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Feeding and habitat selection of the horned grebe, *Podiceps auritus* (Aves), in the breeding season.

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ABSTRACT

Feeding ecology and habitat selection of *Podiceps auritus* was studied in Norway, Iceland (ssp. *arcticus*) and Finland (ssp. *aterrimus*). While ssp. *auritus* is stenotopic, preferring smaller, shallow sheets of eutrophic water surrounded by rich vegetation, ssp. *arcticus*, which lives in regions with no close ecological counterparts, goes down the slopes of its adaptive peak. It extends into any lake type, including open, oligotrophic ones, and may be termed an opportunistic feeder. First-year birds seem mainly to select their habitat from the amount of peripheries of emergent vegetation (nest-sites). Older birds seem to use stimuli which are more essential to their existence and may select very aberrant nest-sites, provided they may benefit upon a local superabundance of food. The significance of learning for the evolution of habitat selection and ecological isolation is discussed.

INTRODUCTION

The aim of this study was to investigate lake-type- and nest-site selection and feeding ecology of the horned grebe, mainly in the isolated populations of Iceland and at the coast of northern Norway. Results of a less extensive study in Finland are included for comparison.

Some morphological differences between these populations have been stated elsewhere (Fjeldså 1973b). While nominate race specimens from the Baltic area and further east to Siberia are small and fine-billed, specimens of the race *arcticus* in Scotland, Iceland, and northern Norway are slightly larger and distinctly more heavy-billed. Both this and other trends of geographical variation are difficult to fit into general ecogeographical rules. The detailed trends of variations of bill dimensions are best correlated with the complexity of the local grebe faunas, in particular with the existence or absence of the red-necked grebe (ssp. *griseigena*, including *schioleteri*). It has thus been interpreted in terms of competitive character displacement (Fjeldså op. cit.).

To state the role imposed by interspecific competition on the evolution of habitat selection, particular attention is therefore paid to differences between

the study areas. Further attention is paid to the mechanism of adaptive changes of habitat selection.

The field work was mainly concentrated upon population ecology in Iceland and northern Norway (Fjeldså 1973a). For a general outline of the study, see this publication.

MATERIAL AND METHODS

Study areas

The study areas are at the coast of northern Norway, 67–69° N; in the Myvatn district in Iceland, 65° 35' N, 17° W; and along the southern coast of Finland, 21–26° E; in all a total of 966 brackish-water bays, slow-flowing rivers, pools, and lakes were visited.

Observations in Norway were in the township of Bodø, from 1958 through 1971; in the Vesterålen region in 1967 (townships of Harstad, Dverberg, Andenes); in the Ofoten region in 1968 (townships of Harstad, Skånland, Evenes, Ballangen, Tysfjord, Hamarøy); brief visits to the townships of Skjærstad (1964, 1971) and Fauske (1970, 1971). Horned grebes bred up to 120 m altitude, so lakes at higher levels, mainly completely devoid of emergent vegetation, are discarded from the analysis. Among lowland lakes 31 are in regions with slowly disintegrating granites; these lakes are for the most part deep, strictly oligotrophic, and with little vegetation. At the other extreme, 47 localities are in lime rock zones or on marine clay deposits, mainly shallow hard-water lakes with richer vegetation and animal life. There are thus considerable differences in morphometry, vegetation, and productivity between lakes in different districts.

The Myvatn district was visited in 1966, 1969, and 1970. This lake is situated at 277 m altitude, on the outskirts of the vast lava deserts of the interior Iceland. Very peculiar limnological conditions are created by the supply of ground water, which is very rich in minerals from both cool and temperate springs. The lake is 38 km² large, but only in a few places more than 4 m deep; it is eutrophic, with rich submergent vegetation and very large amounts of zooplankton and chironomid midges. It is particularly well known for the large breeding numbers of waterfowl (Bengtson 1970, 1972). The coasts are mainly sterile shores of gravel and lava. Emergent vegetation is of very local occurrence, but several hundred pools in surrounding moor- and shrub-land are generally rich in sedges, although less fertile.

In Finland 80 localities were visited in 1972 at Kustavi, Taivassalo, Porkala, Helsinki, Sippoo, and Porvoo. These localities include four areas of extensive, eutrophic brackish-water reed swamps, some more open brackish-water localities, and eutrophic, dystrophic and oligotrophic ponds and lakes in both agricultural land and in coniferous woods. For a broader analysis of

habitat selection in the nominate race additional data from three probably very representative studies (Onno 1958b, Palmgren 1936, Soveri 1946) are included in some discussions.

Examination of the habitats

All lakes were mapped in detail in order to give morphometrical characteristics.

The limnofauna was examined qualitatively at about 125 stations and quantitatively at 36 localities, mainly feeding stations of horned grebes, mainly in July. Bottom samples were taken with a 200 cm², 20 cm high Ekman-Birge dredge, operated by aluminium rods, couplable lengths of each 2 m. The bottom sediment was washed out through a 0.2 mm mesh plankton net. Macroscopic animals were sorted out, and their abundance expressed as individuals per m². This kind of sampling is unfortunately not fully relevant for the present purposes, as it comprises mainly benthic in- and epifauna and scarcely includes nekton. The data include 512 bottom samples. Furthermore, results of about 315 samples, mainly from the offshore parts of Mývatn, have kindly been placed at my disposal by Dr. S. A. Bengtson.

This kind of quantitative study is time-consuming and therefore could not be made for all localities. Instead, I have had to rely upon the assumption that stations corresponding floristically and hydrographically also will have roughly similar general productivity and animal life. Detailed descriptions and species list for both emergent and submergent vegetation (bryophytes, charophytes, thallophytes) were made out for about 400 localities. Some of the plant species may be considered sensitive indicators of alkalinity and supply of nutrients. Hydrochemical investigations include analysis of Ca++ contents (EDTA titration) and humus standard (oxidation of filtered water with KMnO₄ corrected for sulfonic acids) for about 100 stations, measurements of pH (pH-meter 24, Radiometer) at 100 stations, and measurements of electrolytic conductivity (Philips electrode Pr 951 0/00) at 200 stations. For all localities water colour, plankton turbidity, sight depth, and the type of bottom sediment are described qualitatively.

Ornithological studies

The horned grebe populations are recorded quantitatively in most study areas, and many efforts were made to trace all nests. The data include 955 true nests and 729 platforms. Nest sites are plotted on detailed maps and described (position in relation to shore and open water, vegetation type, density and cover, anchorage, water depth). The nesting success was studied for 721 nests to show the significance of nest-site selection. To avoid the bias of overrating

nests on very visible places, only data from regions in districts where about 90–100 % of all nests were probably recorded have been used for analysis of nest-site selection.

The activity-distribution and disposal of areas was studied by plotting the position of the birds at intervals of five minutes on daily maps, using different symbols for different pairs and different activity types. To separate innate and acquired factors in habitat selection it is advantageous to separate age-groups. Ageing is based upon characteristics of the eggs, discussed by Fjeldså (1973a), and as there may be a 20 % joint overlap between eggs of »first-year« and »old« females, the method applies only to part of the population members. Furthermore, it is necessary to reduce differences due to the inability of many first-year birds to set up territories in the best habitats. An establishment failure and migration elsewhere generally delayed breeding by some two weeks (Fjeldså op. cit.). Pairs laying eggs before the annual average have probably been dispersed for other reasons than inability to set up territories, and by using data only from aged early pairs the sources of distortion should be reduced.

For the analysis of interspecific relations also the occurrence of other bird species has been recorded, although mainly qualitatively.

Analysis of stomach contents
The study of food selection is based upon stomach contents of 49 horned grebes taken on breeding localities in northern Norway and the Mývatn district, mainly in July. These include specimens shot on license issued by the Norwegian Directorate for Hunting, Wildlife Management and Freshwater Fisheries in 1971, and some casualties from Norway and Mývatn; further 19 casualties collected during an inventory on waterfowl losses in fishing nets in Mývatn in 1960, kindly donated by Dr. A. Gardarsson, and 5 fishing net casualties kindly donated by Dr. S. A. Bengtson. Unfortunately, as I was issued a shooting license for only one horned grebe and no red-necked grebes in Finland, I was not in a position to make a comparative analysis of food selection in these two close ecological counterparts.

The analysis of stomach contents is complicated as the oesophagus of grebes has no crop which might contain unfermented food. The gizzard contents are mainly feathers and radia and cilia of disintegrating feathers, forming a mush-like substance embedding chitinous crushings, fish bones, microscopical eggs, etc. Whole prey are rather exceptional. In particular nymphs of heterometabolous insects, trichopterans and midges are most often finely disintegrated and must be identified from small fragments. Particular problems involve the counting of specimens. For most insects, including midge larvae, counting is best based upon head capsules, while, e.g., larvae of dy-

Table I. Lake size preference of grebes in the study areas.

Lake area in ha	0.2– 0.9	1.0– 4.9	5.0– 9.9	10– 19	20– 49	50– 99	100– 199	200– 499	> 500
<i>S: Finland and Estonia,</i>									
Number of localities	29	72	33	65	62	30	26	20	25
% with <i>P. a. auritus</i>	10	29	39	22	24	17	23	15	12
% with <i>P. g. griseigena</i>	3.5	1.5	6	3	13	10	27	10	4
% with <i>P. c. cristatus</i>	10	26	33	25	34	72	83	79	84
<i>N. Norway and Mývatn area,</i>									
Number of localities	123	79	23	18	22	15	19	12	12
% with <i>P. a. arcticus</i>	27	65	74	61	77	67	63	58	67

tisids and trichopterans are best counted from mandibles. Finely crushed, empty pupal cases of midges could not be counted.

Large numbers of small Chydoridae, Cyclopidae spp.) in stomachs from Lake Mývatn may have been taken by accident together with other items. Much of this certainly comes from the alimentary canal of fermented fishes. In two stomachs, numerous Cladocera and chironomid larvae actually swallowed out of dissolving sticklebacks, *Gasterosteus aculeatus*. I have by my best judgement tried to discard such items from the diet, but this decision can hardly be objective enough.

Due to the condition of most prey they could not be weighed. However, as most invertebrates except Diptera and Hymenoptera are identified to species level, the length and weight may be taken from live collected specimens. Sixty-two less fermented fishes were measured, and it is supposed that these gave a length distribution representative for the total of 398 fish prey recorded. The regression between length and weight was taken from fresh specimens.

RESULTS

General lake type selection

THE BALTIC AREA. Lake sizes selected by grebes are shown in Table I; the columns for the Baltic area include 80 localities visited in 1972; information has been provided by R. Uusitalo and some local people on the distribution of grebes in the vicinities of Kustavi, Taivassalo, Laitila, Rauma, Lappi, and Kiukainen in southwestern Finland; Palmgren (1936) for the Åland islands; Soveri (1940) for Lammi, southern Finland; Onno (1958b) for Estonia, alto-

gether 362 localities. In a statistical sense the three local grebe species seem to prefer lakes of different size groups.

Horned grebes occurred mainly in smaller pools, 1–10 ha large. This holds true also in districts in southern Finland where red-necked grebes do not breed. Two horned grebe localities, shown to me by Dr. M. Sökkeli and Professor R. Tenovuo, were in the middle archipelago at Kustavi, southwestern Finland, in deeper, brackish-water sounds between isles with rocky shores. The vegetation cover was narrow zones of *Phragmites communis* in sheltered places, however, with richer submergent vegetation, mainly of *Fucus vesiculosus*, *Potamogeton perfoliatus*, *P. acutifolius* and *P. vaginatus*. A similar breeding locality has been described by Hederström (1966) from Sweden. These are extreme localities. Most horned grebe localities visited were enclosed, either small pools or more extensive shallow-water areas interrupted by patches of emergent vegetation. Patches of vegetation covered and average 16 % of the areas outside the shore vegetation.

