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ROHÁČ VELKÝ, PODICEPS C. CRISTATUS (L.), JEHO EKOLOGIE

A HOSPODÁŘSKÝ VÝZNAM

THE GREAT CRESTED GREBE, PODICEPS C. CRISTATUS (L.),

ITS ECOLOGY AND ECONOMIC SIGNIFICANCE

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J A N H A N Z Á K:

**Roháč velký, *Podiceps c. cristatus* (L.), jeho ekologie
a hospodářský význam**

**Экология и хозяйственное значение большой поганки,
Podiceps cristatus (L.)**

(Předloženo 15. IX. 1949.)

Studiem života roháče velkého [*Podiceps c. cristatus* (L.)], zabýval jsem se od roku 1943, avšak hlavním podkladem této práce jsou soustavná terénní pozorování z roku 1948. Jako předmět svých studií zvolil jsem roháče velkého z toho důvodu, že v jeho zajímavé biologii bylo ještě několik nevyřešených a sporných otázek, dále také proto, že se uplatňuje značnou měrou i v našem rybnickém hospodářství. Hlavními body studia jsou: vztah tohoto ptáka k prostředí, ve kterém žije, jeho hnízdní biologie se zvláštním zřetelem na doposud nevyřešené problémy, hospodářský význam pro naše rybníční hospodářství a rozšíření druhu u nás. Většina získaných dat pochází z rybníků okresu sedlčanského a benešovského, zejména z rybníků ležících kolem Bystřice u Benešova. Tyto rybníky — Podhrázský, Semovický, Splav, Nesvačilský, Slavníč, Papírna, Petrovický, zvláště pak rybník prvně jmenovaný, mají každoročně — vzhledem k jejich rozloze — dosti silný stav roháčů velkých. Roku 1943 měl jsem dokonce příležitost podrobně sledovati jejich život na početné kolonii na Podhrázském rybníce. Podkladem pro studia nidobiologická bylo celkem 34 osazených hnízd. Mnoho zkušeností s roháči velkými nabyl jsem také v třeboňské rybníčné pánvi, hlavně na skupině rybníků lomnických. K pozorování používal jsem silně zvětšujícího dalekohledu Zeiss-Asiolarbi 24 ×, jenž mi byl s velikou laskavostí na dlouhou dobu zapůjčen Masarykovou akademií práce, začož na tomto místě vyslovuji svůj upřímný dík. Děkuji také všem, kdož i sebe-menší podporou a pomocí přispěli ke zdaru této práce, v prvé řadě však p. Dr. W. Černému, který mi poskytl množství cenných rad a pokynů týkajících se jak methodiky práce, tak odborné literatury.

Z technických důvodů není mi možno uveřejniti původní podrobnou práci uceleně a v nezkráceném rozsahu. Následující text je souhrnem z původního českého rukopisu, z něhož jen některé partie byly publikovány v různých našich odborných časopisech.

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Следующий английский текст представляет итоги нескольких работ автора о биомии большой поганки *Podiceps cristatus* (L.), которые вышли в разных специальных чешских журналах.

В сравнении с размерами и весом английских и русских поганок, размеры и вес чешских поганок большие.

В отличие от других (не водных птиц) птерилии у большой поганки развиты главным образом на нижней стороне тела. Большие аптерии находятся только на спине. Аптерии в то время, когда поганка не высиживает яйца, развиты в незначительных размерах. Перед гнездованием аптерии увеличиваются, а под ними развивается толстый слой подкожного жира, который однако исчезает как только птицы загнездились. Подкожный жир развит только под частями тела покрытыми перьями, а главным образом на тех частях тела, которые постоянно соприкасаются с водой с целью изоляции против потерь тепла.

Грудина отдельных видов наших поганок бывает различной величины, но грудина у гагар иной формы (смотри работы в «Časopis Národního musea, 1951»).

В Чехословакии на прудах площадью более 100 га приходится 4,24 пары поганок на 100 га, а на прудах меньших чем 100 га, при пересчете на эту площадь приходится 8,90 пары. Густота расселения в некотором биотопе находится под влиянием целого комплекса факторов, из которых главнейшую роль играет состояние и состав прибрежных зарослей. Понятие района поселения приходит во внимание только у птиц, гнездящихся одиночными парами и совсем теряется у птиц, гнездящихся колониями. Участок (район) ограничивается площадью тростниковых зарослей в ближайшем окружении гнезда поганки. Границы участков (районов) добывания пищи точно не обозначены, но при охоте за пищей соблюдаются границы гнездовых районов отдельных пар поганок.

Поганки к нам прилетают уже в парах, а при благоприятной погоде начинают токать сейчас же после прилета. Первый период спаривания (как его обозначает LAVEN) ограничивается временем пребывания на зимовке. Полный период токования имеет 7 фаз. Птицы спариваются на гнезде, а побуждение к спариванию выходит от самки, которая вызывает самца специальным положением тела. Такое положение, при котором самка потряхивает головой и притворяется, как будто ошпыливает себя и вызывающее положение является комплексом инстинктивных движений в смысле эпигамическом. При выпрашивании пищи птенцы занимают специальное целесообразное положение (смотри рисунок). При нырянии большая поганка остается под водой в среднем 24 секунды, максимум 56 сек. Молодые

поганки хорошо ныряют уже в первый день после выхода из яиц. При нырянии поганки работают только ногами, при том обеими одновременно. Время охоты за пищей приходится главным образом на утро, до 10 часов. Потом птицы отдыхают до 15 часов. Интенсивно охотятся снова при заходе солнца. Конечно иногда птицы охотятся и в разное время дня.

При сооружении гнезда принимают участие как самка так и самец. Гнездо иногда бывает построено и в течение половины дня. Можно различать два типа гнезд большой поганки: плавающие на свободной водной поверхности, которые служат только для спаривания, а не для самого гнездования. Птицы в таких гнездах не гнездятся, потому что эти гнезда очень шаткие. Гнезда второго типа служат для высиживания птенцов. У нас большая поганка высиживает только один раз в год. Если снесенные яйца были уничтожены, то самка сносит новые. Как удалось установить, температура в гнезде большой поганки не бывает выше, чем в гнездах других птиц, теплота возникающая при процессах разложения в гнезде не влияет на развитие яиц. Поганка прикрывает яйца в гнезде для защиты их от врагов и для предохранения яиц против охлаждения. Поганки принимают яйца разной окраски, но они замечают эту перемену. Чувствительны только к черной краске. В начале высиживания поганка покидает гнездо при каждой перемене, но со временем сидения стает в этом отношении менее щекотливой. Так например стерпела и перемещение гнезда на расстояние 2,5 м от его первоначального местоположения. Птенцы могут вылупиться и во время долговременного отсутствия родителей на гнезде. Разница между количеством снесенных яиц и числом птенцов в выводке не бывает такая большая, как у поганки черношейной. Писк птенцов в яйцах не притягивает старых птиц — родителей к гнезду.

(О кормлении и воспитании птенцов говорится в английском тексте на странице 28, 29.)

Пища и народнохозяйственное значение: анализом содержания 20 желудков было установлено, что главной составной частью пищи большой поганки являются рыбы и насекомые, которых она ловит без различия видов. Так наз. плевельные рыбы составляют 83% пищи. Наичаще поганка ловит окуней. Величина поедаемых рыб колеблется в пределах около 8 см в среднем. За период своей годовой жизни у нас большая поганка потребляет около 36 кг рыб. Большим поганкам нельзя позволять гнездиться на прудах служащих для воспитания мальков. На больших прудах большая поганка не причиняет значительного вреда. Поганка поедает перья, которые образуют в желудке кашеобразную массу, состоящую из бородок и волосков, которая помогает при извергании острых (колючих) частей пищи (костей и чешуи).

Большая поганка прилетает к нам весной во второй половине марта и первой половине апреля (среднее из 51 данных). Улетает в конце октября.

Было исследовано, как реагирует большая поганка на чучела птиц своего вида, т. е. с целью исследования в какой степени реаги-

ругую на искусственных представителей своего вида. В первый момент поганка считала такое чучело за представителя своего вида, но вскоре сознавала свою ошибку. Главной причиной этого сознания была неподвижность чучела. Если птенцы были со своими родителями, то совсем не обращали внимания на чучело. Если же птенцы были сами, так часто считали чучело за своих родителей. До сих пор не решен вопрос о том, врождена-ли большим поганкам схема товарища (компаньона) или нет.

