the stomachs of 12 Icelandic birds living on fresh-water mainly Simuliidae and to some extent Chironomidae and Trichoptera. As Simuliidae comprise the greater bulk of nutrition of the Harlequin and are strictly confined to fast running waters, it seems reasonable to assert that the occurrence of this group of flies to a considerable extent regulates the density and distribution of the Harlequin in Iceland.

The availability of nest-sites as a determining factor has already been hinted at. However, I think this factor is of secondary importance compared with food. The Harlequin prefers to nest on inaccessible islands surrounded by rushing water. Due to the absence of trees they lay their eggs in caves and holes in the lava, though sometimes the nests are found in rather open situations, although as a rule under dense bushes. Iceland was formerly covered by deciduous forests, which were completely destroyed by the first settlers. The Harlequin may thus have utilized trees and hollow trunks as nest-sites long ago in Iceland.

The preference for inaccessible islands is of certain survival value as parts of Iceland are or have been much haunted by Arctic Fox *Alopex lagopus* which used to be considered as the most serious predator on wildfowl. Recently the Mink *Mustela vison* has spread in Iceland and caused marked decrease in the number of ducks at several places and at Mývatn and its surroundings in particular. The increased occurrence of Mink has even changed the habit of the ducks in a few cases. For instance, the Harlequins in the River Laxá now seem to desert the islands (except for the completely inaccessible ones) and the banks of the river during egg-laying. Instead the females move up along the small brooks which connect with the main river. Nests may be found several kilometres up. The local farmers, who are well acquainted with the ducks, confirm my own observations of this marked change.

The population of the River Laxá

In order to obtain comparable figures as well as for practical reasons a section of the river about 5 km. long, stretching from the outflow in the lake down to the farm named Hofsstaðir, was chosen for the chief studies of the Harlequins. My investigations indicate a regular breeding population of at least 50 pairs in this area. Exact figures are very difficult to give, because the number of breeding and non-breeding birds is very difficult to establish and nest records are incomplete because not all the islands could be visited. The Harlequins breed all the way down the river but nowhere else in concentrations like those close to the lake. Few localities in Iceland support a larger population of Harlequins than this part of the River Laxá, or are better suited for field studies.

I have no first-hand data on the time of return of Harlequins to their breeding places but I have been told by the farmers that the first Harlequins are to be seen at the end of April or in the very first days of May. This date probably varies little from year to year, as the Harlequin is independent of the break up of the ice, since the turbulent rivers never freeze.

To determine the sex-ratios counts were carried out at different times in 1961–64 in the study area. Ideally the counts required more than one observer but I did not always have a co-operative ornithologist at hand. The results from all four seasons are compiled in Table I. The material collected is by no means sufficient but indicates the main patterns in the variations of the sex-ratio. A significant preponderance of males is noticeable. On the basis of all my observations at the River Laxá, the sex-ratio can be estimated as approximately 130

Table I. Sex ratios in Harlequin Ducks on the River Laxá in May and June.

	Data in the form, males: females (% males)		
Year	*20–31st May*	*10th June*	*23rd June*
1961	95:43 (69%)	26:11 (70%)	5:5 (50%)
1962	143:92 (61%)	39:20 (66%)	11:9 (55%)
1963	117:92 (56%)	41:30 (58%)	18:13 (58%)
Sum	355:227 (61%)	106:61 (63%)	34:27 (56%)

males per 100 females, or 57% males and 43% females. The counts in May average about 61% males but the figures from 1961 (69% males) may be too high, due to my inexperience and the fact that females are a lot easier to overlook than the males.

By the end of May some females may have started to incubate while some of them are not to be seen on the water as they are inspecting nest-sites, though usually accompanied by their mates. When the females start to incubate the majority of the males congregate and leave the breeding ground so that the numbers of both sexes that are visible fall. The results also give an idea of the time of laying: after 10th June the number of females decreases markedly but it increases again about mid-July when the eggs hatch.

Predation

The population of Harlequins on the Laxá is well-known. Barrow's Goldeneye breeds regularly in the river (although the majority breeds in the lake itself, especially in parts with plenty of lava-formations) and so do the Long-tailed Duck and Goosander *Mergus merganser*. Most species present on Mývatn occasionally occur in the river, some of them perhaps more often than others, for instance Wigeon *Anas penelope*, Mallard *A. platyrhynchos*, Scaup *Aythya marila* and Red-breasted Merganser.

All local farmers agree that the numbers of ducks (not only Harlequins) have decreased, on the river as well as on Mývatn itself. Gudmundsson (1963) has discussed the reasons for the decreases, which are much more marked in some species than others.

The ducks have few natural enemies in the area. Today only the Mink and some predatory birds are potential enemies. The Arctic Fox is lacking in the immediate vicinity of the lake. The damage caused by the Mink has not been investigated enough. Of course it does a lot of harm as a rapidly increasing newcomer but I think that there soon will be a stabilization. The Mink certainly is a threat to the fishing in the lake, which is very important. I think the Harlequin is more threatened by the presence of Mink than any other duck due to its restricted habitat selection.

Several pairs of Icelandic Gyrfalcon *Falco rusticolus islandus* breed near the lake. Investigations at some eyries indicate that the falcon preys on ducks to a large extent in this part of Iceland but no remains of Harlequin have been found. I have occasionally watched the falcon hunting along the river valley but I never saw it attack any duck. Harlequins rarely take off from the water when a potential predator approaches as Barrow's Goldeneye and other ducks do.

Far more harmful to the ducks are the Arctic Skua *Stercorarius parasiticus*, Great Black-backed Gull *Larus marinus* and Raven *Corvus corax*. The first two species are not very numerous but several pairs of Raven breed. I have no exact figures as to the amount of eggs or young each of these predators take, though investigation is in progress.