Red-necked grebes (ssp. «schioeleri») seem to prefer localities roughly 20–200 ha large, although in many districts, such as in Germany (ssp. *griseigena*) they may frequent small pools (Wobus 1964, p. 37), and in eastern Siberia and North America (ssp. *holboelli*) sheltered bays of larger lakes.

Great-crested grebes may occur in smaller pools, but their requirements usually appear to be localities more than 100 ha large, mainly with vast expanses of open water (see Frieling 1933, Onno 1958a, b, Palmgren 1936). This species is very common in the inner and middle archipelago of southern Finland, and also in similar districts in other places around the Baltic Sea.

Unfortunately, the 80 localities visited in Finland in 1972 do not provide a satisfactory statistical sample for determining lake type preference. Horned grebes were found in three out of six eutrophic ponds and lakes; in four (and previously occurring in at least three additional) out of 14 localities in extensive, eutrophic brackish-water swamps; in three out of eleven humic eutrophic («mixotrophic») woodland pools; in three out of 20 brackish-water localities with less extensive reed vegetation and generally less fertile; in none out of nine dystrophic pools; in none out of eight oligotrophic lakes, and in none out of 12 slightly humic pools enclosed by extensive reed swamps. The general preference for productive habitats may be substantiated from the floristic data by comparing, statistically, the number of times horned grebes occurred together with the separate aquatic plant species, with the number of coexistences expected from a multiplication of their respective constancy figures. Horned grebes showed a clear-cut association with *Alisma plantago-aquatica* (p. 0.01), *Potamogeton alpinus* (p. 0.02), *P. pusillus* (p. 0.01), *P. obtusifolius* (p. 0.001), and *Ceratophyllum demersum* (p. 0.005), which are all considered as «eutrophic» in the graduation of Linkola (1933). No horned

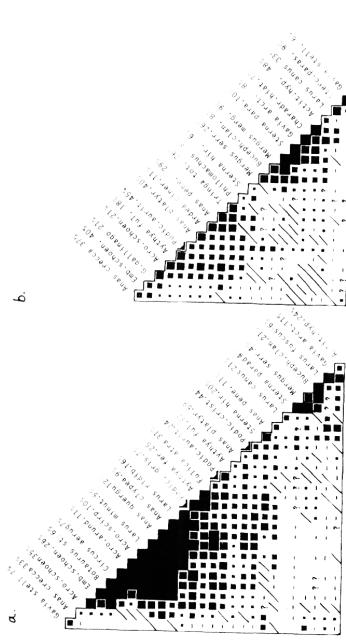


Fig. 1. Avifaunistic associations in 260 marshes, pools and lakes in S. Finland and Estonia (a) and in 170 pools and lakes in N. Norway (b). In (a) data from Onno (1958b), Palmgren (1936) and Soveri (1940) are included, in addition to the results of the authors own investigations. The species are arranged so as to bring the closest associated forms so close together as possible. Figures for occurrence constancy is given for each species; species occurring in < 4% of the localities in (a) and < 6% of the localities in (b) are discarded. Filled square means that the number of localities of coexistence of two species is > 3 × that expected by chance; ¾ filled means coexistence 2–3 × expected; ½ filled means coexistence 1.5–2 × expected; ¼ filled means coexistence < 1.5 × expected, but significantly different (p. < 0.05) from expected; oblique line means that coexistence frequency may be explained due to chance; ? means deficient data; - means coexistence less frequent than expected by chance (p. < 0.05); no sign means that the two species are never recorded in the same lake.

grebes were found in 18 localities where »oligotrophs« occurred (*Sparagnum angustifolium*, *Carex limosa*, *C. lasiocarpa*, *Lobelia dortmanna*, *Isoëtes lacustris*).

The lake type selection, and in particular the differences between the three local grebe species, may be further illustrated by avifaunistic associations. In Fig. 1a data are shown on the association between the breeding bird species in 80 localities studied in 1972, and further supplemented with data from Onno (1958b), Palmgren (1936), and Soveri (1940).

The most pronounced feature of the diagram is the »Nyroca-lake« community of Palmgren (1936), dominated by dabbling ducks, tufted duck, *Aythya fuligula*; pochard, *A. ferina*, coot, *Fulica atra*, blackheaded gull, *Larus ridibundus*, the acrocephaline warblers, and several additional species in the largest reed swamps. This community is typical of shallow, eutrophic (including mixotrophic) localities rich in vegetation. An additional, smaller association, the »Gavia-lake« community of Palmgren, is dominated by black-throated diver, *Gavia arctica*, golden-eye, *Bucephala clangula*, and common sandpiper, *Actitis hypoleucos*. An equivalent mesotaeniate community is dominated by golden-eye, common scoter, *Melanitta fusca* (not in the dia-

gram), redbreasted merganser, *Mergus serrator*, goosander, *M. merganser* (not in the diagram), arctic tern, *Sterna paradisaea*, and larger gulls. These communities are found in deeper, oligotrophic localities, mainly with sterile coasts. Palmgren's »*Podiceps*-lake« community, characterized by the occurrence of great-crested grebes, appears from the diagram to be an impoverished continuum of the »*Nyroca*-community«, in more open, deeper, but still mainly eutrophic habitats.

Both horned and red-necked grebes clearly belong to the typical »*Nyroca-lakes*«, thus differing by habitat requirements from the great-crested grebe. Their associations in the diagram show many strikingly similar details, although there is one main difference. The red-necked grebe is closely associated with many more species. This is for two reasons: It is found mainly in larger localities (Table I) and therefore encounters more other bird species per locality, and it prefers the most highly eutrophic localities with very rich vegetation (note close association with coot and reed warbler, *Acrocephalus scirpaceus*). This result corresponds well with that of Onno (1958a, b). He found red-necked grebes almost entirely in shallow, eutrophic lakes very rich in vegetation, while horned grebes bred both in this type and in shallow pools, rich in vegetation and nutrients, but mainly in more humus-influenced (mixotrophic) localities in uncultivated regions. These species are probably severe competitors (note poor mutual association in the diagram in spite of the great similarity between them in other respects). They may well occur together on the species list of one locality, but this is either because they may live well isolated by vegetation cover in larger swamps, or else because the two species breed in the same pond only in separate years (Onno 1958a, 1960, R. Usitalo pers. comm.). In some districts with mainly smaller lakes the term »mutually exclusive distribution« is maybe a better description of ecological displacement than »segregation«. The horned grebe has virtually disappeared from a number of localities as a result of a recent increase of the red-necked grebe. Interspecific territorialism does occur (Onno op. cit., Wetmore 1924) and naturally the smaller horned grebe is physically subordinate.

NORTHERN NORWAY AND THE MÝVATN DISTRICT. Horned grebes were common in the pothole areas near Lake Mývatn, and the smallest nesting pond measured only 0.033 ha. Most pairs breeding in these areas were, however, »first-year« birds, many of which evidently did not manage to set up territories in the few sedgebeds in Mývatn. Outside typical pothole areas the horned grebes only rarely settled in pools less than one hectare large. As is seen from Table I, localities above this size seem to be selected at random, irrespective of their size. This is a pronounced difference from the selection of smaller pools in the Baltic area. Indeed, the population density per km shoreline is generally very low in most larger lakes, but this is because most shores

are absolutely unsuited for nesting. In these northern regions supra-aquatic vegetation is on the whole restricted to pools or sheltered bays. Actually, the nesting density per km of sedge-fringed shoreline was by far the highest in large lakes.

For the further analysis I use data only from northern Norway, due to some very special conditions in Mývatn. These will be discussed separately later (p. 83). Community studies for Mývatn would reveal little of interest because most waterfowl species are dispersed over the whole area, with only a statistical degree of segregation.

Lakes in northern Norway are mainly oligotrophic; only few approach eutrophic conditions. These are probably better termed »*Potamogeton-Chara-lakes*«, because they are only potentially (hydrochemically) but not climatically eutrophic. Several of them correspond best to the gypso-eutrophic facies of Naumann, moderately rich in nutrients, but very rich in lime. Horned grebes occurred in 27 (64 %) of 42 such lakes; further in 6 (60 %) of 10 mixotrophic lakes; 14 (54 %) of 26 lakes of transitional types; 14 (52 %) of 27 oligotrophic lakes, mainly typical »*Lobelia-lakes*«, oligo- or meso-humic, with soft water; and only 5 (14 %) of 36 dystrophic pools. The latter are mainly small, with peat-filled margins and scanty emergent vegetation, and are thus not fully comparable with the other types. Although the highest breeding numbers are found in richer lake types, the constancy values are about the same for all larger lakes, irrespective of their type. The occurrence of the horned grebe race *arcticus* was, in northern Norway, positively associated with plant species with very different trophic demands, both »eutrope« (*Potamogeton alpinus* (P. < 0.005), *P. pusillus* (P. 0.02) and *Myriophyllum spicatum* (P. 0.02); »semi-eutrope« (*Chara* spp. 0.02), *Potamogeton paelongus* (P. 0.05), *P. perfoliatus* (P. 0.005)); very eurytrophic species (*Potamogeton natans* (P. 0.02) and *Nuphar pumilum* (P. 0.005)); and even character species of oligotrophic softwater lakes (*Urtica dioica* (P. 0.02) and *Lobelia dortmanna* (P. < 0.05)). It was negatively associated with *Eriophorum angustifolium* (P. 0.02) and *Carex limosa* (P. 0.01), two species typical of peat-filled margins of dystrophic bog tarns. The breeding constancy was not correlated significantly with electrolytic conductivity or calcium content of the water, but it was very low at pH < 5.5, which is mainly found in bog tarns. Many breeding lakes have a very poor invertebrate fauna, about 500 benthic organisms per m², and also very little netton.

Fig. 1b shows avifaunistic associations in 170 lakes and pools in northern Norway. The two main communities described for the Baltic area, the »*Nyroca*-« and »*Gavia*-« types, are also found here, although the latter is far more important, and the former is impoverished. The »*Nyroca*-« type is dominated by horned grebe and mallard, *Anas platyrhynchos*, with grey heron, *Ardea cinerea*, wigeon, *Anas penelope*, tufted duck, snipe, *Gallinago*

gallinago, and sedge warbler, *Acrocephalus schoenobaenus*, as associates (indicators). The »*Gavia*«-type is dominated by red-breasted merganser, common sandpiper, and common gull, *Larus canus*, with black-throated diver, goosander, ringed plover, *Charadrius hiaticula*, and arctic tern as associates (indicators). An additional type is dystrophic pools in moorland at the coast, inhabited by, e. g., red-throated diver, *Gavia stellata*, and arctic skua, *Stercorarius parasiticus*. This diagram places the horned grebe among the inhabitants of the »Nyroca-lakes«, close together with sedge warbler and tufted duck, but it also clearly shows an extension into the open oligotrophic lakes, together with the golden-eye, red-breasted merganser and goosander, and even additional species normally found in these lakes. It appears that the horned grebe is, in this respect, outstanding among the representatives of the »Nyroca-lakes«. It may extend into any lake type, provided that it may locally find sufficient vegetation cover for nesting.

Feeding ecology

HABITATS SELECTED FOR FEEDING. Feeding mainly occurs close to those places where supra-aquatic vegetation is sufficient to serve as a nest site, but there is nothing to prevent using additional remote feeding stations.