The Great Crested Grebe, *Podiceps c. cristatus* (L.), Its Ecology and Economic Significance]

This paper is a summary of reports on the biology and ecology of the Great Crested Grebe, published in Czech in several professional journals. Since 1943 I have studied for several years the life of this bird. Most observations used in this paper date, however, from the year 1948. The observations were made chiefly on the ponds of Southern and Central Bohemia. The basis of the nidobiological study were 34 nests of which records were kept.

Systematic Position and Anatomical Remarks.

The Bohemian specimens of the Great Crested Grebe examined show that the principal moulting of this bird falls in the VIIIth month, but it begins already at the end of the VIIth month. All the pinions fall out that time almost simultaneously and grow again very slowly so that in some specimens so many feathers are lacking that the bird cannot fly. This inability to fly lasts for almost a month. During this time we can find on the banks of ponds inhabited by the Great Crested Grebe lots of their feathers, especially pinions. Towards the end of

Weight of some specimens of the Bohemian Great Crested Grebe

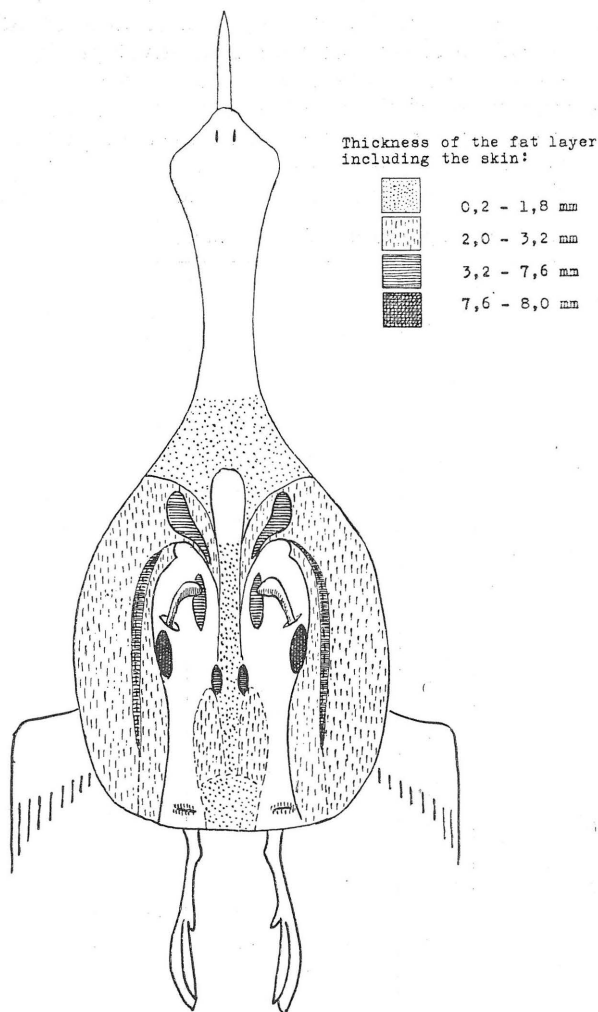
Locality (pond)	Sex	Weight in gr	Date	Leg.
Slavnič	♂	1330	21. 8. 1948	Hanzák
Slavnič	♀	970	21. 8. 1948	Hanzák
Slavnič	♂	1300	21. 8. 1948	Hanzák
Splav	♀	900	21. 8. 1948	Hanzák
Splav	♀	1020	11. 7. 1948	Hanzák
Splav	♂	1350	22. 8. 1948	Hanzák
Podhrázký	♂	1300	20. 4. 1949	Hanzák
Hvězda	♂	890	22. 7. 1925	Musílek
V. Košíř	♂	1400	2. 6. 1929	Musílek
V. Košíř	♀	1125	9. 10. 1927	Musílek
Břehyně	♀	1090	23. 8. 1948	Šarbort

September the birds are as a rule already completely recoloured, and assume the lighter coloured winter plumage. Most of the Great Crested Grebes which return to us in spring are already in mating plumage, but often it is possible to see still in March birds having their winter-plumage. In the text are given the weight and measurements of the Great Crested Grebe hunted down in Bohemia and Moravia. Compared with the measurements and weights of English and Russian specimens ours show on an average higher figures. It should, however, be mentioned that in our case only adult specimens were measured. I studied also the pterylography of the Great Crested Grebe and the distribution of its subcutaneous fat. In view of the fact that the Great Crested Grebe needs for its mode of life a thorough protection because of its constant contact with water, its plumage is unusually thick, and forms round the body a short but thorough envelope. It is also for this reason that the apteriae on its body are considerable reduced. A perfect apteria in the true sense of the word exists only on the dorsal side. The narrow strips adjoining dorsally the ventral pteryla must also be counted as dorsal pteryla. This is shown clearly on the underside of the skin by the direction of growth of the different calami. The direction of the

Measurement of some specimens of the Bohemian Great Crested Grebe

Locality	Sex.	Date	Wing	Beak	Leg.
Slavnič	♂	21. 8. 1948	202	49	60
Slavnič	♀	21. 8. 1948	175	50	56
Splav	♀	21. 8. 1948	183	41	53
Slavnič	♀	21. 8. 1948	204	50	62
Studénka	♀	26. 8. 1948		50	58
Podhrázský	♂	20. 4. 1949	200	48	63
Tisová u Tachova	♀	19. 7. 1936	176	38	58
Březina	♀	6. 9. 1936	185	41	60
Koprník	♂	21. 3. 1925	190	46	62
Březina	♀	16. 3. 1930	194	45	63
Březina	♀	28. 3. 1933	190	41	54
Horusický	♀	27. 7. 1937	172	41	56
Dětenice	♀	10. 5. 1939	176	40	54
Dětenice	♀	1. 4. 1939	188	46	58
Vodňany	♀	7. 1936	174	40	50
Kardašova Řečice	♀	12. 6. 1941	181	41	53
Kardašova Řečice	♀	20. 7. 1941	176	46	53
Kardašova Řečice	♀	20. 8. 1939	190	44	60
Kardašova Řečice	♂	29. 7. 1939	198	43	58
Kardašova Řečice	♀	23. 7. 1938	192	45	57
Dětenice	♀	25. 4. 1941	185	46	52
Jílovce	♀	11. 9. 1939		45	54
Veliny	♀	9. 4. 1921	177	38	58
Čechy	♂		175	42	54

feathers of these strips is opposite to the direction of the feathers of the pterylae gastraei so that the feathers are divided here by a distinct ridge visible on the underside of the skinned skins. The medial apteria dividing the feathered bottom into two parts is very narrow and almost imperceptible. Its width is at the time of rest as a rule narrower than 1 cm., so that apart from nesting time it is almost imperceptible. The nesting naked place develops in birds of both sexes. At first it is protected below by a thick layer of subcutaneous fat, which, however, disappears as nesting proceeds. The distribution of the subcutaneous fat is restricted in the Great Crested Grebe to the feathered places, in the regions of the apteriae it is not substantially developed. The distribution and thick-



Normal distribution of the subcutaneous fat of the Great Crested Grebe — schematically. View of the underside of the skinned skin.

ness of the fat layer is shown schematically in the appended drawing. The table gives the measurements of the sternum of some Great Crested Grebes and Divers of Bohemia.

Measurements of the Sternum of Podiceps and Colymbus.

Species	Sexus	Longitudo maximalis sterni	Latitudo maximalis sterni	Latitudo in loco insertionis ultim. costarum	Latit. minim. sterni	Altitudo cristae sterni	Index: Longitudo st. Altitudo cristae	Index: Longitudo st. Latitudo in loco insertionis ultim. costarum
Podiceps ruficollis		30,5	34	22	22	11,5	2,7	1,4
Podiceps nigricollis	♀	42	40	27	27	16	2,6	1,2
Podiceps auritus		46	44	36	30	20,5	2,2	1,4
Podiceps cristatus	♂	63	54	40	38	25	2,5	1,5
Podiceps cristatus	♀	61	56,5	37	38	24,5	2,5	1,7
Podiceps cristatus		59	56	38	37	27	2,2	1,6
Podiceps cristatus	♀	56	52	34	34	24	2,4	1,6
Podiceps griseigena	♂	50	49	34	33	24	2,1	1,5
Podiceps griseigena	♀	50	49	35	34	25	2,0	1,5
Colymbus stellatus		143	62	53	50	30,5	4,8	2,7
Colymbus arcticus		147	70	56	52	30,5	4,8	2,6
Colymbus arcticus		135	68	57	55	31,5	4,3	2,4

Distribution in Czechoslovakia.