In and around Mývatn extensive egg-collecting is practised but exact figures are not obtainable at present. It mainly concerns the ducks and all collecting is done by the local farmers. Formerly eggs were taken only for consumption. Now, however, agents purchase a lot of them to export for hatching purposes. These transactions are now being controlled by the Icelandic authorities and some species will be banned. Although difficult to keep alive and at present impossible to breed in captivity, the Harlequin is much in demand and the eggs fetch high prices. The majority of Harlequins' eggs exported are collected along the River Laxá, which in the long run is bound to affect the population adversely. By law the farmers must leave four eggs in each nest and this is the reason why so many 'short' clutches and broods can be seen in the area. Whether the Harlequins would lay repeat clutches if all the first eggs were taken is not known. The taking of eggs of ducks around Mývatn is especially hazardous to the Harlequin and Common Scoter *Melanitta nigra*. Other species do not seem to be so seriously affected. The taking of eggs of the two species mentioned will be prohibited very shortly (Gudmundsson, personal communication).

Notes on general behaviour

As a consequence of its extraordinary adaptation to its habitat the Harlequin exhibits several conspicuous specific characteristics.

The drake Harlequin has a spectacular and very conspicuous nuptial plumage which yet matches the whirling and foaming water magnificently so that it is tempting to call it a cryptic colouration. Anyone who has experienced the duck in its natural environment can affirm that the male is not easy to detect either when sitting against a background of green vegetation or rumbling down a river surrounded with foaming water. The female has of course an undeniably cryptic plumage.

Harlequins often sit on stones submerged in the middle of the river or close to the banks. When disturbed they usually move out into the river and let the current carry them away. The pairs normally stick tight together with the female ahead. As they are transported down the rapids they demonstrate great manoeuvring skill; the ducks so to say 'sit high' on the water and no propulsory movements can be seen. They constantly jerk their heads in a way very similar to the Head-nodding referred to above but having no apparent display function. I prefer to call these unritualized head movements simply 'nodding'. They occur in many different phases and situations. The movements described as 'nodding' in a way remind one of other familiar species frequenting similar habitats, for instance the Dipper *Cinclus cinclus* and the Grey Wagtail *Motacilla cinerea*. They are also typical of Torrent Ducks and Salvadori's Ducks.

When moving against the current Harlequins adopt three main types of locomotory behaviour:

(*a*) They dive repeatedly in order to reach the place towards which they are headed. This is not very often done and then only for short distances, as when crossing to the opposite side of the river.

(*b*) They swim directly against the current, trying to make use of the whirls in the most advantageous manner. They stick close to the shores where the current is less powerful or they rush in stages from stone to stone or between small islands, taking advantage of the leeward sides of the obstacles in the river. Constantly they are seen to perform the typical 'nodding' and they make strong propulsory movements with their feet.

(*c*) Where the current is too strong for swimming and no obstacles are in the way they rush straight up the river with their bodies lifted out of the water, running like a fast speedboat. Myres (1959a) very appropriately compared this behaviour to that of ducklings running to their mother. The posture they assume is very distinctive with body and head horizontal.

The Harlequin is an expert diver. Diving technique and foraging behaviour are discussed in a later section.

One of the striking features of the breeding ground is the presence of 'clubs' where paired and unpaired birds spend the first days after arrival and where males and unpaired females (or females off duty) loaf from about 10th June and onwards. Very little activity characterizes the 'clubs' and only when newcomers arrive may the birds act for a moment in some way or another. Preening and sleeping are the only activities an observer will usually see even if he watches a 'club' for several hours. The Harlequin is much less active at the breeding ground than the Barrow's Goldeneye for instance. The requirements of a good 'club' are in general terms a shallow place with a lot of obstacles sticking up in the middle of the river and plenty of rapids. Occasionally a 'club' is situated on an island or on the bank of the river. A big 'club' may be occupied by up to 40–50 birds at a time. The 'club' can be described as a public loafing spot.

Several authors have paid attention to the problems connected with the behaviour and the place of residence of the sexually immature Harlequins in the summer (Salomonsen 1950-1, Gudmundsson 1961). Harlequins probably do not reach sexual maturity until the age of two years and consequently they spend at least one summer as non-breeders. Both in Iceland and Greenland it has been shown that the yearlings spend their first summer at sea, though Gudmundsson states that sometimes the yearlings may accompany the adults into the fjords but no further. I have annually recorded one or two males at River Laxá which definitely were yearlings judging from their plumage, which lacked the bright colours of the adults. I estimate that about two per cent of the males at River Laxá are non-breeding yearlings which disappear together with the adults when they go to sea when the incubation period has started. The one-year-old males show less display activity than the adult males. One-year-old females cannot be identified in the field.

Nobody has so far credited a 'flight-intention' movement to the Harlequin. There is no obvious reason why such behaviour should be lacking in this species although the Harlequin perhaps has fewer enemies than most other ducks. During excitement, as when a potential predator approaches a flock of Harlequins, an

intensified 'nodding' is to be noted with rapid sequences of short elliptic head movements and the neck held at about 70° with the water. When the intruder gets nearer the Alarm-Posture is assumed. This is a stretching out of the neck with the neck feathers slightly expanded which makes the whole appearance look more impressive. No, or very minute, movements accompany the Alarm-Posture. As stated above the Harlequin seldom escapes by flight; their normal way of getting away from an enemy is to swim or dive.

The Harlequins fly low over the water and follow all bends of the river, never cutting off over land and never flying over bridges. The flight, which is somewhat reminiscent of that of the Common Scoter, appears very fast and erratic. It is possible that the speed is exaggerated owing to the short wings and rapid wing-beats of the Harlequin. They use flight as a means of transportation for longer distances only and tend to fly in dense flocks.

They are more liable to fly at the end of May than in the first half of June, probably in consequence of the restlessness that characterizes the period just before egg-laying when the females are very active in searching for nest-sites and the males still have not started to moult and cluster at the 'club'.