To sum up the results regarding activity distribution for feeding, horned grebes are mainly stationary where food is in abundant supply, and feeding is in many such places restricted to the territory almost up to autumn departure. In poor lakes, on the other hand, some erratic feeding far offshore may occur regularly throughout the incubation period, and the territory is often deserted a few days after hatching. In larger, oligotrophic lakes families may, in July, be seen anywhere off coasts with no vegetation cover. Provided that food supply is sufficient, local crowding of nests does not necessarily accentuate remote feeding, but it almost invariably abbreviates territorial cycles.

A most interesting case of remote feeding was found among grebes breeding in small, mainly oligotrophic potholes near Lake Myvatn. During the incubation period their feeding gradually was shifted over to Lake Myvatn. Moreover, the birds did not alight at the nearest coast of the lake, but flew far offshore, probably mainly to those areas which have the largest concentrations of entomostracans and chironomid larvae. Outside the nesting areas horned grebes fished mainly in the southern part of Neslandavík, along the islands of Bolir, and in some places in the central parts of Sydrifjöldi (see map, Fig. 5). However, movements within the breeding season from areas suited for nesting to areas suited for feeding were in general far less pronounced than in the diving ducks of the area (Bengtsson 1971a). The young grebes are reared and fed within the potholes, although in one case a brood was

Table II. Distribution of feeding plots in relation to water depth in sample areas of 80 ha in seven lakes in northern Norway.

Depth in m	0-		0.3-		0.3- 0.8-		1.5- 2.5-		2.5- 3.5-		> 3.5	
	No. feeding plots	Ha area										
No. feeding plots	24	706	805	126	32	4						
Ha area	1.7	15.3	18.6	7.8	19.3							
Feeding plots per ha	14	46	45	6.8	4.1	0.2						

moved across land between two pools, and in one case from a pool across 60 m of land to Myvatn.

Most horned grebe localities, and in particular in the Myvatn area, are in their entirety shallow and soft-bottomed and thus less suitable for analysis of habitat preference for feeding. There were some local depth variations within 80 ha of area mapped in detail outside the nest-sites in the lakes Fjærvatn, Kyrrnesvatn, Laugen, Nyrvatn, Soløyvatn, Skilvatn, and Vatnvatn in Norway. These areas were selected for analysis. The distribution of 1697 feeding plots on maps of activity distribution in relation to water depth is shown in Table II.

Shallow areas, 0.3–1.5 m deep, are clearly preferred. Plots within the 1.5–3.5 m depth range are mainly from the pond Laugen where the food (*Gamma-rus lacustris*) lived pelagically, and there was a tall submergent vegetation of *Potamogeton perforatus* × *praelongus*. The dives were, therefore, less deep than the water depth as such suggests. Tall submergent vegetation is found also everywhere in the offshore parts of Lake Myvatn, and in many other feeding areas more than 1.5 m deep. Although the horned grebe race *arcticus* may well breed in open lakes, which in other regions would be considered typical great-crested grebe habitats, it still differs from this species in being a shallow water or littoral feeder. Onno (1958a) found diving in the nominate race mainly at 0.5–2.5 m deep water.

In deeper pools feeding was generally along the edge of the emergent shore vegetation, and in larger open lakes along the proximal edge of the erosion terrace near the shore. This shallow terrace, eroded by ice in winter, may be stony or sandy, while outside it there may be a fringe of dense submergent vegetation, either *Isötæs lacustris* or *Lobelia dortmanna* in the poorest lakes, or *Nitella opaca*, *Chara* spp., *Potamogeton natans*, *P. praelongus* and *Myriophyllum* spp. in richer lakes. While about 35 % of the bottom in areas less than 1.5 m deep in the seven localities selected for analysis was bare mud or silt, only 6 % of the feeding plots were in such places. Evidently then, the grebe selects places with some vegetation for feeding. Small fishes and vari-

ous invertebrates tend to hide in these places, and the grebes seem to learn to find them there.

FEEDING BEHAVIOUR. The main feeding attitudes are shown in Fig. 2. Feeding is mainly by series of dives, but this technique may be supplemented, to a variable extent, by snatching insects from the supra-aquatic vegetation or from the air (a), by picking floating items from the water surface (b), or by skimming in places where the water is covered by masses of, e.g., chironomid pupal cases (c). Commensal feeding between two horned grebes and a male surf scoter, *Melanitta perspicillata*, has been described by Paulsen (1969).

Feeding dives in horned grebes vary technically. From a normal surface position (e) the plumage is sleeked, making the curvature of the back more apparent, and the neck is curved (f, g). The bird glides gently into the water, with no splash. On rough sea, or when diving into swells at a coast, the dive is more violent, springing, so that the entire body may be out of the water (cf. Lawrence 1950 for the western grebe, *Aechmophorus occidentalis*). At very shallow feeding stations the dives may be incomplete, sometimes with only the head and neck submerged, or the bird may swim about with the head (d) or even the entire neck submerged.

Under water a horned grebe may proceed about one metre per second using the feet synchronously, normally keeping the wings closed, and the neck stretched forwards (h). During more slow searching for prey the neck is held vertically, nodding to and fro, and the feet are used alternately (i). Surfacing is passive, without using the feet, and in an attitude like (j).

Feeding is mainly solitary; even members of a flock normally disperse for feeding. Only in places with large shoals of small fish have I seen flock members dive close together. Synchronous diving of large flocks of horned grebes into the swells at the coast of a lake in Korea is described by Bergman (1936).

The time of feeding dives is variable, 1–73 sec., although most often within the range 7–25 sec. The intermittent pauses are minimum 3 sec. and mainly 6–15 sec., and not closely correlated with the time of the previous dive. As feeding is mainly near the bottom, except in places with tall submergent plants, the diving time may depend on the water depth, although not closely, as a bird may sometimes dive and emerge about in the same place, while at other times it may travel a considerable distance submerged. As a grebe under water must seek, chase, and catch individual prey, the diving time is far less dependent on water depth than in bottom-feeding ducks. It depends more upon the ease by which food is caught. Data to show this are best collected when a grebe dives for food for its young, because it then surfaces for each prey caught. Furthermore, data are selected only from stations about one metre deep. At benthos densities of < 1000 animals per m² bottom, grebes spent

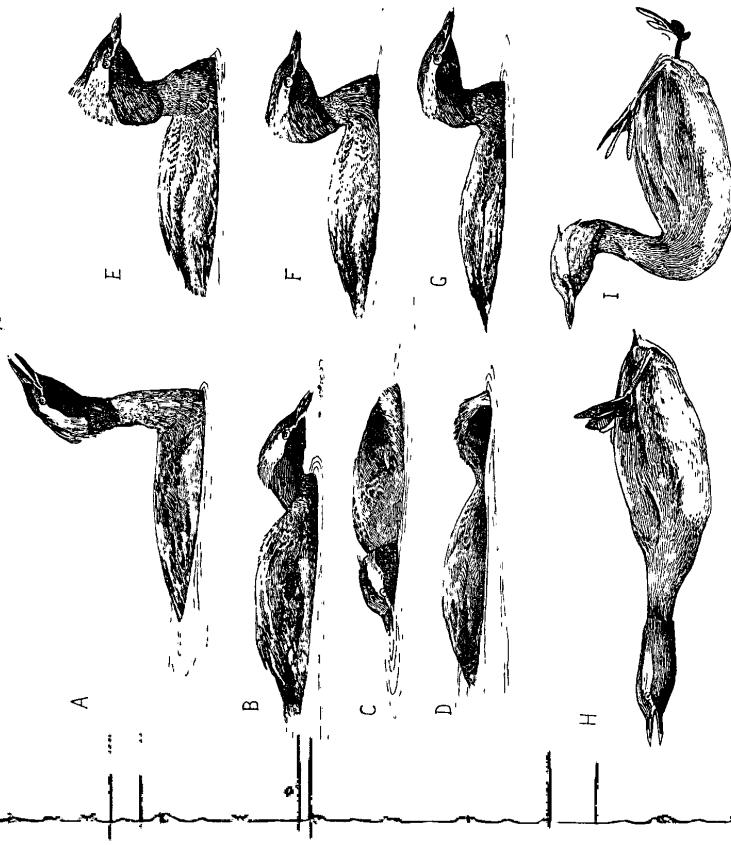


Fig. 2. Feeding behaviour of the horned grebe: Snatching of insects from the air (a); picking (b) and skimming (c) from the water surface; capturing submergent prey from surface position (d); normal surface position (e) and intentions to dive (f, g); rapid (h) and slow (i) swimming under water.

an average of 22 ± 10 sec. submerged per prey brought to the young (n 290); at benthos densities 1000–4000 the time was 13 ± 7.5 sec. (n 173); at benthos densities > 4000 it was 7.4 sec. (n 153). The correlation coefficient for average diving times in 36 series of each ten dives and benthos densities is $r = -0.79$, which is highly significant ($P < 0.001$). If only density data for crustaceans, amelabolous insects, coleopterans, trichopterans and fish are used, the coefficient is $r = -0.81$. Diving times compared with pH of the water give $r = -0.88$; compared with KMnO₄ oxidation figures for humic substances give $r = 0.80$. These latter parameters are, of course, by themselves irrele-

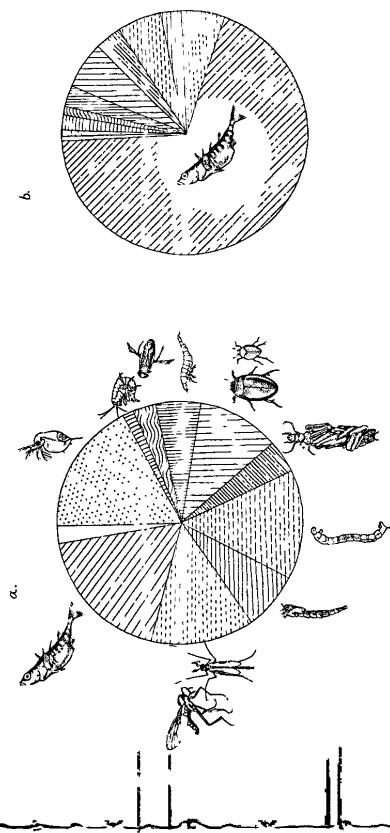


Fig. 3. Pie-graphs showing composition of the diet of horned grebes in N. Norway and the Myvatn area, Iceland, by numbers of prey (a) and by weight (b). The categories are, clockwise from the top, cladocerans, amphipods, aquatic heteropterans, dipteric larvae, aquatic coleopterans, imagines, trichopteran larvae, chironomid larvae, chironomid pupae, aerial insects, mainly picked from the water surface, fish, and various other foods.

vant. It is nevertheless consequent that food is most easily obtained in the rich and alkaline lake types, while the birds must make an effort to capture their necessary food in oligotrophic and, in particular, dystrophic localities. This result corresponds to the difference in stationarity between the lake types (P. 66).

It follows that studies of the time and effort necessary to satisfy the daily caloric needs may be a most practical parameter for characterizing the optimality of feeding stations.

STOMACH CONTENTS. Feathers were found in all stomachs, with an average number of 28. The birds would pick up small feathers from the water surface whenever they saw one, and feathers which loosened during preening were also eaten. These were mainly the short, satiny white ones from the underparts.