(Density of Population and Relation to Environment, Colonies, Question of Territory.)

The Great Crested Grebe is a definitely aquatic bird. In Bohemia and Moravia it is of common occurrence on all larger suitable ponds. In nesting-time it keeps to standing waters only. It is remarkable that the number of nesting pairs varies considerably from year to year on the different ponds. Thus they are abundant one year, while next year they may almost have disappeared. Also on two ponds of equal size the number of these birds may differ considerably. Thus f. inst. on the Podhrázský Pond (District Sedlčany) their number has varied in the different years as follows:

1942	not nesting at all,
1943	17 pairs in a colony,
1944	8 pairs,
1945	5 pairs,
1946	15 pairs,
1947	7 pairs,
1948	5 pairs.

Another pond in the same district—the Musík—whose area is almost equal to that of the Podhrázský Pond, is almost every year inhabited by only one, at most two pairs. But we find similar conditions also on other ponds, as f. inst. on the South Bohemian ones.

Thus the question arises as to the cause of this variation. Here the following factors come into consideration:

- area of the pond
- state and kind of the littoral vegetation
- method of cutting this vegetation
- depth of the water
- undisturbed surroundings
- density of population of other birds
- amount of food
- height above sea-level
- type of region

In the journal *Naturae tutela* for 1951 a survey is given of a number of Bohemian and Moravian ponds, stating the number of pairs of the Great Crested Grebes which nested on them.

It is noteworthy that the largest Bohemian ponds compared with the ponds of medium size have not a correspondingly larger number of grebes. Thus f. inst.

Rožmberk	720 ha.	15 pairs
Bezdrev	510 ha.	15 pairs
Horusický	439 ha.	5—10 pairs
Velký Tisý	342 ha.	12 pairs
Nesyt	322 ha.	30 pairs
Máchovo Jezero	200 ha.	12 pairs
Koclířov	192 ha.	5 pairs
Lenovský	190 ha.	10—20 pairs
Jedovnický	120 ha.	1 pair.

In these ponds of an area exceeding 100 ha. there are 4.24 pairs per 100 ha., whereas in ponds of less than 100 ha. there are on an average 9.90 pairs on 100 ha. The cause of this relatively small number of grebes on the large ponds lies in the fact that the narrow reed fringe, which determines the abundance of these birds, is small in comparison to the size of the water surface. When one of these large ponds has a strong reed-growth (Nesyt, Bezdrev), a greater number of grebes nests on it simultaneously.

The dependence of the number of nests on the area of the reed-cover is clearly shown by ponds whose population of grebes remains almost constant for several years, and whose littoral plant covers are formed by the same type of vegetation. Thus f. inst. in the Benešov District the Slavníč Pond with an area of 11 ha., with a *Typha* growth of about 25% of the total area, harbours every year 5—7 pairs, whereas the Semovický Pond (32 ha.), nearly twice as large as the Slavníč, whose *Typha* growth forms 5% of its total area, has as a rule only 3—4 pairs. On the Podhrázský Pond (48 ha.) with 5% of *Typha* growth one usually finds 5—17 pairs, the Musík (42 ha.) has always

one pair only, as it lacks any taller reed growth, and has only borders of sedge and rush. The same applies also to many South Bohemian ponds. Too overgrown ponds, where the water surface is restricted to a small area by the luxuriant growths, do not attract the grebe, and the number of nests on such ponds is never large.

Of 52 nests which the author saw in recent years (1948) the vast majority (39) was established in *Typha* growths, 7 in *Phragmites*, 3 in *Acorus*, one in *Equisetum limosum*, two in *Carex*. The Great Crested Grebe is often satisfied also with very shallow ponds (1 m.). Thus f. inst. the pond "Láska" at Lomnice nad Luž. with an average depth of 1 m. is inhabited by one pair.

The cutting of the pond growths is very detrimental to the grebes, and has a considerable influence on their total number. When the reed remains standing in winter, the grebes nest in the following year very quickly after their arrival. Thus f. inst. in 1947 (in 1946 the *Typha* had not been cut) six occupied nests were found as early as on 27-IV, whereas in 1948, following a complete cutting of the *Typha*, the first nests were found only on 24-V, i. e. a month later. In such years the birds have to wait until the *Typha* has grown to a certain height so that it may hide their nests. Thus nesting becomes much retarded.

The cutting of the reed has, however, still another unfavourable influence on the nesting. When the reed is cut in the autumn, it does not reach its original density in the following year, but is much thinner. Thus it comes about that the nests floating in it are not protected by its density, and it often happens that a strong wave breaks them completely, and the clutches fall into the water. Waves inflict on the grebes very sensible losses and play a large rôle in their total number.

The grebe does not visit too dense and dark growths. It prefers to establish its nests in more open spots. The dependence of the grebes on good littoral growths is so great that they do not mind even the nearness of frequented roads, railway lines, or even the neighbourhood of human habitation.

HARRISON and HOLLUM (1932) maintain that *Fulica atra* does much harm to the English grebes, destroying their eggs and nests so that a multiplication of *Fulica atra* results always in the disappearance of the Great Crested Grebes. I cannot confirm this from my experience, as I have often met with cases where in the immediate neighbourhood of grebe-nests *Fulica* nested, and it even nested regularly in grebe colonies. Also SCHUSTER (1933) maintains that the presence of *Fulica* has no great influence on the number of grebes.

When checking the amount of small fish in the ponds I found that the amount of food available is not a factor which influences in any way the density of distribution of this species.

From a survey of the Podhrázský Pond (Central Bohemia), fished every other year, it is evident that the amount of fish has no influence on the number of birds. The years of fishing the pond, when there is most weed-fish, do not correspond to the largest grebe populations.

When the grebes of a certain pond are prevented from nesting on it because it is summered or has insufficient water they shift to the

nearest neighbouring pond. Thus their number on the surrounding ponds increases where the water conditions are normal.

The density of population of the Great Crested Grebe in a given biotop is not influenced by one factor, but by a whole complex of agents of which some, f. inst. the state of the littoral growths and their character, manifest themselves most, the others play a subordinate rôle. In most localities also the interference of man manifests itself to a considerable extent. Thus it is in most cases difficult to say why on some ponds the number of nesting pairs is great and on others quite insignificant.

In our country grebe colonies are rare, and were found only on two ponds (maximum 17 nests).

In the question of districts the Great Crested Grebes have a special position due to the closedness of the biotop in which they live, and to their exclusively aquatic mode of life. The normal phenomenon in a grebe population are birds living in separate pairs. In such cases the size of the territory is clearly delimited and defended by each pair. The size of the defended nesting territory varies for different pairs, and it is usually restricted to the immediate neighbourhood of the nest. The nesting bird does not suffer a strange individual to approach directly into its own reeds, but as long as the intruder keeps to the open, it can approach quite close. Thus the shape of the defended territory is not circular, as is so often the case f. inst. with singing-birds, but it is elongate-elliptic. The birds defend mainly the margin of the reeds (in solitarily nesting grebes on an average 50 m), and a not too wide strip around it. It is interesting to see that in ♂ and in ♀ the conception of the size of the nesting territory is different, so that each of them defends a section of different size, ♂ of course always the larger one. The size of this territory differs, as already said, and is in direct ratio to the shape and size of the reed cover in which the birds nest. With grebes it is of course necessary to distinguish between the nesting territory and the hunting ground, i. e. the section in which a given bird hunts. The hunting ground varies according to the size of the pond. In smaller ponds the grebes hunt over the whole area and generally preserve amicable relations with each other hunting. F. inst. every morning they hunt preferably at the dam of the pond, and do not persecute each other at all. Thus it is not possible to speak of hunting grounds in such small ponds as the hunting ground is usually the whole pond. The limits of the nesting territories are, however, respected also when hunting. Also on large ponds the hunting grounds are not accurately delimited; usually the birds hunt in the neighbourhood of their nests, but the grounds of the different pairs distinctly overlap. LUNAU (1933) states that at the time when the Great Crested Grebe educates its young it takes them for flights over the neighbouring water for hunting purposes; nothing similar has ever been observed in our country.