The Harlequin is extremely unwilling to use its wings as a means of escape when at the breeding ground, in contrast to its behaviour in winter.

Territory

Myres (1959a), quoting Darcus, states that each pair has its own territory at least for a short period of the season. I have found that on the Laxá the territorial boundaries are very indistinct and sometimes seem to be lacking. This might be a result of the relatively sociable behaviour of the species at places with concentrated populations. In places where only a few pairs breed the maintenance of territories seems more pronounced and each pair occupies and defends a small section of the river. This can be seen when you walk along the river and encounter a pair of ducks. You then drive them in front of you until they reach the outer limit of their territory when they turn against you and swiftly pass you and return to their original spot.

The pairs on the Laxá that do maintain territories are mostly birds breeding on the periphery of the area. In the densely populated central parts of the breeding ground I am often inclined to relate the 'territorial behaviour' of the male to its mate rather than to a certain area.

At places where more than one pair dwell the pairs stand well apart and the mated birds close together. When a female leaves its mate and by chance approaches a strange male her mate immediately assumes an attitude which besides being a display of courtship origin probably has some bearing on 'territorial behaviour'. He lowers his neck and head and performs repeated Head-nodding and approaches the strange male swimming or walking (depending on the circumstances). Normally no other activities take place but the male and female return to their starting point to preen or sleep. Both when a male defends a certain area and when he limits his 'territorial behaviour' to the female he maintains a loafing spot (cf. 'defense-of-the-mate-behaviour' in Velvet Scoter *Melanitta fusca* (Koskimies and Routamo, 1953)).

Courtship and agonistic behaviour

The different displays of the Harlequin are inadequately known and described in the literature. The most detailed description of the sexual behaviour of the Harlequin is that by Myres (1959a) whose terminology is adopted in this paper.

Bretherton (1896) has described a complex display in which the male throws his head back and then forward with a jerk and simultaneously the bill is opened and he utters a call. The wings are said to be slightly expanded. I refer to this paper because it has been much quoted. So far I have never recorded any such behaviour or any similar. However, his description is not very detailed. Yeates (1951) recorded 'many scurryings, divings and displays with heads thrown back into scapulars and whipped forward with a quiet whistle'. This also is a very vague description. Michael & Michael (1922) published an account in which they state that a pair they watched bobbed their heads and bowed to each other and swirled round uttering chatty sounds and dipped their bills in the water. My own observations have more in common with this description than with those referred to above.

The male displays (except copulatory behaviour) in the tribe Mergini show few similarities and relationships cannot be inferred from them. The most striking feature of the display of *Histrionicus* is the paucity of visual activities. This lack of elaborate displays is evidently compensated by a vocal display superior to most of the other diving ducks. In this respect the Long-tailed Duck can be compared to the Harlequin. Both species form monotypic genera. It is suggested by Myres (1959a) 'that paucity of visual displays is an

indication of isolation from related groups, due to ancestral divergency'.

The Head-nodding is undoubtedly the fundamental display movement of the Harlequin in most situations (cf. winter observations above). Myres (1959a) believes that this is the only male display. The Head-nodding is present in both sexes. The motivation of the Head-nodding is not yet satisfactorily studied and its degree of ritualization is in many cases doubted. I have not been able to record enough courtship and agonistic displays at the breeding ground to separate these two components from each other with certainty.

The 'ordinary', fully performed, Head-nodding movement describes an elliptic course with the long axis parallel to the surface of the water and the bill held horizontally. However, as pointed out before, there are many modifications in the Head-nodding. The behaviour shows similarities to the Rotary-movement in Barrow's Goldeneye (Myres 1957, 1959b and own observations). The absence or paucity of lateral head movements requires further attention as the Harlequin certainly does not lack conspicuous patterns on the head. The crescentic white patches on the sides of the head and the reddish back of the head could have significant signal functions (cf. Barrow's Goldeneye as to the white head-patches).

Many ornithologists claim the Harlequin to be rather pugnacious. Encounters occur frequently at the breeding ground throughout the season. When, at the 'club' for instance, two birds compete for a certain stone to loaf on or when a newcomer alights nearby the birds perform Head-nodding. The same form of Head-nodding behaviour occurs whenever two birds or more get in close contact. The Head-nodding in such cases consists of rapidly performed movements of the neck and head which do not seem to be complete: they are not so extensive as in many other displays and look stiffer. Myres (1959a) suggests that the Head-nodding also serves as a greeting. I think it is a form of hostile behaviour, because, if the opponents are not discouraged by each other's Head-nodding (which they usually are), Threat-Posture is assumed. This posture comprises two phases: first a lowering of the head and neck to the horizontal and second the actual attack when the bird slowly approaches the opponent (walking or swimming), sometimes with its bill open. The Threat-Posture may continue into a fierce attack when the duck leaps or rushes at its opponent with water spouting. The length of the 'rush' varies from 2 to 30 feet. When fighting, Harlequins dive a lot but I have never seen them performing underwater attacks, as Barrow's Goldeneye regularly does.

In the encounters both males and females are generally involved but fights between males are more common than 'mixed' conflicts or encounters between females only. Encounters with only males involved are as a rule of the type described above in connection with 'threat-behaviour'. Apart from incidents at the 'club', etc., encounters frequently occur in 'courting-parties' or where a pair is attended by a single unpaired male. Normally a conflict ends in a 'rush' from one of the combatants and only rarely does it lead to a serious fight. A female may in connection with display activity perform a 'rush' at a foreign male, or occasionally a female. The 'threat-behaviour' of the female is seemingly identical to that of the male but is more seldom recorded.

Males frequently chase females but these actions are not only aggressive since courtship displays and copulatory behaviour presumably involve quite a lot of aggressive tendencies.