The significance of feather-eating in grebes is still disputed (e.g., Hanzák 1952, Harrison & Hollom 1932, Madsen 1957, Simmons 1956, Storer 1961). Madsen (1957) considered physiological explanations superfluous and assumed that the habit had simply arisen as a non-adaptive by-product of preening behaviour which did not hinder the grebes in the struggle for existence. An approximate function might be to keep the stomach comfortably full when the food had passed on into the intestines. From the present material the hypothesis might be supported by the fact that, with one exception, stomachs with a large number of feathers (more than 35) contained only small amounts of finely fragmented and mainly unidentifiable chitin and few fish bones, an average of 18 identifiable prey. Stomachs with less than 20 feathers had an average of 63 identifiable prey. One stomach with 70 unfermented and one fermented prey had three feathers only. Similar cases were described by Madsen (op. cit.). It follows that feathers must be eaten between the meals at the time when the stomach contents are partly dissolved and emptied into the intestine. However, this is no argument against a physiological function, say the »strainer-effect« theory of several writers. It may be irrelevant to argue that other fish-eating birds survive without the habit of feather-eating. It is worth noting that the number of feathers per stomach averaged 35 in Myvatn where sticklebacks, *Gasterosteus aculeatus*, were the staple food, while it averaged 21 in localities where fish was not taken. Furthermore, the habit of feather-eating is most pronounced in the most typical piscivorous grebe species.

It is not absolutely clear what happens to the feathers after being eaten. Evidently they disintegrate rapidly. Microscopical examination of the contents of the intestines by Hanzák (1952) and Geiger (1957) shows that neither remnants of feathers nor undigested roughage pass the pyloric stomach. Storer (1961, 1969) has given evidence that the feathers aid in the formation of pellets, although definite observations of pellet-casting in grebes are few

(Storer op. cit., Onno 1960) and the pellet is unknown. I have no certain observations of regurgitation.

After regurgitation Storer saw much drinking and thereafter feeding, and birds shot after this feeding period had a large number of food items and few feathers in the stomach, apart from the small feather plug which is always found like a filter in the pyloric lobe. It is not known how frequently pellors may be cast.

Vegetable matter, fresh and decaying, was occasionally found in the stomachs. There are per stomach an average of about two vascular plant fragments, 0.5 seeds, 1.2 sand-grains or small stones and often some tiny, filamentous algae and some detritus. Such items are so few that they probably do not form part of the normal diet, but are more likely taken by mistake or together with other food.

Alltogether, I have recognized 2864 individual prey in my material of 49 stomachs from northern Norway and Iceland. The importance of various categories, by numbers and by weight, is shown in the pie-graphs Fig. 3. By numbers (a) the diet is dominated by cladocerans (17.7%), various aerial insects which may have dropped to the water surface (17.6%), larvae (15.3%), and pupae (7.8%) of chironomid midges, small fishes (14.1%), and aquatic coleopterans (12.3%) and their larvae (5.1%). By weight (b) the fishes dominate completely (69.1%), while cladocerans gave only 0.5%,

aerial insects 5.5 %, chironomid larvae 5.3 %, pupae 3.7 %, aquatic coleopterans 7.4 %, and their larvae 2.7 %. A detailed list of prey is given below.

Bivalvia (*Pisidium* spp.); 19 Notostraca (*Lepidurus arcticus*); approximately 2671 limnic organisms are as follows: 9 Oligochaeta (*Tubifex tubifex*, *Peloscolex ferox*, *Lumbriculus variegatus*, *Stylodrilus hirundianus*); 11 Gastropoda (*Lymania peregra*, *Bathyomphalus conortus*, *Gyraulus acronicus*); 9 larger Cladocera (*Daphnia longispina*, *Eurycerca lamellata*); 38 Amphipoda (*Gammarus lacustris*); 6 larvae, 8 imagines Ephemeroptera (indet., *Ephemerella vulgaris*, *Caenis* sp.); 1 larva, 1 imago Zygoptera (*Coenagrion* sp.); 9 larvae, 8 imagines Plecoptera (*Nemoura* sp.); 75 Heteroptera (*Gerris thoracicus*, *Arcotocoris carinata*, *Sigara* sp.); 143 larvae, 189 imagines Dytiscidae (among the imagines 135 belonged to 9 small *Hydropsyche* spp., length 3–6 mm; 54 to medium-sized, 8–17 mm long, species, viz., *Agabus arcticus*, *A. bipustulatus solieri*, *Ilybius fuliginosus*, *Platambus maculatus*, *Ranthis bistratus*, *Colymbetes dolabratus thomsoni*); 153 Halipidae (*Haliphus fulvus*, *H. ruficollis*, *H. flavicornis*); 2 small Hydrophilidae (indet.); 5 Staphylinidae (*Stenus* sp.); 2 larvae, 30 imagines Donaciinae (*Haemorria mutica*, *Donacia* sp.), *Plateumaris discolor*); 2 larvae, 21 imagines Neuroptera (*Sialis* sp.); 86 larvae, 15 pupae, 113 imagines Trichoptera (only eruciformous types, mainly *Limnephilus* spp., but there were no remains of larval cases in the stomachs); about 430 larvae, 220 pupae, several thousand empty pupal cases, 136 imagines Chironomidae (indet.); 2 larvae Ceratopogonidae (indet.); 5 Culicidae (indet.); 9 Nematocera (indet.); 1 larva Brachycera (? *Climocera stagnalis*); 4 Hydracaridae (indet.); + Ectoprocta (32 statoblasts of *Plumatella fungosa*); 398 fishes (19 *Salmo trutta* fry, 1 *Anguilla anguilla*, 278 *Gasterosteus aculeatus*); few eggs of *Gasterosteus aculeatus*.

The 190 terrestrial insects are as follows: 12 Hemiptera (Cicadina indet., *Oribezia artica*, Heteroptera indet., Saldidae indet.), 21 Coleoptera (indet., Carabidae indet., *Patrebus* sp., *Phyllodecta polaris*, *Aphodius fimetarius*, *Otitophryncus* sp.); 112 Diptera (Triplidae indet., *Bibio marci*, *B. pomona*, *Empis* sp., Cecidomyidae indet., Brachycera indet., Syrphidae indet., Tetracoridae indet.); 45 Hymenoptera (Oryssidae, Braconidae, Ichneumonidae, Ophionidae, Agriorypiidae, Cynipidae, Formicidae, *Lasius* sp., *Bombus jonellus*).

The food of small chicks may be judged from 14 stomachs, mainly from the potholes near Lake Myvatn. Five of them were empty; the remaining contained an average of 5 feathers each, and further 5 % crustaceans, 6 % corixids, 37.2 % coleopterans, 14.1 % trichopterans, 28.4 % chironomids, 4.9 % terrestrial insects and 4.4 % *Gasterosteus aculeatus*. In some localities the chicks were seen to be fed mainly with fish. Small chicks are fed by their parents, and the data give no particular reason to believe that particular food was selected for them.

In the literature, information on the food selection of the horned grebe is

given mainly by McAtee & Beal (1912), Wetmore (1924), and Onno (1958a).

McAtee & Beal (57 stomachs, Canada, ssp. *cornutus*) found 23.3 coleopterans, 12 % other insects, mainly heteropterans, trichopterans, larvae of chironomids, and various nymphs, 20.7 % crayfish (*Cambarus*, *Potamobius*), and 13.8 % other crustaceans and 29.8 % fish. Wetmore (122 stomachs, Canada, ssp. *cornutus*) found 46 % insects and 43 % fish, but his material was from all months of the year, except July. In summer amphipods, corixids, gerrids, belostomatids, halipids, dytiscids, hydrophilids, trichopterans, chironomids and land insects dominated, and also some crayfish were taken. Onno (56 stomachs, Estonia, ssp. *auritus*) found mainly amphipods (*Gammarus*) and aerial insects, and some *Donacia* and zygopterans, but no fish. Dementjev & Gladkow (1951) (Sachalin, ssp. *auritus* \geq *cornutus*) mention mainly Gammaridae and Dytiscidae and their larvae. Some of the differences between the sources, especially the presence or absence of crayfish, are, of course, simply due to limnofaunal differences.

The average size of the invertebrate prey in the present diet list is small compared with lists given by other writers. Only few exceeded 0.5 g by weight (19 *Lepidurus arcticus*, 25 *Colymbetes dolabratus thomsoni*, 1 *Bombyx joneillus*). Certainly this is mainly due to the fact that larger aquatic arthropods are uncommon in these regions. I have found larger dytiscids (viz. *Colymbetes pulex*, *Achlyus salicatus*, *Dytiscus marginalis* and *D. lapponicus*) only in very few lakes in northern Norway, and none of these large species occur in Iceland. The average size of 171 aquatic Coleoptera and Heteroptera taken in supposed random samples in the study areas was 7.1 ± 2.5 mm, while the average for 447 reconstructed specimens from grebe stomachs was 7.0 ± 2.1 mm, which is very similar. However, the average length of 67 sticklebacks collected in Myvatn was 28 ± 16 mm, while more constant, 29 ± 7 mm, for 62 unfermented specimens from grebe stomachs, suggesting a selection of medium-sized specimens among the fishes.

At sea the winter food is, according to Wetmore (1924), mainly small fishes, especially sculpins (Gadidae and Cottidae), and some mysids, amphipods, and Decapoda Natantia.

Information on the food of the most likely food competitor of the horned grebe, the red-necked grebe, is given mainly by Madsen (1957), Markuze (1965), Onno (1958a), Smogorzewski (1959), and Wetmore (1924). The investigation by Markuze in fish-ponds near Astrakhan (73 stomachs) showed 92–100 % invertebrate food, mainly Notostraca (*Triops* sp.), Conchostraca (*Esteria* sp.), heteropterans (especially *Ranatra linearis* and *Nauclera cimicoides*), dytiscids and hydrophilids and their larvae, *Donacia* spp. and curculionids (*Lixus* sp.) and some amphibians, mainly tadpoles, and few fishes. A very similar result was arrived at by Smogorzewski, and also by Onno (fish remains only in one out of 45 stomachs). There may be some local variations

Locality	Samples	Percent composition of the samples
Other items		
Gasterosteus		
Terrestrial insects		
Chironomid im.		
Chironomid larvae		
Trichopteran larvae		
Trichopteran im.		
Sialis sp. im.		
Various nymphs		
Corixidae		
Dytiscid im.		
Haliplid im.		
Cladocera		
Lepidium arcticum		
Pisidium spp.		
Gastropoda		
Hirudinea		
Oligochaeta		
3 stomachs with 243 prey	0 0 1.5 0 0 1 0 1.5 30.5 1.5 0 6.5 1.5 36.5 0.5 3.5 10.5 2 3	
22 bottom samples, giving	0.6 0 19.5 10.5 0 0 0.2 0 >0.2 >1.8 >0 0 1 - 59 - - - >0 5.5	
21 bottom samples, giving	6.8 5.1 2.8 59.4 0 >0.3 0.3 >0 >0.3 >1 >0 0 1.7 - 16.3 - - - >0 7	
2 stomachs with 325 prey	0.6 0 0 0 0 0 2.8 1.5 34 147 0.3 0.6 11 17.5 9.8 25.5 2.2 7.4 0.9 1.8	
15 bottom samples, giving	2.4 2.0 4.5 65.3 0 >0.5 0.3 >0 >0.5 >0 0.3 3.1 - 16 - - - >0.2 5.1	
2 stomachs with 330 prey	0.3 0 0.3 0 0 0.3 0 0.7 0.9 8 3.9 2.1 1.8 19.4 34.8 0.9 23 3.6 0	
4 bottom samples, giving	4.3 0 1.5 37 0 >0 0 >0 >0 >0 0 1.5 - 52.7 - - - >0 0	
9 stomachs with 248 prey	0 0 0 0.4 0 2 0 6.5 49.4 5.2 3.6 0 2 4.4 3.6 + 8 1.2 13.4 0	
33 bottom samples, giving	19.5 0.8 0.3 26 0 15.5 0 >0.3 >0.8 >0.3 0 0 0.3 - 37.2 - - - >0.3 0	
11 stomachs with 522 prey	0.4 0 0.4 0 2.5 13.6 0 0.8 1.2 4.4 0 0 1.5 1.5 15 (3) 5.4 10.6 39.9 0	
88 bottom samples, giving	7.9 0.2 1.4 4.1 0.2 >5.9 0 >0 >0 >0 0 3 - 76.5 - - - >1 0	
5117 animals per m ²	80 bottom samples, giving	26.304 animals per m ²
12 stomachs with 811 prey	0.3 0 0.4 0.6 0.8 30 0 0.3 0.6 1.4 0 0 1.7 0.4 14.5 (20) 5.3 5.3 16.5 0	
7		