In the cases where the nesting is in colonies, the limit of the nesting district is of course effaced. In such cases the grebes get on together very well at their nests. This is also mentioned by VENABLES (1933 and

1936) in the case of the English grebes. It is thus evident that with the grebe the conception of territory is not sharply defined and that it can be influenced by outer circumstances. It is of course impossible to say whether there are not certain grebe populations which habitually nest in colonies while other grebe populations have solitary nesting. To settle this question it would be necessary to study it for several years by means of marking the individual birds.

Behaviour when Nesting.

(Occupation of nesting sites, pairing, movements, manner of movements in the water, daily activity, manner of hunting.)

The grebes reach the Central Bohemian ponds usually towards the end of March (earliest arrival I recorded was March 15, 1943) and in the beginning of April. On the other Bohemian ponds they arrive at the earliest at the beginning of March. According to knowledge so far obtained the Great Crested Grebe is a bird migrating solely at night. It appears on the ponds overnight, usually during clear nights, either isolated or, more frequently, in pairs, but also in greater numbers. The grebes return to their nesting places already paired and the formation of pairs for most nesting individuals takes place in their winter-quarters.

Courting does not necessarily begin immediately on arrival, as it is influenced by favourable weather (besides by the activity of the gonads). It has not yet been ascertained whether the pairs remain together several years, but this is the most probable.

In contradistinction to most bird species both partners participate in the courting. (It has been proved that a similar phenomenon occurs very frequently in birds with small sex dimorphism.) The courting is always begun by ♂. It is possible though difficult to come to observe the whole process of courting. Of a total number of about 70 cases of courting observed only seven were complete with all phases. A feign pecking when both partners turn their heads over their backs and with jerky movements feign to ruffle in the feathers of the back was often observed in courting, though in the descriptions of the courting of the grebes it has not yet been mentioned. At the end of the courting both birds like to dive and seem to pursue each other under the water. Once I observed that ♂ did not follow ♀ in diving, but only feigned to dive and emerged in an instant at the same place whereas ♀ appeared about 20 m. farther away.

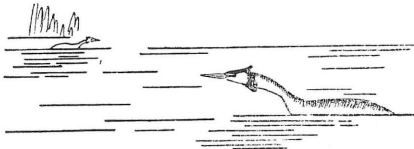
When a foreign ♂ appears unexpectedly in the vicinity of the territory of a given pair close to the ♀, the ♂ of the ♀ drives it away with great determination. After such an intrusion, and when the intruder has safely been chased away, the attacked pair always exhibit one symptom of courting in that they take up the position with raised necks touching each other. ♂ probably wants by this (♀ is always invited) to produce a negative reaction in the intruder and a

positive one in the partner. Also in other birds it is in some cases striking that courting is more intensive when an unpaired individual is present (LORENZ 1935).

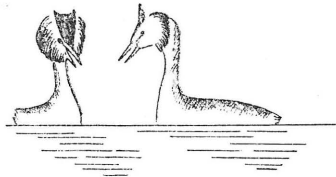
According to my observations the sequence of the different phases of courting is as follows; but it must be added that it is only very rarely that full courting is completed.

1. ♂ and ♀ distant, often up to 30 m.; ♂ provokes ♀ in a position with stretched neck low above the water level, ♀ repeats this position, and they swim together.
2. With unfolded collar and upstanding crests they swim towards each other, shake their heads with a quick jerking movement and call out a sharp *ket-ket-ket*.
3. They dive and carry up in their beak a bundle of plants. With these in their beaks they place the stretched necks close together, the head-shaking is repeated. The calling is more rapid.
4. They swim up to each other till their breasts touch and then they "tread water".

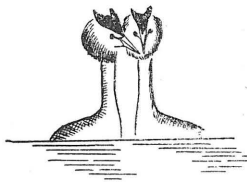
Invitation to courting



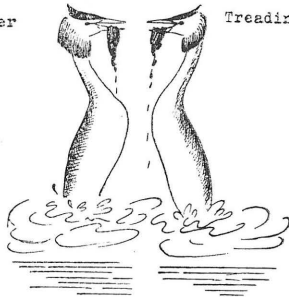
Shaking of heads



Position with necks placed close together



Treading water



♂ after courting has ended

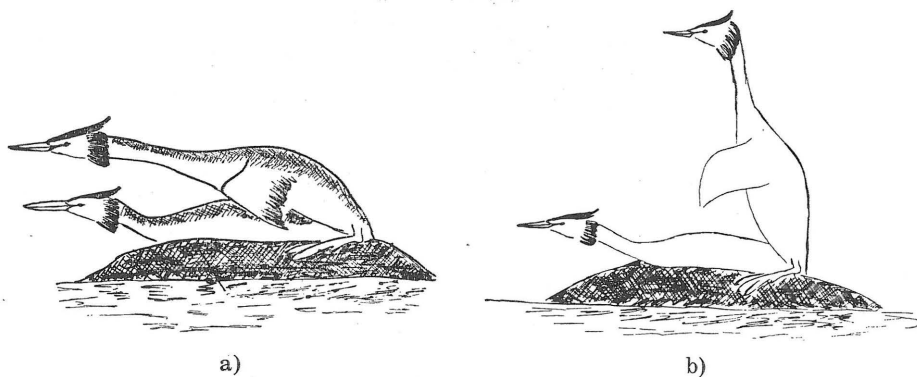


Different phases of the courting of the Great Crested Grebe

5. They let the plants fall from their beaks.
6. ♂ dives while ♀ swims around with swelled wings and S-curved neck with drawn-in collar or jumps away abruptly from ♂ and swims around in the described position.
7. Mutual diving.

The courting of the grebe may also take place at night, but only on clear nights.

The courting of birds is usually restricted only to the time before nesting, though it may continue for a short time while nesting. The Great Crested Grebe forms in this respect an exception, as its courting continues during the whole nesting period, often not dying away even during the time of leading out their young so that in June and July it is still a current phenomenon in our regions. But the whole course of courting is found only in the pre-nesting period. Later there is but a part-courting (position with raised necks). Part-courting was observed as late as August 23. In one case (27-VII) the pair observed courted in the position facing each other with stretched-out necks. In doing so the courting birds drove away and pecked at one of their own fledglings which came in their way. The late courting is probably only a consequence of the dying activity of the gonads.



Mating of Great Crested Grebes
(b after HESSE)

Pairing takes place in this species exclusively in the nest. HESSE (1910) described very fully the copulation of the Great Crested Grebe, but his description differs somewhat from my own observations.

STANĚK, who witnessed several times the copulation of the Great Crested Grebe, maintains that ♂ helped to keep its balance in copulation by movements of the wings. HESSE (1910) made a sketch of copulating grebes where ♂ stands on ♀ in an almost upright position with spread-out wings. In the text he states that ♂ in the culminating sexual excitement swings the wings forward. That this need not always be so is shown not only by my own observations but also by Černý's records of 10-IV-1949, according to which ♂ in an upright position did not move

the wings at all. In this case after the coitus ♂ ran along the back of ♀ and jumped over her head into the water. Immediately after this an incomplete courting took place, in which, however, ♀ remained sitting on the nest and jumped down only later.



Special epigamous position of ♀ on the nest

Copulation was always connected with preliminary nest-building. Birds copulating in the nests among the reeds always betray themselves by the characteristic throaty voice of ♂ sounding like a creaking *ee eee*.