In about 80% of the cases where both sexes display mutually the male is the initiator. Both birds perform sequences of Head-nodding ranging from 2 to 17 movements and with a duration of 8 to 15 seconds. The Head-nodding of the female is generally less elaborate than that of the male but even a little Head-nodding by the female markedly influences the male's activity.

Whereas the sexual displays of the female seem to be limited to Head-nodding and Inciting, the male seems to possess at least a few other displays which probably are ritualized. The male has been recorded as performing Head-nodding and lateral shaking of bill in the water ('Water-twitch' of Myres 1959b?). I have seen this behaviour of the male when the birds displayed mutually. Frequently the male assumes a 'look-for-food-posture' as he dips his forehead into the water and, as it were, skims the surface. This posture is often assumed when he is excited and then he may also exhibit an attitude which seems identical to Threat-Posture. Occasionally he opens his bill and utters a squeaking sound at the same time.

It is not quite clear how much the aggressive 'rush' in connection with pair-maintaining displays is ritualized. Possibly this behaviour is mostly confined to pre-copulatory behaviour since copulation may follow immediately after. (Copulatory behaviour is treated below.)

Quite frequently during mutual Head-nodding the male has been seen to Upward-

stretch, with flapping of the wings. This display is rather weak and often interrupted and it may just be a comfort movement, though the frequency with which it has been recorded in connection with sexual displays, except copulatory displays, favours the possibility that it is ritualized.

Preening sometimes occurs during courtship and agonistic displays. Both preening dorsally and behind the wing have been recorded but it is not yet clear whether these activities are highly ritualized. Some of them are probably only comfort movements. An action which probably is to be regarded as a 'two-wing-stretch' (also observed in Barrow's Goldeneye and several other species of ducks) has apparently no display function. Stretching of one wing and the corresponding leg also occurs in the Harlequin.

The only specific display of the female, other than copulatory behaviour, I have noted is Inciting. This has not previously been described for *Histrionicus* (Johnsgard 1960). The movements involved are similar in principle to the Inciting of Goldeneyes. The female lowers her head and neck, often touches the water with the throat, and performs distinct Head-turns (easily distinguishable from Head-nodding), alternating from one side to the other. This has been seen on four occasions (twice in summer and twice in winter) while in a fifth case the female just pointed the bill at an interfering male without any Head-turns. In a sixth case the Head-turns were followed by a 'rush' of two or three feet, after which the female repeated the Inciting. The usual response of the male to the Inciting was Head-nodding and twice he assumed Threat-Posture. During Inciting a female was once heard to utter a harsh call. The performance of the displays common to both sexes is as a rule weaker (not so elaborate) in the female than in the male.

An elaborate 'flight-display' compared to that of many other ducks evidently does not occur in the Harlequin. 'Courting-parties' chasing a female through the air have been recorded several times but no distinct behaviour patterns have been attributed to these flight chases. Possibly the Harlequin possesses a 'flight-display' which is more elaborate during winter and early spring when the birds are at sea.

Copulatory behaviour

The copulatory behaviour of ducks is regarded as highly conservative and can thus be used as a possible criterion of relationship. Very few ornithologists appear to have seen copulation in the Harlequin. This is not only due to the remoteness of the breeding grounds because even rather extensive observations seldom result in seeing a copulatory sequence. Possibly the copulatory frequency is highest at the beginning of the breeding season and then rapidly decreases. My own material includes seventeen interrupted copulatory sequences but I have so far recorded only five more or less completed copulations, two in May, two in June and one in July. The earliest attempt was seen on 20th May and the latest on 2nd July. Most copulatory activity apparently takes place around 10 a.m. and between 3 and 6 p.m. Attempted copulations have been recorded at places where parties of ducks have been present but all five completed acts occurred in secluded spots with no more than two pairs.

Pre-copulatory behaviour can be initiated by either sex, though most frequently by the male. The performance commences with mutual Head-nodding. The Head-nodding of the female is more irregular and is less pronounced than that of the male. It seems to serve mostly as a stimulus to the male. I have once seen a female use a head-movement as a defence action when the male became aggressive during copulatory display. This mutual Head-nodding may last for five to thirty minutes, but eventually the birds lower their necks and heads to 10–15° with the water. In this posture they have been seen to perform mutual 'bill-dipping' with lateral movements of the bill (in eleven interrupted and four completed copulations). This may last for 30 seconds or more. The actual dipping of the bill involves 3–5 dips in rapid sequence.

The most striking pre-copulatory behaviour of the Harlequin is the 'rush' of the male which seems identical with those occurring in courtship and agonistic encounters. The male skids towards his mate with his bill widely open and uttering a sound reminiscent of 'a group of fighting mice' (Myres 1959a). The male tries to grab the nape of the female who usually seems to struggle to avoid capture. The aggressive element in copulatory behaviour is very pronounced in the Harlequin. No definite rape has been recorded, but it is often difficult to draw a line. In one case that occurred on 18th June, 1964, the male chased the female (later observations proved that they were paired) by 'rushes' until she took off, followed by the male. After a short pursuit-flight she alighted near a small island and the male tried unsuccessfully to mount her. All the time the male called constantly. The female ran up the slope (45° angle) of the island

nearby pursued by the male. After a few rounds on land the female got out of the male's sight for some time. A 'foreign' female happened to be in the water near the island and the male caught sight of her and displayed energetically in front of her without any response. Suddenly the male spotted his apparent mate again and made a rush at her. Soon after that the sexual activity declined and they began to feed together. However, after a very short time the male again commenced to perform Head-nodding and rushes and at this time an under-water-pursuit even occurred. More chases on land took place (the Harlequin is very agile on land) and again the male tried to mount without any success. Hence it seems as if a male Harlequin in an aggressive state might even copulate on land occasionally. The pair was first seen at 3.00 p.m. and at 5.40 p.m. the male still showed aggressiveness, although less extreme.

Copulation may be preceded by 5–20 'rushes' extending over a long time (10–30 minutes and exceptionally even longer).