Table III. Percent composition of herring goby stomach contents as compared with percent composition of the bottom fauna in the same places. The localities are: (1) The oligotrophic river Nivaara near Bodø, Norway, with prey rich vegetation of *Boguscium filiforme* and mosses; (2) Shallow bays, mainly with gravel bottom covered by vegetation of *Lobelia dortmanna*, in the large, oligotrophic Lake Fjærvatn near Bodø; (4) The lake Lærdalsvatn near Bodø, with dense submergent vegetation of *Isotoma lacustris*, *Potamogeton perfoliatus* and *Mgriophyllum alterniflorum*; (5) Oligotrophic pools, rich in sedges, *Carex spp.*, and submergent vegetation, mainly of *Chara spp.*, *Potamogeton gramineus alterniflorum*; (6) Close-shore parts of Lake Myvatn, eutrophic, about one metre deep, with dense submerged fields of *Potamogeton filiformis* and *Mgriophyllum spicatum*; (7) Offshore parts of Lake Myvatn, eutrophic, mainly 2-3 m deep, and *Mgriophyllum alterniflorum* near Lake Myvatn, Iceland; (8) Close-shore parts of Lake Myvatn, eutrophic, about one metre deep, with dense submerged fields of *Potamogeton perfoliatus* with *Peltiphyllum perforatum* overgrown with *Potamogeton perfoliatus*, *P. filiformis*, and *Ranunculus aquatilis*. For lake Myvatn data from the abnormal summer 1970 (see Bengtsson 1971b, 1972) are discarded from the table, but they are mentioned in the text.

as, e.g., Madsen and Wobus (1964) found more fish, but generally spp. *grisea*, notwithstanding its large size, has a diet very similar to the horned grebe. The winter food comprises more fish (Madsen 1957), and the data of Wetmore (1924) (46 stomachs, Canada, spp. *holboellii*) support the fact that the red-necked grebe is mainly piscivorous in North America, thus being probably an ecological equivalent to the great-crested grebe.

The great-crested grebe differs clearly from its relatives in the Baltic area in its food requirements, being largely piscivorous (Geiger 1957, Hanzák 1952, Harrison & Hollom 1932, Madsen 1957, Markuze 1965, Ono 1958a, Smogoriewski 1959).

DIET IN RELATION TO AVAILABLE SUPPLY. In most of the localities from which horned grebe stomachs are taken, the bottom fauna was studied quantitatively at the same time of the year (July). Unfortunately, the comparison of food selection and supply stated is not fully relevant as the bottom dredge takes mainly in- and epifauna, while the nekton, and in particular the fishes, are much underrated. This bias must be taken into consideration in the following discussion.

Table III summarizes data from seven localities briefly characterized in the table legend.

It is clearly seen from the table that the benthic fauna (Oligochaeta, *Pisidium*, some Chironomidae species) together with Hirudinea is nowhere selected. The infaunal species are eaten only occasionally, and their share in the diet does not appear to be proportional to their dominance values in the bottom samples. Gastropods are also taken rarely, but maybe their role as food is correlated with local abundance: *Lymnaea peregra* constituted 1.5 % of the food in Nyvatn, where it was abundant (99 per m²) and very conspicuous. *Bathyomphalus contortus* and *Lymnaea peregra* constituted 16 % of the contents of one stomach from Lake Myrvatn (co. Skåneland), where both species abounded on decaying litter (385 per m²).

In some places larvae of trichopterans may be eaten selectively, and the imagines are frequently caught from the emergent vegetation or from the water surface. The data do not show for certain whether their share in the diet is in proportion to their dominance values. In coastal parts of Myrvatn trichopteran larvae were eaten only occasionally, notwithstanding an average density of 154 larvae per m². This may be due to a superabundance of other foods, mainly sticklebacks. Nymphs of Plecoptera and Ephemeroptera are scarce in the stomach samples, but they are also very scarce in bottom samples.

There is a pronounced selection of *Lepidurus arcticus*, *Gammarus lacustris*,

the table the lumped values for these nektonic organisms in the diet lists are roughly proportional with their lumped dominance values. In Myrvatn, where sticklebacks occur in large shoals along most coasts, this is by far the most important food, by weight. In the nearby pothole areas corixids, halophilids, dytiscids and small sticklebacks, living among the shore vegetation, are the staple food. In the pools Laugen and Kvannesvatn near Harstad, where the amphipod *Gammarus lacustris* abounded, even pelagically, this was, judged from direct observations, almost the only food taken. At some breeding sites situated near brook inlets in the lakes the grebes fed much upon trout fry, *Salmo trutta*. On the other hand, in Lake Vikevatn near Harstad, where nekton seemed to be scarce, one grebe stomach contained 20 % *Haemona mutica*, a Donacinae beetle which clings tightly to the submerged vegetation.

Chironomid larvae and pupae may be eaten in considerable numbers, probably from the submerged vegetation (see Nyvatn, Vatnet, Liatjønn, Myrvatn). In some lakes these insects seem to constitute a buffer food as their share in the diet is varied. The share is not proportional to the dominance values in the bottom samples, but maybe rather with a scarcity of other foods. Myrvatn is an exception. Here the midge larvae are certainly eaten due to their extreme abundance, in normal years (1968, 1969) average 24,000 per m² in offshore portions in July. The chironomid larvae found in the bottom samples further become important later, during the hatching periods. About half of the stomachs from Myrvatn contained innumerable finely fragmented pupal cases (the value 20 % in the table is set rather arbitrarily). Also in the potholes feeding upon midges from the water surface was, on some few days, the main feeding technique. Naturally, these items must be of low caloric value. Nevertheless the hatching peaks seem to be very attractive as they represent enormous numbers of very easily available items. The attractiveness of such feeding prospects is clearly illustrated by the selection of offshore portions of Myrvatn for feeding among the grebes breeding in the potholes (Fig. 5).

Feeding from the water surface is also seen during periods of nice weather when many land insects are blown out over the lakes. This appears clearly from the table, especially for Liatjønn.

Larger cladocerans (*Eurycerus lamellatus* in some pools, *Daphnia longispina* in offshore Myrvatn) are eaten when they occur in very large concentrations.

In 1970 the Chironomidae failed completely in Myrvatn. The density of larvae in July was only 6 % of that of the previous two seasons (Bengtson 1971b, 1972). In four horned grebe stomachs analysed there were only 17 Chironomidae larval heads and some very few fragments of pupal cases, no sticklebacks, but 271 *Daphnia longispina*. This may indicate a shift to a zoo-

plankton diet in the offshore parts of the lake. Near the coast the food was, as in normal years, mainly sticklebacks (direct observations).

Altogether, the feeding of the horned grebe ssp. *arcticus* appears to be unspecialized and very flexible. Although the normal food is nektonic, including both arthropods and fish, it may shift to what is in abundant supply and easily available.

DIET IN RELATION TO BILL DIMENSIONS. Heavy bill in ssp. *arcticus* and a fine bill in the nominate race in the Baltic area and further east (Fjeldså 1973b) has been interpreted in terms of character displacement. This interpretation rests upon the assumption that a fine bill is an adaptation facilitating specialized feeding in areas with food competition with other grebe species.

Food selection in birds may presuppose some innate search images (e.g., certain size groups, movements), but is probably mainly acquired by trial and error. Both nidifugous chicks and nidicolous fledglings first try to eat a variety of objects, and in the main they learn by experience which of them are edible, and also which food is obtained most economically (Hinde 1959). The ontogeny of food selection and feeding technique is thus mainly a matter of experience and very dependent on the available supply of food; segregation by feeding is thought to be maintained by morphological characteristics of beak, feet, musculature, and innate motor patterns which determine which food may be most economically obtained.

My assumption regarding the horned grebe races is supported by a comparison of the present diet list with the results from 56 Estonian horned grebe stomachs (Onno 1958a). These contained mainly amphipods, aerial insects, *Donacia* and zygopterans, and no fish, suggesting a preference of medium-sized arthropods. The diet lists given by McAtee & Beal (1912) and Wetmore (1924) for the American race *cornutus*, which has also a thin, although longer and more variable bill, do not differ much from the present.

As mentioned on p. 60, I was not in a position to make a comparative analysis of the food selection of the two European races. Instead I have tried to demonstrate the significance of bill thickness by comparing the food of specimens with extreme bill measurements from the *arcticus* series. The samples consist in stomachs of 12 grebes with a height of the closed bill, at the base, more than 9.5 mm (553 prey) and six grebes with a bill height of 7.5–8.0 mm (n 299 prey) (Fig. 4). It appears from the histograms of length distribution of the prey that the most fine-billed specimens selected medium-sized prey (average only 7.3% fish), while heavy-billed specimens took prey of more variable size (average 29.5% fish). The result supports the assumption that a fine bill assists specialized feeding habits, although the data are few and not fully conclusive as the specimens are not all caught in the same place.

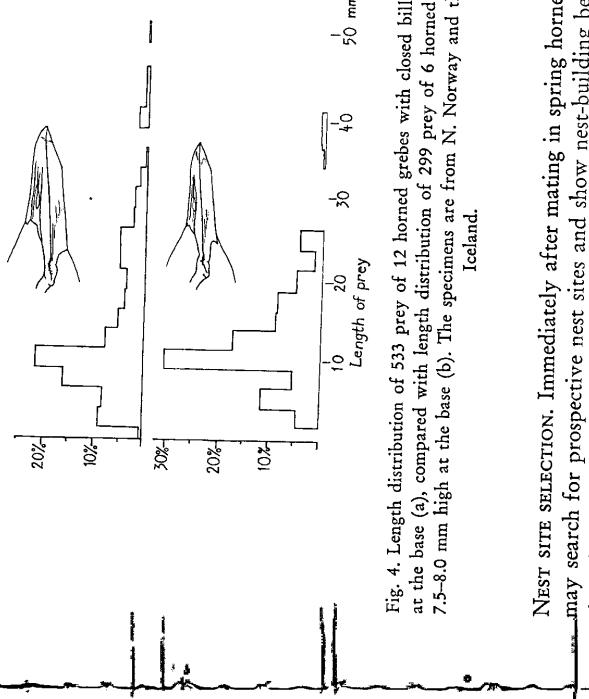


Fig. 4. Length distribution of 553 prey of 12 horned grebes with closed bill > 9.5 mm high at the base (a), compared with length distribution of 299 prey of 6 horned grebes with bill 7.5–8.0 mm high at the base (b). The specimens are from N. Norway and the Mývatn area, Iceland.