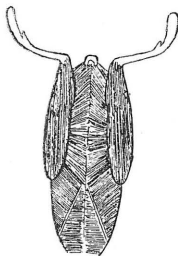
At the time of copulation the grebes use a special position, taken up only by the female sitting in the nest; ♀ in the presence of a ♂ swimming round stands upright in the nest and bends its neck so that it lays



Inviting position of ♀ before mating

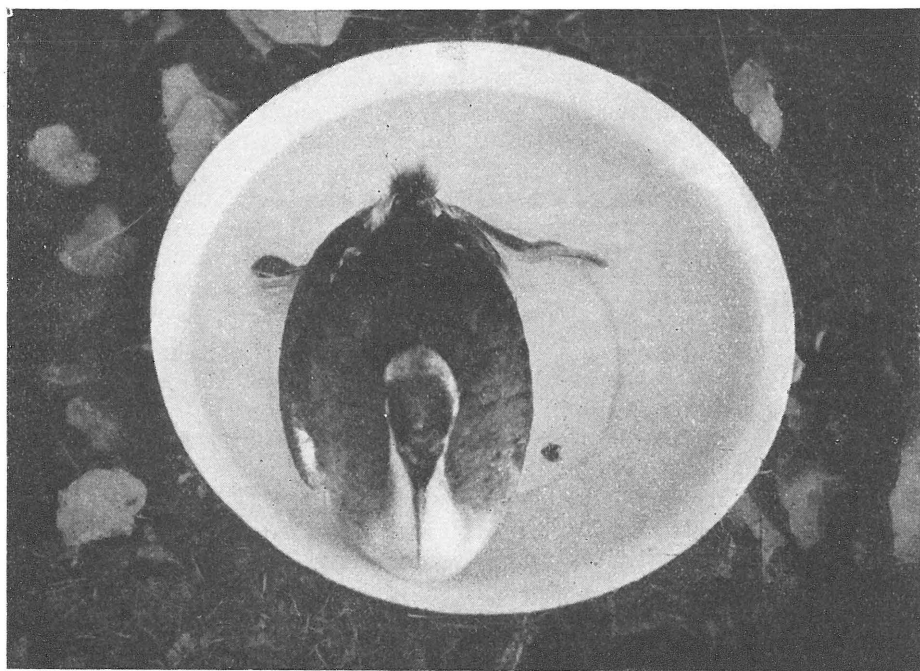
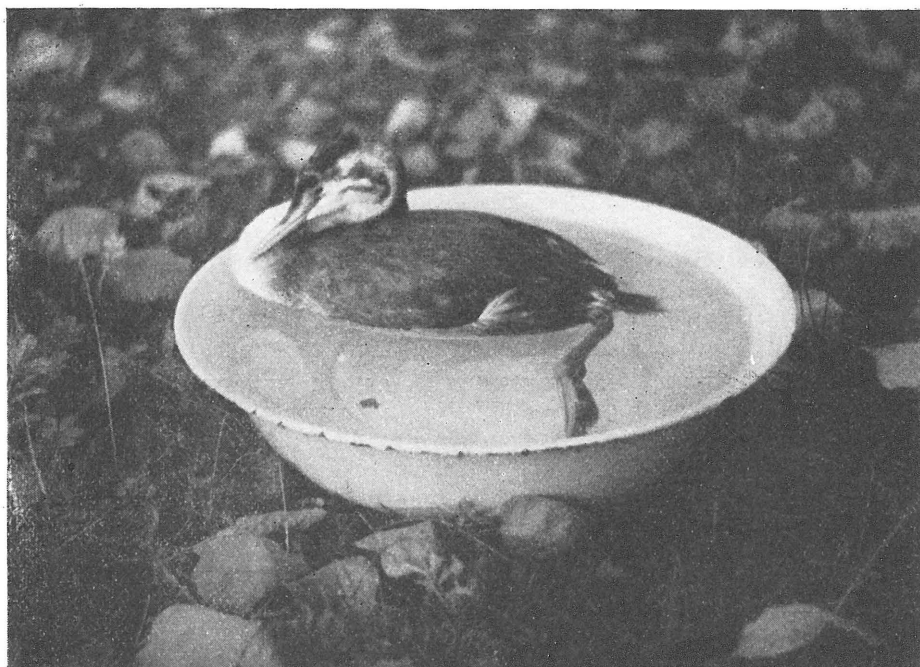
its head on its underside. The beak nearly touches the nest. This is very reminiscent of the position in which the grebe arranges the eggs under itself, but in this case it is more upright and does not reach the nest with the beak. The Black Necked Grebes use this peculiar position, and it is closely connected with copulation time.

Also from the other remarks on the copulation of the grebes it is evident that the immediate impulse for copulation comes from ♀. The



Body of the Great Crested Grebe without the skin (after HEILMANN ex STRESEMANN)

position in which ♀ lies on the nest with the neck stretched above the water level is for the grebe one of the most typical ones. By means of it ♀ excites ♂ to copulation. The neck of ♀ is not always stretched straight above the water level, but is sometimes bent in an S-shaped



Way of holding the legs in swimming

form. ♂ does not let himself be lured at once to copulation, but swims round the nest as if undecided, approaches and again draws away, until by a sudden movement he jumps with both legs at the same time into the nest and on to ♀. In many bird species one has found that the initiative to copulation comes from ♀. I have not been able to observe in the grebes the two-sided pairing which often occurs in species with a small sex dimorphism and mentioned also in connection with the Great Crested Grebe (NIETHAMMER, 1942).

Attention was paid in the Great Crested Grebe to the question of movements chiefly because these movements are influenced to a large extent by the peculiarities of the anatomical structure of the body, especially by the configuration of the hindpair of the extremities. Most movements described are relatively difficult to express in words.

The different types of movements may be divided into instinctive (symbolic, purposeless) movements and purposeful movements. Unfortunately the majority of the most valuable and interesting instinctive movements take place during the time before pairing, and are restricted to the time before the grebes arrive in our region. This is of course only an assumption, as there are no detailed works at all about their behaviour in their winter quarters. Nevertheless the study of their life has shown that instinctive movements occur in this species also after the formation of a pair, in the time before nesting. The culmination of these acts is the courting already described, which is really composed of a whole series of such movements, and as it occupies a special position it has been described first. But there exists also a whole series of instinctive symbolic movements which, if true, have been observed only to a small extent, but which the grebes presumably use all their life.

To these instinctive movements belong: feign-pecking, shaking of the head, provoking position in the epigamic sense, and special position of ♀ before mating in the nest.

The feign-pecking of the feathers on the back and the shaking of the head have to be placed in the series of epigamic expression movements occurring often but not always in connection with courting.

The feign-pecking is as a rule preceded by a position with slightly raised neck, after which the bird with a quick movement bends the head above the back, raises the back feathers slightly and with quick movements feigns to ruffle them. It does not push its beak deep into the feathers but touches only their ends. This action takes place always between two individuals of different sex (only in the time before nesting), both birds shaking their heads simultaneously.

The shaking of the head is also a purely epigamic movement. It occurs in the grebe very often also in the time after nesting, and is also usually connected with courting. The shaking is done in quick jerks with the beak turned downward by a sideways movement. It is usually accompanied by a sharply expressed *ket-ket*. It is analogous to the "pumping" of heads in ducks. Both these phenomena can be observed only when also the second partner is present. In connection with the time of mating the author found still one other, very interesting, position

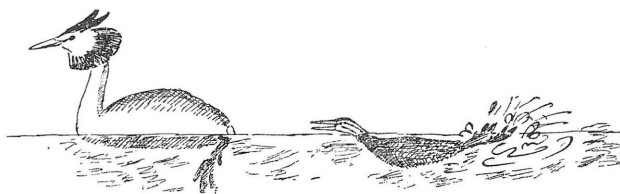
whose significance cannot well be judged. In it ♀ sitting on the nest rises so that it stands quite upright, bends the head downward so that the neck lies almost against the underside. The beak is directed forward, not high above the nest. With the neck so curved it rocks the head several times from side to side. Immediately after ♀ lies down in the nest and provokes ♂ to mating.

This position is surely one of the many ceremonies which in most cases we find difficult to understand, exclusively connected with the mating period.

The "provoking position" consists in contradistinction to the preceding three positions solely of epigamic movements only partly bound to the time of propagation. In connection with the sex manifestations it is the starting phase in courting, used by both partners. The collar, crests and also all other feathers are regularly appressed. Head and neck are stretched far forward so that the lower part of the collar sometimes dips into the water. This position is often accompanied by a *ket-ket-ket* which gets quicker the nearer the birds approach to each other. It is used at a distance. At close range, at a distance of less than 10 m., it can rarely be seen between two birds. This position is very reminiscent of the action of HEINROTH's Koketierschwimmen and LORENZ's Nickschwimmen described for wild ducks (*Anas platyrhynchos*).

With this I have described all the instinctive movements I was able to observe. The other movements described in another paper are purposeful movements.