In a pre-copulatory sequence I once recorded a form of 'body-up' without wing-flap. The male had been displaying to a female for about 15 minutes when he performed this 'body-up' display five times in less than a minute. He then 'rushed' at the female and renewed his displays. The posture was very much reminiscent of pre-copulatory 'rearing' behaviour in Steller's Eider *Polysticta stelleri* (Johnsgard 1964). The neck seemed to thicken and the feathers on the back of the head were ruffled, giving the bird a very peculiar appearance. The 'body-up' posture could have been only a comfort movement unconnected with copulatory behaviour at all as it has only once been recorded.

No male displays definitely suggesting exhibition of the metallic plumage have been noted. I think the pivoting and turning in front of the female is over-estimated because of the spectacular colours of the male and the unwillingness of the female in early stages of the copulatory behaviour. This may even lead to small combats with the female trying to grab the tail of the male while he attempts to clutch her nape.

Female pre-copulatory behaviour includes brief sequences of Head-nodding and sometimes dipping of the bill while lowering the head and neck. She does not normally assume a Prone-Posture until immediately before treading, or in some cases not at all. Occasionally I have seen the female in Prone 10–20 seconds in advance.

The copulation takes 2–6 seconds (5 instances) and during treading no calls have been noted. The male presses the female almost under the surface of the water and his wings are slightly expanded (in two cases not at all). No flapping of the wings has been observed in connection with the act.

Post-copulatory behaviour is poorly developed in *Histrionicus* and presumably absent in the female. Rotary-movements by the male like those of *Bucephala* (Myres 1957) have been recorded twice, but it is possible that these motions occurred on account of the female's struggling to release herself in interrupted copulations. After coition the female may bathe (dive) and preen for some time but this behaviour is very variable and may be lacking completely. No distinct post-copulatory displays have been attributed to the female.

Nor does the male Harlequin exhibit any specific displays after copulation. He may dive a couple of times and thereafter repeat the aggressive parts ('rushes') of the pre-copulatory display but with less intensity. If the female rejects the courting both birds eventually preen themselves. I have never seen two copulations in succession. The aggressive post-copulatory behaviour of the male Harlequin is very characteristic.

The paucity of visual displays in *Histrionicus* is apparently compensated by a rather great vocal activity. Elaborate and conspicuous aquatic displays would be difficult to perform in a fast running river where the Harlequins breed. The male sexual displays in the sea ducks are in all but a few species very elaborate. The Long-tailed Duck, which is not confined to rushing streams, has at least two fairly distinct and conspicuous, though not very elaborate, visual displays (Johnsgard, in letter). The Barrow's Goldeneyes which breed in the study area on the River Laxá are only seen to perform their displays at sheltered places where the water is smooth.

The unique habitat selection of the Harlequin and its lack of close relatives perhaps reduce the importance of displays as an isolating mechanism to prevent hybridisation. No hybrid Harlequin has been recorded.

The vocal ability of the Harlequin is indisputable, as is that of the Long-tailed Duck, which supports the idea that vocal displays compensate for reduced visual displays. It is of interest to note that the Common Scoter possesses both vocal and visual displays of high degree. To be of any importance the vocal display of the Harlequin must be very pronounced as the river noises interfere not only to human ears but very likely also to the Harlequins'.

Concerning the copulatory behaviour of our species more observations are needed. However, in view of the facts presented above it is suggested that the genus *Histrionicus* should be placed close to *Polysticta* and form a link between Steller's Eider and the *Clangula-Melanitta-Bucephala* assemblage on the basis of behaviour characteristics.

Nest-site selection

As early as in the middle of May some of the females may begin to lay eggs. During the latter part of May the majority start to prepare for egg-laying. Harlequins' nests are always found very close to the water. In Iceland they nest among lava blocks or, more often, directly on the ground under a layer of protecting bushes or other types of ground vegetation, for example *Angelica* sp.

Owing to the fact that most nests are situated on inaccessible islands in the river, it has not been possible to examine very many. However, my observations indicate that there is a strong tendency of the female Harlequin to return to the same nest-site for consecutive years. My statement is based on several observations at nest-sites which are so concealed and unusual that it must have been the same bird returning year after year. It should be noted that so far no banding of adult females on the nest has been done. The great homing tendency in hole-breeding ducks is well-known (cf. Erskine 1961).

The nest consists of a thin layer of grass and occasionally a few dry twigs and leaves. It is lined with white down with reddish tips. The amount of down never reaches the quantity found in nests of Eiders. The most prominent feature of the nest is that it is mostly protected from above by dense vegetation. This has been proved to be of survival value during cold spells with snow-falls (Bengtson 1963).

No interspecific competition for nesting places has been noticed, though eggs of Goosanders have been found in Harlequins' nests (Gudmundsson 1961).

The females alone choose the nest-site. In the latter part of May females attended by their males are seen exploring sites. The Harlequins' search for sites differs in one major respect from that of Goldeneyes in that the birds are never seen flying over land as the latter species frequently do. Concerning the Barrow's Goldeneye at Mývatn it has been established that immature females (and possibly even some mature ones) spend a lot of their first spring season looking for nest-sites. Due to the lack of trees they investigate crevices in the lava chimneys and ventilators in the farmhouses. These flights have been proved to occur predominantly in slight drizzle (Gudmundsson 1961 and my own observations). Harlequins have shown no such weather preference.

When Harlequins look for nest-sites they walk on the islands or on the river banks for an hour or more at a time. They disappear into every cave and behind every rock and bush. Every now and then they stop and remain motionless for several minutes looking out over the area. The males follow their females continuously, though without paying so much attention to the holes and caves as do the females. They mostly stay on guard. When disturbed the birds dash down to the river. They walk or run on land without any difficulty even for quite long distances. When looking for sites along the small brooks recently resorted to for nesting the pair swims up into the brook. The noisy behaviour of the Harlequin during these explorations is striking.