NEST SITE SELECTION. Immediately after mating in spring horned grebe pairs may search for prospective nest sites and show nest-building behaviour. Pairing platforms may even be built in the littoral *Fucus* zone in marine habitats before breaking up of the ice on the lakes. Arriving at fresh water at an advanced stage of reproductive development, these pairs may settle immediately to breed. Many nests are thus built when new and withered vegetation scarcely reaches above the water surface, and they may be visible from far away during the early part of incubation. For the entire population, however, the selection of nest sites is protracted from medio May to ultimo July.

Nests and platforms are as a rule built floating, anchored to the emergent vegetation, as far offshore as possible, although still sufficiently within the vegetation to be protected against waves. The depth of water was, for 573 Norwegian nests and platforms, 0–120, $\bar{x} 43 \pm 19$ cm; for 615 Icelandic nests and platforms, 0–125, $\bar{x} 45 \pm 26$ cm. Before the new-grown vegetation gives sufficient cover, the birds seem to select shallow patches within the vegetation zone. This may be advantageous as shallow places may indicate dense future vegetation.

In order to study vegetation preference for nest sites the relative abundance of separate vegetation types in lakes in northern Norway was recorded by measuring along the offshore edge of the vegetation the sections dominated by each type (Table IV). (Nest site selection in the Mývatn district will be discussed separately later (p. 88) due to some peculiarities and very little variation in the types of supra-aquatic vegetation there. Data from Finland

Table IV. Types of vegetation selected for nesting in northern Norway.

Dominant plant species	km vegetation zone	nests per km	platforms per km
<i>Eriophorum angustifolium</i>	1.5	0	1.3
<i>Carex lasiocarpa</i>	5.0	0.4	3.0
<i>Comarum palustre</i>	0.5	2.0	2.0
<i>Menyanthes trifolia</i>	3.1	3.9	5.2
<i>Carex rostrata</i>	23.0	6.2	8.1
<i>Carex</i> and <i>Salix</i>	0.5	24.0	30.0
<i>Salix</i> shrubs	0.4	10.0	27.5
<i>Lysimachia thyrsiflora</i>	0.5	6.0	6.0
<i>Equisetum fluviatile</i>	26.8	3.7	2.7
<i>Phragmites communis</i>	9.3	4.2	5.5
<i>Scirpus lacustris</i>	2.5	0.4	1.6

are too few for analysis.) A total of 72.3 km of systematically examined vegetation zones is used for analysis. Only very few nests were placed in other kinds of vegetation than those shown in the table, *Carex aquatilis* and *C. vesicaria*, *Caltha palustris*, floating peat or absolutely open, anchored only to submergent vegetation. Only five nests and five platforms were found along 286 km of shoreline with no helophyte zone.

To interpret the table it is necessary to consider the normal succession of vegetation in the lakes of this area. The incipient littoral growth of a boggy coast mainly consists of a narrow zone of sparse *Eriophorum angustifolium*, *Carex lasiocarpa*, *C. limosa*, *Comarum palustre* or *Menyanthes trifolia*. In such places true nests are very scarce, but occasional pairing platforms may be found. Such a narrow zone may develop into a broader and denser zone of *Carex rostrata*. This is clearly favourable for nesting (6.2 nests per km), especially in fertile localities where this plant species is lush and broad-leaved (var. *nitriculata* (Bott.), 10 nests per km). Still more frequented are *Carex* stands interspersed with willow shrubs, *Salix* spp. (24 nests per km). The very high selection is mainly due to the cover given by the shrubs even before foliation and sprouting of the sedges. A high proportion of pairing platforms per nest in places with localized shrubs but no sedges (10 nests and 27.5 platforms per km) indicates that these are not fully satisfactory, and are selected mainly due to a shortage of sedgebeds.

A wide helophyte zone with complete succession of vegetation has most often an outer portion of *Equisetum fluviatile*, with undergrowth of various

HABITAT SELECTION OF PODICERS AURITUS

Table V. Widths of helophyte zones selected for nesting in northern Norway.

Dominant plant species	km vegetation zone	Width of helophyte zone, m	> 100					
			< 2		2-5		5-10	
			Km investigated	Nests per km	Platforms per km	Platforms per km	Platforms per km	Platforms per km
<i>Eriophorum angustifolium</i>	1.5	10.9	9.8	10.8	12.7	10.1	4.5	2.5
<i>Carex lasiocarpa</i>	5.0	0.5	2.8	4.8	6.5	7.3	8.2	8.4
<i>Comarum palustre</i>	0.5	1.8	3.4	5.1	5.2	7.3	12.7	6.0

pleurocarpic bryophytes and *Lysimachia thyrsiflora* in dense platters. Such dense *Equisetum* zones constitute favourable nest sites (6 nests per km in places with *Lysimachia*), but as *Equisetum* vegetation is in many places less dense and generally sprouts late in the spring, the average nest density is low (3.7 nests per km). Instead, early pairs may place their nests in smaller nearby *Carex* stands, or in the *Carex-Menyanthes* zone frequently following inside the *Equisetum* zone. Of nests with egg-laying before the annual average, 69 % were in *Carex* vegetation, 17.5 % in *Equisetum* vegetation, while of nests with egg-laying later in the season these values were 47 % and 34 %, resp.

In some few lakes the *Equisetum* zones are replaced by reeds, *Phragmites communis*, (4.2 nests per km) or by *Scirpus lacustris*. (Low nesting density here is not much worthy of attention as this plant is found in only three of the lakes included.) Both these plants sprout late in the spring, but withered reeds ordinarily give sufficient cover early in the season. Reeds are mainly less than 2 m high and scanty in this region.

To sum up, vegetation selection for nesting in lakes in northern Norway seems mainly to be due to position differences in the succession of shore vegetation, i.e., preference for well-developed helophyte zones to scanty ones with a pioneer community, and a preference for localities with *Salix* shrubs, *Carex rostrata* and *Phragmites*, which may remain emergent throughout winter and give cover as soon as the ice breaks up in the spring.

Preference regarding the density of vegetation may be illustrated indirectly by the relative abundance of pairing platforms, i.e., incomplete intentions to breed. In scanty vegetation where the birds must penetrate some distance into the sedgebed to find sufficient shelter, there averaged 1.93 platforms per true nest. In medium-dense vegetation the ratio was 1.13, while in places with a dense barrier along the outer vegetation border it was 0.56. The nests were mainly placed just inside the barrier, or even floating in an open patch inside it. In very small, isolated sedgebeds the ratio may be still lower, but this may mainly be due to a shortage of alternative sites for nest-building activity.

Preference regarding the width of the helophyte zone in lakes in northern Norway is shown in Table V.

Breeding nests appear to be scarce in very narrow helophyte zones and most numerous in the very widest zones. However, the ratio between plant forms and true nests stabilizes in zones only 5–10 m wide, and there is only a slight increase in nest density in zones more than 10 m wide. This shows that zones more than 10 m wide will generally be satisfactory. The best extensive, shallow areas became overgrown with uniform, dense vegetation of *Equisetum* after an auxotrophication. Horned grebes preferred smaller patches of *Carex*-vegetation to the *Equisetum* swamps. In Finland no horned grebes were found along the borders of extensive, dense reed-swamps. Maybe this species is too weak to force its way through such vegetation. Although the horned grebe does not shun cultivation and generally will benefit by erophiation from surrounding agricultural land (Olsoni 1928, Soveti 1940), a large-scale overgrowing may be adverse. Thus the requirements are met neither in the first stage of littoral growth nor in the climax type of unbroken vegetation, but in the intermediate sere stage. There is a clear-cut preference for shallow lakes with numerous small, offshore patches of vegetation (Olsoni 1928). Here the situation of nests is independent of the proximity of the shore. Such places are few in lakes in northern Norway. In a 2.2 km periphery of sedge isles and areas of patchy offshore vegetation there were 20.8 nests and 7.8 platforms per km.

The relative importance of innate and acquired factors in habitat selection

The relative significance of innate and acquired factors in habitat-selection may be analysed by an examination of possible age differences in nest-site selection. A prerequisite is to exclude birds which did not succeed in setting up a territory in preferred habitats. As stated on p. 60 this bias may be largely reduced by using data only from pairs laying eggs earlier than the annual mean.

Among early pairs an average of 55 % of 226 «aged» females were »old«. Below I will give »old«-female percentage values for various kinds of nest-site habitats, and these values should be compared with this average as a standard.

There is a general preference for nesting in wide helophyte zones (Table V) and in particular in offshore mosaics of open water interrupted by emergent vegetation. This preference is evidently fortunate in most lakes, judged from a 81.5 % average nesting success in offshore sedge-isles and 75.5 % success

in helophyte zones more than 50 m wide; as compared with only 51 % success in scanty zones less than 1 m wide. As »old« birds are generally superior in setting up territories in the spring, we might expect the wide vegetation zones to be mainly at their hegemony. This does not appear to hold true: Among early nests placed in longer helophyte zones the »old« bird percentages in zones < 5, 5–15, 15–25, 25–50, and 50–150 m wide were respectively 53 % (n 32), 55 % (n 60), 50 % (n 28), 44 % (n 16), and 47 % (n 17). The »old« bird percentage is only slightly higher, i.e. 59 % (n 29), in offshore sedge-islets, and it is slightly higher in dense than in scanty sedge beds. On the other hand the »old« bird percentage may be very high at nest site types which, judged from the preceding preference analysis, would seem abnormal. Of nests hidden among high tussocks at the shore, or in holes or crevices in a peaty shore, 72 % (n 14) belonged to »old« birds; of those placed in a similar way on isles, 91 % (n 11) belonged to »old« birds; of those placed in very small but dense *Carex* stands near an otherwise sterile shore 88 % (n 8) belonged to »old« birds; and of those in dense willow shrubs with no sedge vegetation 85 % (n 13) belonged to »old« birds. Common to these sites is a localized cover, in some cases only just sufficient to hide the nest. Nevertheless, many such nests were difficult to find, and the nesting was very successful: Hatching took place in 87.8 %.

The nature and significance of the possible age difference in habitat selection may be best illustrated by a comparison of environmental factors and the distribution of grebe nests in the Mývatn area.

Fig. 5 compares the distribution of helophyte vegetation, areas with abundance of sticklebacks, and distribution of July bentos densities (a) with the distribution of feeding areas and »first-year« and »old« female nest sites early in the breeding seasons (b). The maps include only the northern half of the district, as more than 90 % of the grebe population of the area nests here. Age-group figures in the text are, however, calculated for the whole area.

East and north of Lake Mývatn there are mainly lava coasts. Other coasts are mainly peaty or gravel shores, influenced by the action of strong waves. Only in restricted bays of the west coast of Ytriþófi are there several dense vegetation zones of *Carex rostrata* var. *utriculata*. Also other lakes in the area have mainly sterile coasts, except near the outlet from Lake Sandvatn, where marshes of *Carex chordorrhiza* and *C. saccatilis* and *Salix* shrubs are broken up by channels and small sheets of open water with a patchy cover of *Carex rostrata*. To the northwest of Mývatn there are moors and shrubland with several hundred pools and flooded marshes with a general richness of *Carex* vegetation.