More grown-up fledglings use special positions in demanding food. These movements are connected exclusively with the request for food and occur only in hungry, more grown-up fledglings. Hungry and begging fledglings near the old bird stretch their beaks towards it under continuous wheedling shrieking. When the old bird does not show any great inclination to feed them and tries to swim away, the fledglings stretch themselves as far as they can, and finally end by submerging their whole body under the water level so that only part of the neck with the head rises above the water; the back is completely submerged. With the legs the fledglings kick in the direction out of the water so that from time to time they are above the water level and spray the



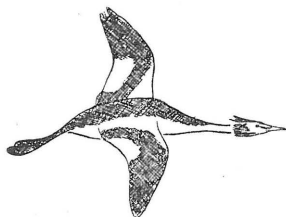
Special movement of a hungry fledgling in soliciting food

water behind them about 15 cm. high. At the same time they move but very slowly, as the legs do not fully take hold. Usually the old bird does not pay any attention to the fledglings. In one case a begging

fledgling maintained its position with submerged trunk for about 30 seconds while calling out pitifully the whole time.

This reaction to feeding awakens in fledglings only when they have the old bird within sight at a small distance of 1—2 m.; this is different from the behaviour of the fledglings of some species which beg even when they cannot see either of their parents. It occurs only in larger fledglings, aged about one month or older.

The Great Crested Grebe moves usually with a speed of 3—7 km. per hour. With regard to diving the three main questions are: the duration of diving, the interval between the dives, and the depth.



Great Crested Grebe in flight

There is no correlation, at least in the Great Crested Grebe, between the length of the dive and the interval between the different dives. The rapidity of the individual dive is individual and depends certainly also to a large extent on the hunger of the diving bird. When the bird is not hungry it does not dive so often.

The times measured show that the length of the dives depends in no case on the depth of the pond. There is no correlation between the times measured for ponds of different depths. The mean time of 52 measurements was 24 sec., the maximum time 56 sec., where the specimen (an old ♂) covered a distance of about 50 m. Once an individual was observed which dived 14 \times in 8 minutes and caught in this time two small fish.

GROEBBELS (1932 a, b) maintains that a quite young grebe does not dive. From his text it is not clear whether he thinks here only of diving connected with hunting for food. I observed that also very young grebes can dive well in danger. Already fledglings one week old dive quickly and dexterously when pursued by a boat. But the depth of the dive is of course always so small that the fledgling moving under water can always be seen well. On June 6th I found in a nest a freshly hatched fledgling about a day old. The other was just struggling out of its shell. Already the grebe a day old dived well and swam 4 m. under water at a small depth below the surface.

The Black Necked Grebe holds its neck under water a little bent in an S-shape. As far as I personally observed the Great Crested Grebe has under water its neck stretched straight forward.

As in swimming so also in diving the Great Crested Grebe uses exclusively the legs. When under water the wings are pressed close

to the body and pushed into pockets formed by the lengthened feathers of the sides of the lower part of the body.

The Great Crested Grebe belongs to the group of birds which feed regularly at a certain time of day and then rest long until they get hungry again. The hunting and chasing for food in general are limited (but not consistently) to the early morning hours and the time of evening twilight. At dusk all grebes on a pond are always busily hunting. But they never hunt in the dark. As the dusk deepens the grebes become very active, none of them sleeps and most of them hunt. They seem to be twilight birds. Often they also fly about.

Round noon, at the time from about 10 a. m. to 3 p. m., most of them rest, sleep or trim their feathers. At night the grebes sleep always near the reeds, on the water-surface, and never (except at nesting time) among the reeds. Also during the day the paired grebes rest in places where they want to nest or where they already have finished nesting. These are their preferred stations.

The grebes hunt for food preferably in the neighbourhood of the shore rather than in the middle of the open surface. This fact is certainly directly connected with the crowds of weed-fish which move usually along the shores. It is also for this reason that the grebes keep near the dams and shores of the ponds early in the morning and in the evening.

From several observations it is possible to say that probably the grebe often first sees the fish under water, and only then dives for it.

The hunting birds sometimes push as much as half of their heads into the water so that the eyes also are submerged, perhaps in order to see better into the water when the wind ruffles it.

I have often observed grebes behaving like this, but always only in windy weather. On a quiet surface the grebe very probably can see down to a certain depth in the water.

The grebe swallows the hunted fish alive, easily or with considerable difficulty according to the size of the fish. It grips its prey behind the head with its beak and holds it always in this position while shaking it violently so that one often receives the impression that it kills it. It swallows the fish always head first. When the prey is large it takes sometimes fairly long (62 sec.) before it succeeds in swallowing it. It happens not rarely that it has to let the fish go, because it cannot swallow it on account of its large size. After swallowing it drinks several times. In feeding the fledglings it dives often, holding the fish in the beak.

Very often the grebes can be observed hunting or more accurately collecting insects on the surface. It is certain that some kinds of insects are caught also below water.

The main feeding (hunting) time of the grebes is in the morning till about 10 a. m. Then follows a rest until 3 p. m. Later in the afternoon they are more active. They hunt again intensively only at sunset. Occasional hunting is of course not excluded at any time of the day.

Behaviour during Nesting.

(Building of the nest, the nest, the clutch, experiments with colouring the eggs, behaviour during sitting on the eggs, hatching and education of the fledglings.)

The larger share of nest-building in the reeds falls to the ♀ while the opposite is the case with nests floating free on the surface.

The grebes need several days to build their nest in the reeds. In the four cases controlled the grebes had the nest ready in 6—8 days. But nests floating free on the surface form a special group. These nests are sometimes even 20—50 m. distant from the shore, often, however, they are also found on the middle of the surface. Grebes were not observed to nest in them, for in the slightest wind the nests are shattered by the waves. But it is striking to observe with what speed these useless nests are built on the open surface. Sometimes the grebes build so fast that in half a day the nest is capable of holding a grebe sitting on it. In building the grebes often mount the nest, perhaps to ascertain its firmness. One building pair brought in the course of five minutes 21 materials for building (*Potamogeton crispus*).

The grebe collects the building material in the neighbourhood of the nest (within a radius of up to 20 m.), mostly directly on the surface, or it carries it up from the bottom diving for it. Generally the birds build by sitting on the surface and placing the material with the beak on the nest. When the building is already considerably advanced, it happens not rarely that the grebe jumps on to the nest, slaps its edge with the legs, and with the beak shifts the material from the edges into the middle.

Nest building does not end with the laying of the first eggs, but continues during the time of egg-laying as well as during the time of further hatching so that often the nest grows to a considerable size.

The nest of the Great Crested Grebe is built of aquatic plants; but material found in the neighbourhood is also used. Thus nests in *Typha* growths are mainly built of *Typha*, floating nests on some ponds exclusively of *Potamogeton crispus*, nests in *Equisetum* growths of *Equisetum*, etc.

The following plants were ascertained in the nests examined: *Typha*, *Phragmites*, *Acorus*, *Potamogeton crispus*, *Equisetum limosum*, *Polygonum*, *Carex*, *Batrachium*, *Alisma*, *Sagittaria*, *Rumex aquaticus*, *Glyceria*, *Spirogyra*.

Occasionally also other plants were used, tree-leaves fallen into the water and twigs of various kinds of bushes and trees.

In some nests only material of one species is used, others are composed of quite a number of plant species.

The foundation of the nests of normal type is usually the coarser parts of *Typha* or *Phragmites*, always material of the preceding year, very often already rotting, carried up from the bottom or collected on

the surface. But this is not to say that remains of fresh plants are lacking, even though these are found only to a small extent.

Two fundamental types of nests must be distinguished as far as shape is concerned:

- a) relatively low nests, built of rotting plant fragments, forming a compact "cake". — The most common type.
- b) Nests built largely of dry fresh material, which acquires the shape described sub a) only after longer use. These nests are more rare.