Egg-laying

The Harlequin is a comparatively late breeder. As in various other high boreal and arctic breeding birds, the egg-laying extends over quite a long period. One can expect to find fresh clutches in Iceland from the second half of May until mid-July (approximately an eight-week period). The majority of females start to lay in the last week of May. Some authorities are of the opinion that egg-laying is not finished until the second part of June (Hantzsch 1905, Gudmundsson 1961). The regularity with which downies occur in the first weeks of July indicates that many females have already completed their clutches in the very last days of May and the first week of June. Hantzsch (1905) refers to a set of eight eggs collected at Mývatn (identical to River Laxá) on 30th May, 1898. The egg-laying seems to take place simultaneously in Alaska and Iceland although Bent (1925) mentions a clutch of seven eggs found on the west coast of North America (Washington) on 7th May, 1924. In the latter instance the egg-laying must have commenced about 20th April or even earlier. My own observations in Iceland indicate egg-laying from 10th May until 8th July with the majority in the first days of June.

I have been able to follow up the egg-laying in only three nests (in one case from the second egg only). I have found the intervals between the eggs to be two to four days. A lapse of three days seems normal but two-day intervals also occur quite frequently. Only one four-day gap was recorded. I believe that females may

lay two days in succession on rare occasions although this has never been directly observed. The local farmers have also found the interval between the eggs to be two to three days.

The clutch seldom exceeds nine eggs. The number of eggs in eleven nests I have examined ranges from three to seven, average 5.5 (Table II). It should be noted that clutches with four eggs or less may have been depleted by the egg-collecting farmers, as permitted by law. Table II also includes some broods observed when the young were so small that it may be presumed that the number of young reflected the (minimum) clutch-size. As can be seen I have recorded females with nine to ten downies and as no robbing of young from each other apparently occurs in the Harlequin these observations are, I think, good evidence for large clutches. Gudmundsson (1961) has found nests with eleven and twelve eggs but he adds that they may possibly have been laid by more than one female.

Incubation

Incubation starts before completion of the set. At this time the female begins to pluck feathers and down from her breast with which to line the nest-cup and to cover the eggs when leaving the nest. The incubating bird generally sits very tight throughout the incubation period and can sometimes be touched by the observer without being flushed. When disturbed on the nest she may utter a hissing sound and try to bite the intruder. If flushed she generally leaves the eggs without splashing them with excrement as do most other ducks.

After most females have begun incubating very few Harlequins are to be seen on the water. The males have departed (or are just about to) and the females on eggs very rarely leave them. No continuous observations have been carried out in order to establish how often the incubating females leave their nests to feed. However, certain observations indicate an interval of 48 hours between the feeding pauses of an incubating bird.

Once I watched a female leaving her nest after having covered the eggs with down. She swam straight to a nearby waterfall where she foraged for 26 minutes and then climbed up on a ledge and preened and rested for 38 minutes. Then she continued to feed with brief pauses for nearly one hour before she finally returned to the nest. In total she stayed away from the eggs for about two hours.

Unfortunately I have not been able to establish the length of the incubation period in the Harlequin with desirable exactness. The available literature states that it takes 31–32 days (Scott and Boyd, 1957) or even 33–34 days (Witherby *et. al.* 1958) for the eggs to hatch in an incubator. My own investigations indicate a period of 28–29 days which is a rather long time considering that some bigger ducks require less than 30 days. However, 'hole-breeders' tend to have longer incubation periods than ground-nesting species. It would be of great interest to get sufficient information on the length of the period in Harlequin.

Behaviour of the males after incubation has started

From about 12th June a new phase starts on the River Laxá in that the females disappear to their incubation duties and the drakes and non-breeding birds begin to moult and congregate at the 'clubs' and other favourable feeding places. The females that are seen at the 'clubs' I believe are non-breeders as those that still have not begun or finished egg-laying do not frequent such places.

Sometimes a male may spend a day or two in the vicinity of his incubating female and accompanying her on her feeding time but very soon he deserts her.

At the end of June I once observed a solitary pair of Harlequin in a river near the mountain Herðubreið (north-east Iceland). Nothing indicated that the female had started egg-laying but she could have done so. The male was still in full nuptial plumage. It would be of interest to know whether the tendency of the males to remain with their mates is greater in isolated pairs, where the sociability of the moulting males is not so favourable as at the River Laxá.

The males do not remain for long at the breeding grounds after they have abandoned their females. After a few days at the 'club' they depart for the sea. The majority leave around 20th–24th June and at the beginning of July only a minor portion of

Table II. Numbers of eggs in nests and young in broods seen along the River Laxá, 1961–63

	Number of eggs or young								
	3	4	5	6	7	8	9	10	mean
Clutches	1	1	3	4	2	–	–	–	5.5
Broods	–	5	3	3	2	1	1	1	5.7

the males in the population is left (late breeders).

They are now more social and when disturbed (as by my arrival) they cluster together and if the intruder gets too close to their loafing place they all leave in a dense flock swimming or flying. The social behaviour they exhibit at this time of the season at the 'clubs' probably prevails through the autumn and winter until pair-formation starts. During the last days before departure a marked tendency to fly has been noticed among the not yet moulting males.

After a visit to the River Laxá in 1958 Sellick (1960) opposed the hypothesis that the males go to sea when the females begin to incubate. He found 60–70 males, in eclipse, at a secluded spot a little way down the river. He suggested that the belief about the males making for the sea arose because no, or very few, males are seen at the breeding ground at that time. In his opinion this could be owing to difficulties in distinguishing the sexes when the males moulted. I have never observed any flocks of Harlequins in the river after the third week of June, only scattered males, and I think it is quite possible to determine a moulting Harlequin as to sex and age in the field.

The males that remain at the breeding ground until early in July are late breeders still in full plumage and may peeform various displays and attempted copulations.