The distribution of food (cf. Table III) differs very much from that of emergent vegetation. Lake Mývatn is eutrophic, with a very high production of diatoms and bluegreen algae, *Anabaena flos-aquae*. In the central parts

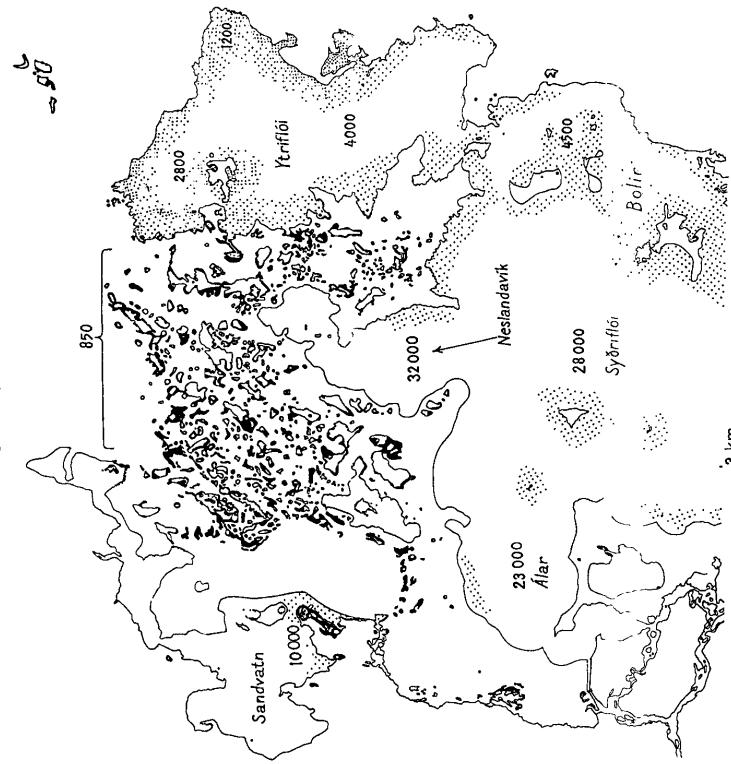


Fig. 5. Comparison of some environmental factors (a) and distribution of feeding and nesting of horned grebes (b) in the northern part of the Mývatn area, Iceland. In (a) black colour shows occurrence of emergent aquatic vegetation, mainly *Carex rostrata*; stippling shows areas with abundance of sticklebacks, *Gasterosteus aculeatus*; figures show average benthos densities, mainly chironomid larvae, in some subdivisions of the area, in July. In (b) the main feeding stations of horned grebes are stippled; arrows show direction of feeding excursions from nesting areas; open symbols show location of nests with »first-year« females; filled symbols nests with »old« female. Only nests where egg laying took place before the annual average is included, to reduce the number of nest-sites selected due to the inability to set up territories in preferred habitats.

of Syðrjóli, Neslandavík, and Alar the soft diatomite bottom is extremely rich in chironomid larvae; in certain places the density may exceed 50,000 per m² bottom in late July, and also cladocerans are very numerous in late summer. In the eastern and northeastern parts, Bolir and Ytriðjóli, these organisms are less numerous, but sticklebacks are very abundant, especially near temperate springs in three bays at the east coast of Ytriðjóli. Lake Sandvatn

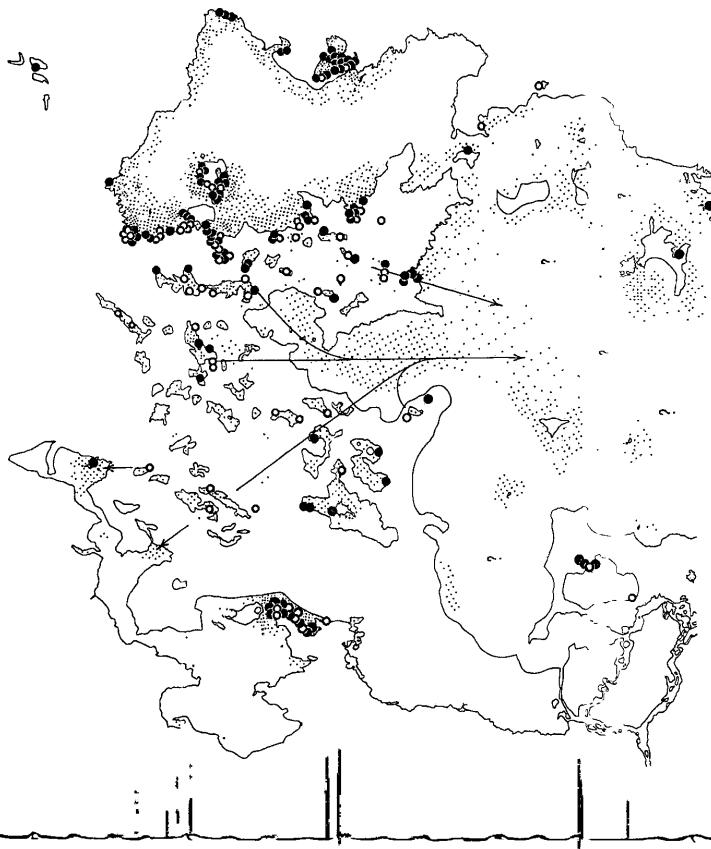


Fig. 5b

is less fertile, although one series of samples in late July showed 10,000 Chironomidae larvae per m² (S. A. Bengtsson). The pothole areas are infertile, with benthos densities mainly well below 1000 specimens per m².

The total »old« bird percentage among early horned grebe pairs in Lake Mývatn was 65% (n 125), against 44% (n 66) in the pothole areas. This difference may be due to some extent to the early breaking up of the ice in Mývatn as compared with the pothole areas (the eastern coast of Ytriðjóli is never frozen), and the earlier arrival of »old« pairs in spring. Among data from nest sites within helophyte zones in Mývatn there were 48% »old« birds (n 69), which is very similar to the pothole area value. However, the average age group at nest sites with no helophyte vegetation in Mývatn was 86% (n 56) »old« birds.

There seems to be a tendency that the »first-year« birds are very dependent on the occurrence of supra-aquatic vegetation. They further tend to settle in

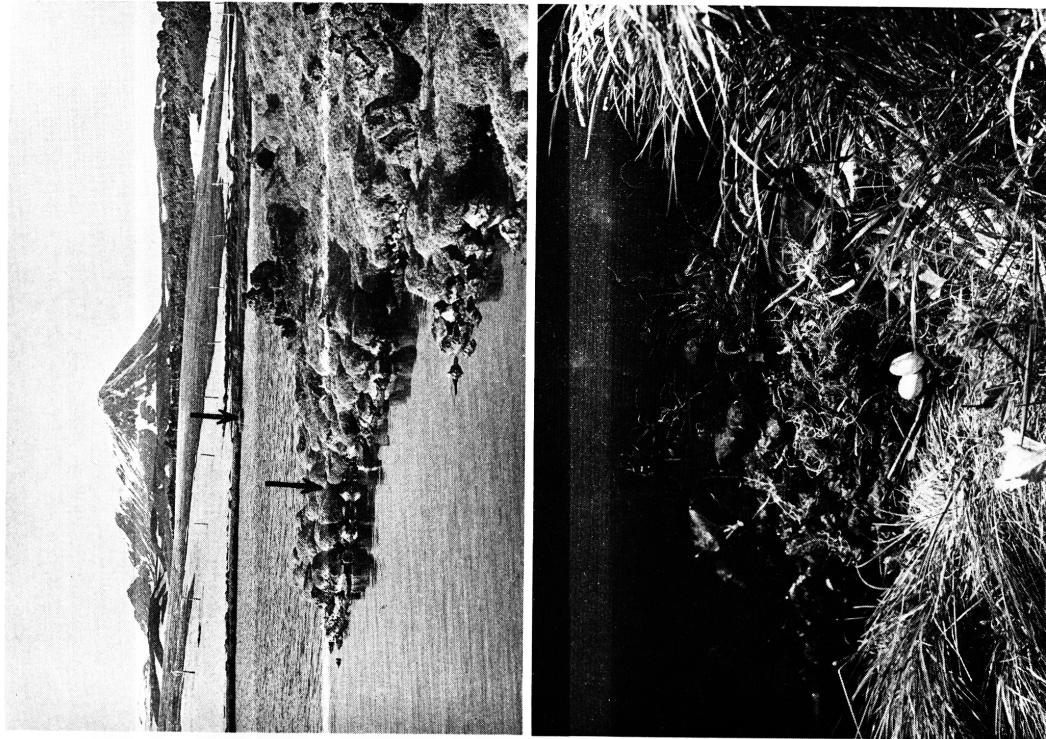
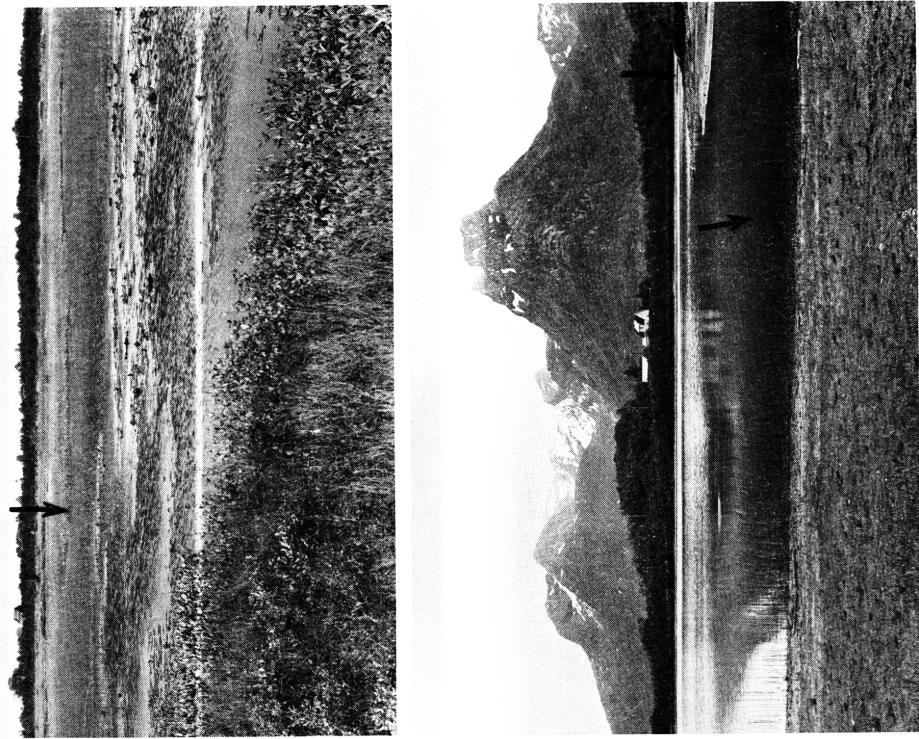


Fig. 6. Breeding habitats of horned grebes -nest-sites indicated by arrows. A shows a mesotrophic moorland lake (Seinesvatn near Bodø, Norway) with mosaics of open water, patches with floating leaves of *Nymphaea occidentalis* and emergent vegetation of *Equisetum fluviatile*, *Carex rostrata* and *Menyanthes trifoliata*. B shows an oligotrophic lake (Liatjønn



near Bodø) with mainly sterile shores, and only small, local beds of *Equisetum fluviatile*. C shows a bay in lake Mývatn with springs of temperate ground water. Here the horned grebes breed on hummocks in the water or in crevices among lava stones. D shows a nest placed at an exposed peaty shore in Mývatn.

places with less extensive sheets of open water. In places with less than 50 m expanse of open water, measured along a perpendicular from the nearest outer vegetation border, there were only 45 % (n 100) »old« birds; in places with 50–500 m open water expanse 65.5 % (n 128) »old« birds; in places with more than 500 m open water expanse 75 % (n 36) »old« birds (data from early pairs from both Mývatn area and northern Norway). Thus »first-year« birds probably prefer to see themselves completely surrounded by emergent vegetation.