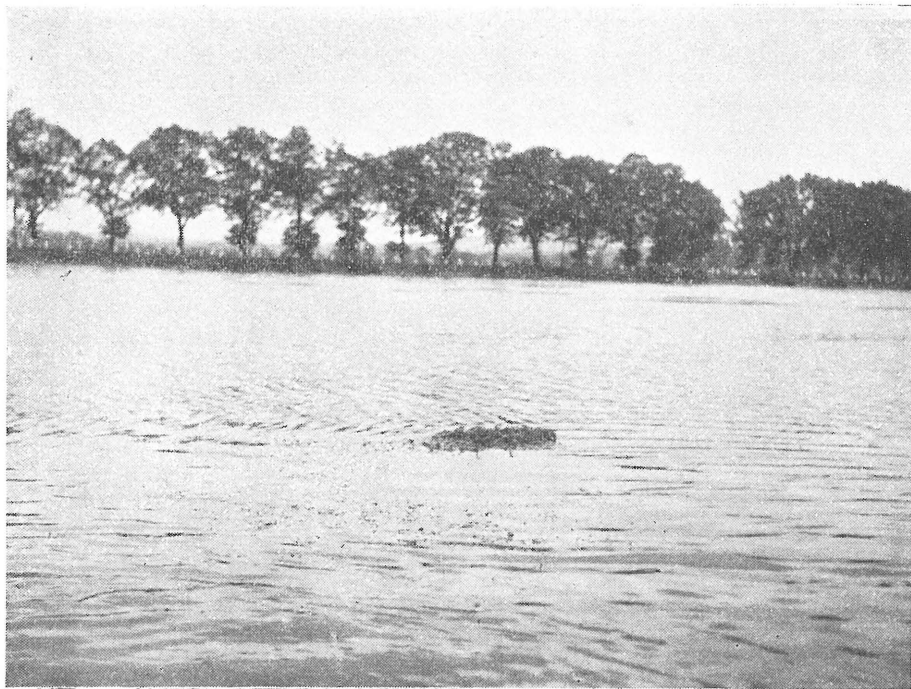
Of 31 nests only 3 were of this type.

The total height of the individual nests is sometimes so great that they reach to the bottom (80 cm.).

The distance from the shore and the margin of the reeds varies according to the state of the plant cover, but as a rule the nest is situated closer to the open surface than to the shore.

The depth of the water in the vicinity of the nest is usually not great especially because the littoral vegetation does not extend to places of any depth. Also the floating nests were built in places 1—1.5 m. deep.

The nests floating on the open surface deserve special attention. Even though the littoral plant covers are in certain places suitable, and though every year several pairs nest in them, yet individual birds establish their nests in the middle of the water surface. But it never



Free floating nest. Pond Splav, May 28, 1948

comes to nesting. Perhaps the grebes come to build such nests in order to mate. Mating takes place on them very frequently and intensively. Presumably also many half-built "nests" in the reeds not used for nesting are made only for this purpose. They are presumably only formations enabling mating, as the copulation of the Great Crested Grebe is, as already said, possible only in a nest. When the free floating nest is destroyed by the waves, the grebe starts already next day on erecting a similar construction.

The main time of egg-laying is in our area May and June. As already mentioned the state of the reeds on one or the other surface plays here a by no means negligible rôle. Of 43 records of nesting from Bohemia ten belong to the first half of May, eleven to the second half of May, seven to the first half of June, five to the second half of June. The most belated eggs were found in the first half of July (three cases). Earliest nesting on 27-IV. (six occupied nests). Sometimes we meet also with a considerably belated nesting. On September 16, 1948, I found fledglings about a week old; this corresponds to an egg-laying in about the middle of August. The old birds were in this case already in their winter coat. Thus sex activity had already ceased, and yet the fledglings were educated quite normally.

The Great Crested Grebe nests in our area only once a year. But when the first clutch is destroyed, a substitute clutch in another place is almost always the rule.

Of 38 clutches in Bohemia 15 were of three eggs, the same number of four eggs, four of two eggs, four of five eggs.

The measurements of the 114 eggs of Bohemian origin vary within the following limits:

Average	54.80	×	36.82
Max.	62.2	×	37.0 and 58.9
Min.	50.0	×	37.3 and 55.0

The temperatures of the nests and eggs of the Great Crested Grebe during nesting were controlled for ten pairs. But the opportunity offered itself to observe these conditions in detail also in a closely related species — the Black Necked Grebe (*Podiceps nigricollis* Brehm).

From the values measured it is possible to settle several questions.

Temperature of eggs measured in different species of birds

Species	Temperature of eggs	Number of cases	Measured by	Body temperature	Measured by
<i>Podiceps cristatus</i>	28,8	12	Hanzák	40,3	Hanzák
<i>Podiceps nigricollis</i>	24,5	31	Hanzák	40,0	Hanzák
<i>Fulica atra</i>	27,0	2	Hanzák	42,01	Löer
<i>Gallinula chloropus</i>	22,02	16	Schiermann	41,03	Löer
<i>Arenaria interpres</i>	33,8	18	Bergman	41,0	Bergman
<i>Sterna hirundo</i>	28,8	4	Bergman	40,5 (?)	
<i>Ixobrychus minutus</i>	20,5	5	Schiermann		

1. Is the temperature in the nests of grebes really strikingly higher than the temperature in the nests of other birds?

2. Has the rotting plant material in the nest a great influence on the development of the eggs or not?

3. Has the covering up of the eggs before leaving the clutch an influence on the maintaining of the heat in the nest?

The table in the text gives the temperature of the eggs of the grebe and of other birds.

The maximum temperatures in the nests of grebes are as follows:

Great Crested Grebe	33.8°
Black Necked Grebe	27.5°

The results obtained show beyond doubt that the temperature of the eggs (nests) of the Great Crested Grebe is normal when compared with that of other bird species. The average of the measured values equals the average of the measurements measured by BERGMAN for *Sterna hirundo*, i. e. in a species in which the temperature of the nests cannot come into consideration as the nests are quite dry. The conditions are also quite normal for the Black Necked Grebe.

The high temperature of the eggs spreads of course also to the surrounding nest material, so that the layers of the nest immediately under the eggs are very warm. Even the water, the surface of which sometimes penetrates into the hollow part of the nest, is heated to a considerable extent. Thus in one case the water in the hollow had a temperature of 23°, whereas the water around the nest had only 17° (insolation?).

Temperature decreases in the direction from the eggs in the nest.

In ornithological literature one frequently finds a discussion of a possible influence of the rotting material in the nest on the temperature of the nest, thus helping to develop the clutch. The conception of such an influence probably arose from the observation that the grebe is rarely to be found actually occupying the nest, that it strays far from it, and that even in nesting time it roams about the ponds. These facts, however, cannot in any way be taken to point to a warming of the eggs by heat developed by the decomposition of the material of the nest, as the grebe in the first instance sits fairly steadily on its nest, and secondly as the eggs are covered up when the parent bird leaves the nest so that the heat engendered by sitting is prevented from escaping. Thus there is no reason for seeking for any further explanation in a possible development of heat by rotting material. Moreover any such influence is excluded by the following fact:

A comparison of the temperature of the eggs with that of the nest (always measured in the hollow in the layer immediately under the eggs) shows that the temperature of the eggs and of the nest is not the same, even when the old bird is sitting on the eggs. The nest is invariably cooler than the eggs. The smallest difference measured was 1°. If we assume that the heat engendered by decomposition actually exists, then old grebe nests, abandoned by the birds, should also be warmer than their immediate surroundings immediately after

the hatching; but as this is not the case, we must take it that the rotting material in the nest has no influence on the temperature of the nest. Neither in the part below the water level nor above it was there any rise in temperature. Thus we must conclude that the temperature of the nest plays no rôle whatsoever in the development of the clutch. We are forced to the same conclusion also by the fact that many grebe nests have no rotting material in them at all. The above conclusion is based on many measurings which I undertook for this purpose.

The main reason for covering up the clutch seems to be protection against an enemy from the air, crows, birds of prey of the genus *Circus* etc. which may attack the clutch from above, and which would easily discover the light eggs without any protective colouring. There is no doubt that this is one reason why the clutches are covered. The same is also shown by the fact that in many cases only a few halms or leaves are very thinly dragged over the eggs so that they are not covered by a whole layer of rotting plants, which could protect the eggs from loss of temperature. But a heat protection of the eggs cannot be excluded. In many cases, also for the Black Necked Grebe, where I measured the temperature of the eggs in the nests, I also studied the question of how far the covering up of the clutch acts on its temperature.

The fact that by covering the eggs these are protected against quick cooling cannot be denied. Also SCHIERMANN (1927) arrived by measuring at this conclusion.

We may also safely surmise that the plant layer placed over the clutch maintains the humidity in the environment around the eggs.