Feeding methods

In a previous section it was stated that the staple diet of the Harlequins in Iceland were pupae and larvae (and to some extent imagos collected from the surface of the water) of *Simulidae* and *Chironomidae* in particular which are both very abundant in certain districts (around Mývatn almost a plague) with suitable hatching conditions.

Harlequins use three different methods of feeding: (*a*) skimming off the surface combined with dipping of the head under water; (*b*) actual diving and (*c*) 'up-ending' as in the surface feeders. In shallow places they use the first method and scrape the surface of stones with their bills in order to obtain edible items. This method of feeding gives an impression of being less effective than diving and can be characterized as 'inactive feeding'. Diving is the normal way of obtaining food and can be practised almost anywhere in the river. Not even the most turbulent and strongest current or falls form any apparent barrier and the Harlequins readily find their way along the bottom of the river. They dive with their wings open and from the steep slopes of the river I have often had excellent opportunities to watch their activity in the clear water. They make use of their wings under water, as far as I can tell not for propulsion but to keep their balance as they move on the bottom like a Dipper. Even when feeding in strong currents Harlequins manage to emerge in almost exactly the same spot from where they dived. At least they seldom emerge downstream. The 'precision diving' is amazing and very typical of this species. The third method, 'up-ending', is identical with that used by dabbling ducks. It is rarely practised. When they do Up-end they dip their heads only on most occasions as a cupplementary method. 'Up-ending' was never recorded by Pool (1962) but Michael and Michael (1922) mention it.

Michael and Michael (1922) give 15 sec. as the average duration of the dives and state that they rarely exceed 25 sec. Cahn (1947) frequently timed dives of 30 sec. or more. The duration of the dives may of course differ from place to place and season to season. In the River Laxá Harlequins normally dive for 15–18 sec. The longest dive I have recorded was 39 seconds. As the female seems to dive first when a pair is feeding simultaneously in 48.3% of 1,210 recorded dives and both birds submerge about the same time, the dives of the female tend to be slightly longer than the dives of the male.

No correlation between the duration of the dives and the depth of the water has been established. The Harlequins do not show any apparent preference as to the depth of water in which to feed. As in the case of swimming on the surface, the Harlequins try to take advantage of the lee-sides of stones and islands when diving for food. This may also be a consequence of the greater tendency for the larvae and pupae of insects to be attached on the lee-sides of underwater obstacles.

The Harlequin was claimed by Alford (1920) to be mainly a 'day-feeder'. Pool (1962), from observations on the Laxá, disagreed. In mid-July, 1961, Pool was impressed by the rarity with which the Harlequins were to be seen feeding at all and found them to be most active just before sunset (10.30–11.00 p.m.). My more extensive observations on feeding activity of the Harlequins are compiled in Figure 1 into a curve showing the daily rhythm in this respect. It is obvious from this diagram that they feed with a two-peak frequency, one maximum being around 6 a.m. and the other at 5–6 p.m., the latter being the more pronounced. Apart from these two peaks a less marked one seems to occur at midnight. No variations in the

daily rhythm in the course of the summer have been established. The problems connected with feeding activity in ducks deserve further attention.

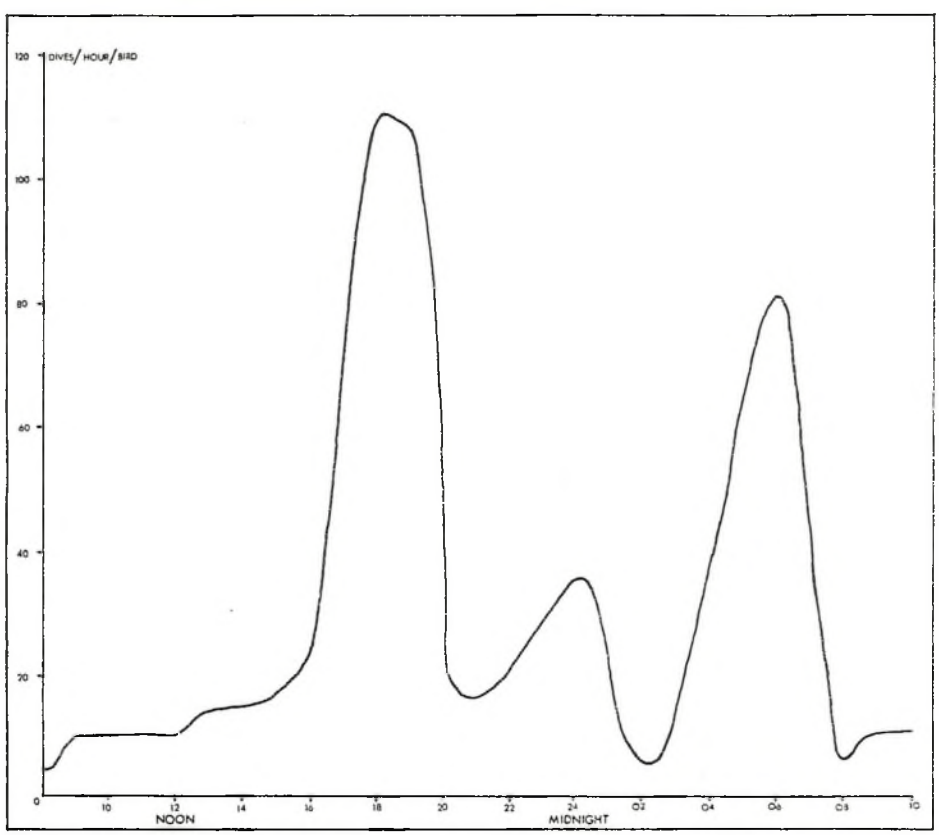
It seems as if the females are more active than the males as they often continue to feed a long time after the males have stopped. This has, however, not been statistically proved.