»Old« birds, on the other hand, preferred to place their nests in dense, protective patches of vegetation, irrespective of how extensive these were or close to the best feeding stations, irrespective of whether there was emergent vegetation at all. Many nests were placed in deep crevices between tufts of *Carex juncella* and *C. lyngbyei* or *Caltha palustris* at the main shore or at the shore of an islet, among lava rocks overhung by shore vegetation of, e. g., *Angelica archangelica*, or even on firm ground. (Nesting on firm ground may further be due to the flooding or destruction of traditional nest sites, cf. Nero, Lahrmann & Bard 1958 for western grebes.) Such sites are shown on the photographs Fig. 6, p. 87, together with two more normal sites. As stated above these aberrant nest sites proved fully protective. Probably, »old« birds have learned to judge the protectivity of vegetation cover from other factors than its extension or the distance from firm ground. The lack of normal nest sites is compensated for by the prospects of benefiting from a superabundance of food in the closest vicinity. This enables the broods to remain on the territories, using the nest sites for resting.

Birds settling on more »normal« nest sites in the pothole areas had a much lower nesting success (66 %), and during the incubation period they showed an increasing tendency to leave the pools, flying to the offshore portions of Neslandavík and Sydriflói to feed (p. 66). The young necessarily had to be fed within the pools, but if the data were homogenized as to age-groups of the parents, the chick survival was not much different from that found in Mývatn. Survival data (Fjeldså 1973a) show that even very small pools would suffice to raise a brood, but according to the studies of feeding behaviour (p. 69), the parents will necessarily have to spend much effort to satisfy the requirements here. While the specialization of experienced birds in localities very rich in food need not be strictly necessary for the raising of young, it may demonstrate a preference for comfortable living conditions.

The progress of breeding in Mývatn after the annual mean of egg laying may be briefly summarized here (see Fjeldså 1973a, Figs. 2–5 for details). The main bulk of »first-year« birds in the district dispersed westwards into the pothole areas so that the lumped age-group for both early and late pairs was here 37.5 % (n 96) »old« birds. Some »first-year« birds also settled in late June at peaty shores on the west coast of Ytriflói, but they did not show the

same ingenuity as »old« birds to find safe nest sites here. Their nesting success was only about 50 %. There was also an increment of birds at the east coast of Ytriflói throughout June into July, but the late settlers here were mainly »old«.

The apparently much higher valency of extensive vegetation for habitat selection in »first-year« birds than in elder birds does not exclude the opinion elaborated elsewhere (Fjeldså 1973a) that first-year birds dispersed into the pothole areas because they could not establish territories in the crowded sedgesbeds at the west coast of Ytriflói.

DISCUSSION

The role of interspecific competition in the evolution of habitat selection cannot be evaluated in detail here. The investigation in Finland was too deficient to indicate directly the nature of competition between the local grebe species. The prevailing explanation of competitive ecological displacement, including displacement by habitat selection, rests upon the assumption that the size of populations is regulated directly by environmental resources, in particular food, together with, in some cases, harmful interferences between the species (e. g., Nicholson 1957, Lack 1970 and several papers in the 1940's—DeBach 1966, Slobodkin 1962, Mayr 1948). The importance of the food factor to horned grebes should appear clearly from the description of habitat selection in the Mývatn area, and further from the inverse correlation between the abundance of food and aggressive levels, direct effects of crowding upon breeding in individual pairs, extension of feeding excursions and vagrancy of families with young, stated elsewhere (Fjeldså 1973a). But although many aspects of breeding ecology as well as average population levels are clearly correlated with the abundance of food, there are cases where the *actual regulation* of population numbers is evidently mediated by territorial behaviour. The population may be kept at a level securing optimal feeding conditions rather than at the highest possible level which could be maintained (Fjeldså op. cit.). This condition does not fully satisfy the above-mentioned premises for displacement.

In all cases, the existence of several ecological differences between the grebe species in the Baltic area is documented (see further Onno 1958a, 1960). The horned grebe ssp. *auritus* appears to be stenotopic, selecting smaller open spaces of water (Table I) fringed by rich vegetation, mainly eutrophic or mixotrophic, typical »Nyroca-lakes« (Fig. 1a). It is fine-billed (Fjeldså 1973b), and the comparison of the present diet list from northern Norway and the Mývatn area with that from Estonia given by Onno (1958a), together with the examination of prey size in relation to bill dimensions in ssp. *arcticus* specimens (Fig. 4), supports the theory that this may be an adaptation assi-

sting specialization in an arthropod diet. In northern Norway and the Myrtn area, in a situation with no close ecological counterparts, the horned grebe seems »to go down the slopes of its adaptive peak«. It may extend into any lake type provided that it may locally find sufficient cover for nesting. This resembles the often cited case of the meadow pipit, *Anthus pratensis*, which in Iceland and on the coastal isles of northern Norway, where possible competitors are scarce, invades several kinds of habitats, including forests (Timmerman 1949, Jenkins 1953). The diet of the horned grebe ssp. *arcticus* includes both various arthropods and small fishes. Although food is mainly nektonic, feeding appears to be unspecialized. If nekton is in sparse supply, there may be a shift to other kinds of food. The birds feed on what is abundant and easily available (Table III) e. g., large concentrations of Chironomidae larvae and Cladocera, or masses of aerial insects or Chironomidae pupal cases on the water surface. They may thus be termed opportunistic feeders.

The habitats selected by »first-year« birds suggest simple innate key stimuli for habitat recognition. The most valent stimulus may be a complete periphery of emergent vegetation. As judged from the nesting frequency in places with a patchy vegetation the attractiveness of a locality may to some extent be due to the amount of »peripheries« of vegetation. This schedule may well resemble the habitat recognition in the Baltic area. The geographical differences in habitat selection (Fig. 1a, b) need, therefore, not necessarily be innate. One frequently cited factor in the evolution of new patterns of habitat selection is early experience (e. g., Klopfer & Hailman 1965, Hildén 1965). As stated by Klopfer (1963) for the chipping sparrow, *Spizella passerina*, and by Wecker (1963) for the prairie deer mouse, *Peromyscus maniculatus bairdi*, mechanisms of habitat selection are in part innate, in part acquired; the acquisition of an attraction towards »new« habitat types was shown to take place mainly during a sensitive youth period.

Although this imprinting component certainly plays some role in fixating new traditions in the population, it cannot be directly supported by the present results. Indeed, its effects seem to be slow, on the population level, as judged from the fact that 25 % of the juvenile grebes in the Myrtn area are raised at aberrant nest site types, while only 10.5 % of the early »first-year« birds settle there to breed. Thus the advantages of settling near the temperate springs and the large concentrations of food found there must to some extent be learned by each new generation. The primary factor of adaptations to peculiar local conditions seems to be a selective retention of experience throughout the life span. The birds learn to select vegetation mainly due to the protection it may give rather than due to its general abundance. Furthermore, they learn to select habitats from factors not closely associated with the nest site as such, e. g., feeding prospects for future convenient living. The

evolution of new traditions by, e. g., the imprinting component, may come subsequently.

Key stimuli for habitat selection are likely to relate to simple features, although a heterogeneous summation of several factors probably takes place (Timbergen 1948), securing a certain flexibility. According to the present results a wider spectrum of potentially vicarious stimuli is used by »old« birds, and these stimuli are mainly more essential to the existence of the species than the supposed innate key stimuli. Learning may bring about an ontogeny from a rigid to a more opportunistic habitat selection.

Returning to the question of the evolution of ecological isolation and the basis of adaptive radiation, the results raise a possible reason to suppose that food need not be in short supply for competitive displacement to take place. Individuals may, by the influence of learning, currently adjust their habitat selection according to what is convenient, not to what is absolutely necessary for survival. In addition to the probable role of young individuals in establishing the species in extrazonal areas, it seems likely that learning by later experience is instrumental in adapting the populations within established areas to the special advantages of these areas. They may learn where and how to find prospects of superabundance of resources for self-maintenance and reproduction, and thus also how to avoid resources or habitats heavily exploited due to the presence of ecological counterparts, even prior to the maximum utilization taking place. The adaptive reaction due to learning does not tend towards a maximum utilization of the area by the population but rather towards the securedness of optimal or convenient living conditions, that is, a counterpart to the supposed effect of evolution. This change in habitat selection is, of course, particularly likely to take place in case of active interference, such as interspecific territorialism. The evolutionary role of so-called aggressive neglect in case of excessive interference with a second species is discussed by, e. g., Ripley (1971).

The genetical survival of individuals is not simply determined by environmental hazards as such. Their effects are steered by what an organism *does* in its environment, i. e., by the *adaptive* reactions stated above. Thus, acquired habits will canalize the effect of selection, thereby giving selective advantage to any innate character that might support fortunate acquired habits. The process of preadaptation is described under the term »genetic assimilation« by Waddington (1942). As explained by Braestrup (1971), this means of »modificatory steering« of evolution by the means of acquired habits is not neo-Lamarckian.

The results further raise viewpoints concerning the interpretation of statistical ecological differences between sympatric species. In situations with a superabundance of food commodities, some degree of ecological differences will still occur, due to segregation having taken place in the past. Neverthe-

less the absence of actual competition may probably be detectable by a study of ecological agegroup differences in the sympatric forms; i. e., a tendency among experienced representatives of the ecological counterparts to use more similar resources than unexperienced representatives. In a situation of direct competition for limited, common resources the reverse may hold true.

SUMMARY

- (1) Feeding ecology and habitat selection of the horned grebe was studied in northern Norway (1958-1971), Iceland (1966, 1969, 1970), and Finland (1972), with particular attention to ecological differences between ssp. *arcticus* in the two former areas, and ssp. *auritus* in the latter area.
- (2) The ssp. *auritus* is stenotopic, selecting smaller, open spaces of water surrounded by rich vegetation, shallow, mainly eutrophic or mixotrophic. Evidence is given that the fine bill, typical of this race, supports specialization on an arthropod food.
- (3) The ssp. *arcticus* has its optimum in the richer lake types, but extends into any lake type including open, oligotrophic ones, provided that it may locally find a sedged bed for nesting and some shallow feeding areas. This heavy-billed race appears to be an unspecialized feeder. Its staple food is small fishes and nektonic arthropods, but it may shift to what is abundant and easily available, such as chironomid larvae, aerial insects or Cladocera.
- (4) The reason why this race »goes down the slopes of its adaptive peak« is probably the absence of close ecological counterparts. The opportunistic feeding habits, extension into larger lakes, a plastic activity distribution and adaptive variations in territorial behaviour are factors which permit it to maintain stable populations even in very infertile lake types where food is in scarce supply.
- (5) Nest-site vegetation is selected according to the protection it may offer early in spring. Offshore sedge islets are highly preferred, but shore sedge frings more than ten metres wide will generally be fully satisfactory. The requirements are met neither in the first stage of littoral growth nor in the climax type of unbroken vegetation, but in the intermediate sere stage.
- (6) In ssp. *arcticus* »first-year« birds seem to prefer enclosed localities which give a complete periphery of emergent vegetation. This may correspond to a simple, innate key stimulus for habitat selection. Older birds evidently choose their habitats by a heterogeneous summation of stimuli which are probably more essential to their existence. They may learn to specialize on very aberrant nest sites, provided they may benefit on other commodities, e. g., a local superabundance of food.

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