During the winter at sea the social feeding behaviour of the Harlequins is a predominating feature. At the breeding ground they normally do not feed in parties unless there are so few suitable feeding-areas that they have to frequent the same place. If possible the pairs feed well apart from each other, or occasionally two pairs together.

In Figure 1 a simple method of expressing feeding intensity was used, just the number of dives being recorded. A 'feeding-rate' has also been estimated by watching birds (one at a time) when feeding and timing the dives during a selected period during which uninterrupted feeding occurred. The time spent diving has then been calculated as a percentage of the length of the entire observation period so that the figures obtained are the ratio between the dives and the intermediate pauses. As a rule the 'feeding-rate' is very high in the Harlequin; about 80% (or dives of about 15 sec. with 2–3 sec. long pauses). A bird may feed constantly for 5–50 min. but the 'feeding-rate' decreases slowly and the feeding is interrupted for periods during which the bird preens and rests on a ledge. These resting periods gradually increase in length until the feeding is stopped completely.

In order to further illuminate the adaptation of the Harlequins to their environment, the feeding behaviour of other species of ducks in the study area has been examined in the same way. The comparison of feeding efficiency in Table III, using the measures devised by Dewar (1924), shows quite indisputably that the Harlequin is superior to the other species in most respects. From field-observations it is quite clear that other ducks do not have the same skilful way of diving and

Figure 1. Daily rhythm in feeding activity of Harlequin Ducks on the River Laxá: Based on times of 2,450 dives in the summers of 1961-64.



swimming in rushing streams as do the Harlequins and consequently no other species can occupy this ecological niche. Dow (1964) studied the 'diving efficiency' (measured by the dive/pause ratio) of some North American diving ducks in still water and found the Long-tailed Duck (ratio 4.1:1) to be superior to species like the common Goldeneye *Bucephala clangula* (2.2), the Red-breasted Merganser (2.2) and Surf Scoter *Melanitta perspicillata* (1.8). Yet in rushing streams the Long-tailed Duck is outclassed by the Harlequin.

Parental care and behaviour of the young

The first broods as a rule can be seen from the first week of July and onward, though a single young was observed on 24th June, 1962, and on 25th June, 1964, a female with downies was reported from the River Laxá (Santeson, personal communication). I have about ten records from the first days of July but most eggs do not hatch until 20th July. By the end of the month females with broods are frequently seen. Hantzsch (1905) saw downies from mid-July. The yearly variations are small as would be expected.

I have no personal observations on the behaviour of the female and young in the first hours after hatching. Millais (1913) states that the newly hatched Harlequins are fed directly by the duck. He bases this statement on observations of small downies pecking with their bills at the bill of the female. Even very small ducklings (approximately one to two days old) which I have watched have never done this. They have been seen taking food directly from the surface. The female alone takes care of the young and I have never seen a male escort his mate with a brood (the males are only rarely present at the breeding ground then).

The average number of downies in a brood corresponds to the average clutch-size. Females with nine to ten downies have been recorded but normally they have two to four. As is the case in several other genera of sea ducks (e.g. *Melanitta*, *Somateria* and *Mergus*), the Harlequin shows social tendencies when rearing young. Quite frequently two or three females will have a mixed group of downies in common in which all sizes of young may occur. No tendency to 'rob' downies from each other has been noticed. The aggressive behaviour of the females in a group of broods is not very pronounced and no real combats have been recorded. Females unsuccessful in breeding sometimes participate in the rearing of broods.

The female takes her brood as soon as possible to a secluded part of the river where they stay for some time, moving about very little. The duck is very anxious about her offspring and when the brood is in danger she assumes what looks like the Prone-Posture and utters a jarring sound (Barrow's Goldeneyes behave in the same way). She is then very bold and I once approached to within eight feet of a female in this posture.

The young grow very fast and according to Faber (1822) they are fledged after 40 days. Very early they show the same excellent adaptation to their habitat as the old birds. Their pre-fledging mortality is probably rather low and their worst enemies are the Mink and bad weather. The mortality in five broods (or more probably, seven, since two were each accompanied by two females) was recorded. Of the 37 ducklings in these broods, 24 survived one week and 19 two weeks from the date when first seen, indicating losses of at least 35% in the first week but a much reduced mortality rate thereafter.

To catch a young Harlequin with bare hands when it is in the water is almost impossible because even when quite small they dive with great skill in very turbulent rapids. They use the same technique as the adults when avoiding an intruder; that is they let the current carry them downstream.

Table III. Feeding efficiency of diving ducks in the River Laxá. An observation period is a time during which constant feeding takes place. The dive/pause ratio is the quotient of the average period of a series of dives divided by the average length of the corresponding series of periods spent at the surface of the water during a spell of diving.

	Observation periods (min.)			*Number*	*Duration of dives (sec.)*		*Dive/pause*
	number	*lengths*	*total*	*of dives*	*mean*	*range*	*ratios*
Harlequin Duck	34	12–31	510	1028	16.2	3.7–34.2	4.0
Long-tailed Duck	17	7–19	148	302	10.1	4.1–22.2	2.2
R.-b. Merganser	11	4–13	91	221	11.2	3.1–19.1	1.9
Barrow's Goldeneye	27	3–17	310	652	8.7	2.7–18.4	1.9
Common Scoter	8	5–11	75	210	8.7	2.4–11.1	1.0
Tufted Duck	7	3–8	42	182	6.0	2.6–8.1	0.7
Scaup	18	5–12	133	440	6.4	2.1–9.2	0.9

Usually they first try to hide under the dense curtain of vegetation hanging down from the banks of the river and islands.

Young Harlequins are hardly ever seen on land but they may loaf on the shore within a foot of the water or on ledges in the river. All the time the female and young remain on the breeding ground they live a very inconspicuous life. Not until the young are fledged does the female take them down to the sea according to Gudmundsson (1961) who also states that females with fully fledged young may occasionally be met with far inland as late as 20th September.

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