From the many experiments I have made with the colouring of eggs I can state definitely that the Great Crested Grebe as well as the Black Necked Grebe are not sensitive at all to a change of the colour of their eggs. But it cannot be maintained that they do not perceive such a change, on the contrary, it is striking in both species described that when they approach a clutch changed in this manner they move around very distrustfully for a while and call out loudly. There is no doubt that they recognise the change. They are especially sensitive to black colour. With eggs coloured black the bird does not dare to approach the clutch as quickly as with eggs given any other colour. The Great Crested Grebe was so frightened by the black colour used for its whole clutch that it did not return at all to the nest. With other colours, whether the whole clutch was given the same colour or each eggs was coloured differently, no such abandonment took place. However, that there are exceptions to this rule is shown by the abandonment of red and green eggs of a clutch in the Black Necked Grebe.

The indifference which the grebes show to almost all colours is probably due to the fact that the grebe eggs change colour during the time of hatching.

The grebes do not react at all to a change in the number of eggs. They continue to sit even when only one egg of a clutch of four is left for them. Also an increase of the clutch by 1—2 eggs is suffered. One pair sat the whole time on a rather large chicken egg added extra

to the number of eggs already there; the pair did not appear to notice it at all. An angular stone of about equal size as the egg of the Great Crested Grebe was, however, thrown out by the old birds. Also the Black Necked Grebe throws foreign objects out of the nest, and carries them away from its vicinity.

At the time of the actual hatching of the fledglings the experimental pair suffered a shifting of the nest of 2 m.

The Great Crested Grebe is used to a change of the position of the nest; a certain power of resistance to a change in the position of the nest must be inborn in it when we remember that the nest itself is not stable. The inborn tendency of building freely floating nests brings with it also a certain resistance in the sensitivity to a change in the position of the nest.

Much depends of course on when during the period of hatching the disturbing interference is introduced. At the beginning of hatching the grebe abandons its nest very often already on account of a small disturbance. But towards the end of hatching the birds sit very steadily, and visits at the nest have no unfavourable consequences.

Just as in the large majority of birds so also in the Great Crested Grebe both birds take part in the hatching of the eggs. The share of ♀ in sitting on the eggs is, however, distinctly greater, so that in most cases we find ♀ on the nest. There is no regular time when ♀ and ♂ sit on the clutch. But in the morning hours ♀ sits more frequently. When the bird sitting on the nest sees its mate approaching it tries to draw its attention to itself by moving its head from side to side and by straightening itself up in the nest. Often it jumps at once from the nest. Sometimes it leaves on these occasions without the mate taking its place. In such cases the eggs may remain uncovered even for rather a long period. It is not rare that it takes 15—20 minutes before one of the parents appears near them.

♂ scared away from the nest usually returns to it later than a scared away ♀, which is a little more confident. They mostly approach the nest by diving in front of the reeds and emerging in its immediate vicinity. But this need not always be so.

When in danger the grebe does not take refuge in the reeds, but on the open surface.

In one case the fledglings hatched from the eggs already on the 22nd day, which is less than the period recorded in literature.

At the time of hatching the peep of the fledglings in the eggs is very striking, especially in the vicinity of grebe colonies. It comes from the still unhatched fledglings within the eggs. On this striking phenomenon HEINROTH (1928) expresses the opinion that it is to prevent the old grebes from leaving the nest. Owing to the considerable interval between the hatching of the individual fledglings there is a very real danger that the old birds may leave the nest with the first fledgling, even though it contains still unhatched eggs. When we remember that the peep of the fledgling in the egg is not limited to the grebe but occurs also with feeding birds, we must treat this opinion with a certain reservation. If the calling of the fledgling in the egg had really this

significance most of the grebe pairs would have to lead out as many fledglings as they had eggs. It is quite well known that this is not the case either with the Great Crested Grebe or with the Black Necked Grebe. The phenomenon is still more striking in the Black Necked Grebe. SCHIERMANN is of the opinion that the difference between the size of the clutch and the number of fledglings led out is due to the fact that the parents abandon the other eggs when leading out the first fledgling. The factor of abandoning the clutch certainly manifests itself most in this matter. The eggs are really abandoned — of course only in some cases — by the old birds, and the calling of the fledgling in the egg has no influence on the behaviour of the old ones. The developed embryo of the grebe can stand not being warmed for a considerable time and may be hatched successfully also in the absence of the parents, which in any case do not help it into the world, and then the fledgling dies in the neighbourhood of the nest.

The old grebe sitting on the nest is disturbed by the first fledgling, which immediately on hatching climbs of its own accord on to the back of the old bird, and this may be the cause of the premature abandoning of the clutch, especially when the mate shows no great inclination for a longer sitting.

Very often a non-fertilized clean egg has been ascertained in the total number of eggs. Also this phenomenon might account for the small number of fledglings. In the Black Necked Grebe, however, not one non-fertilized egg was found in the whole colony (20—25 nests).

But it is not rare that the grebes lead out the full number of fledglings (3—4). On the ponds of Bystřice near Benešov this is an almost normal phenomenon. In Bohemia a small number of fledglings is a local phenomenon, limited to certain populations only.

After the hatching of the fledglings the old grebes remove the shells, and carry them away from the vicinity of the nest.

The young grebes pass the first day on the back of their parents under the wings or in the pockets on the sides of the body. Later the fledglings venture alone on the surface of the water or are thrown off the back by a special shuddering movement of the old birds. Even four weeks' old grebes may still try to creep in under the wings of the old ones. The reports that the old birds dive with the fledglings on their back are true. Once a flying grebe was shot down in a duck-hunt; it had a living fledgling on its back.

The old birds take an equal share in bringing up the fledglings. ♀ carries them on the back and passes almost the whole time in their company, while ♂ provides the food. Sometimes the old birds change tasks. In the first days it is almost exclusively ♀ which feeds the fledglings. The fledglings are always associated with the entire pair, and the families are not divided.

Ornithologists differ as to the way in which the fledglings are fed. The results obtained in this investigation may be summarized as follows:

1. In the first days of their life the fledglings are fed with small fish and insects collected on the surface. These are placed gently in

their beak. They may be fed also by one parent while sitting on the back of the other parent. The fledglings are led out by ♀ and ♂.

2. Fledglings aged several days are given feathers torn from the underside of the body or collected on the surface so that they get them straight into the beak. Often the feathers are first moistened. The fledglings begin to swallow their own feathers only when the feathers of the contour dress begin to appear in the first down-garment.

3. Most of the food is provided by ♂, especially small fish; quite small grebes are mostly fed by ♀.

4. The small fish are given alive. The old birds hold them in carrying them behind the head and give them to the fledglings head first.

5. At a more advanced age the fledglings can drag out and eat feathers of the old birds as well as their own. But even then they are fed by the old ones.

6. Feeding takes place at the time of hunting (morning and towards evening) on an average $7 \times$ an hour.

7. The fledglings beg strenuously from the old ones. In extreme cases the begging ends with a special movement of the fledgling (described in the section on movements). They hurry from afar to the old bird carrying food.

8. When the old hunting grebe is some distance away from the nest, it sometimes dives to swim the rest of the way under water with its prey, using the cover given by the reeds.

9. The first diving for food was observed in fledglings on the 20th day of their life (HARRISON & HOLLOM report diving only in the sixth week).

10. In the Bohemian grebe the families stay together till well into the autumn. A separation of the fledglings into ♂ and ♀ was not observed in any case.

The problem of non-hatching birds is still not settled. Some ponds have a greater number of individuals than really nest on the pond. All are paired, however, and most of them show a quite normal courting.

The main cause of this striking phenomenon has to be found in the inability (especially of the young birds) to find suitable nesting places. This is proved by the many unsuccessful attempts at nest building.

I discovered, however, that non-nesting grebes occur only in some places, i. e. they are a local phenomenon.

Food and Economic Significance.

An analysis was carried out of twenty grebe stomachs. I compared the results obtained with those of other authors, both from Czechoslovakia and from abroad. A survey of the stomach contents is given in the table.

The quantity of fish consumed per day is considerable. At the time of hunting, in the morning and towards the evening, the grebe can

Table of the contents

Place and date when hunted down	Sex and age	Weight of the dry content	F i s h
Podhrázský, 20. IV. 1949	adult. ♂	7,30 g	bones of <i>Perca fluviatilis</i> and further whole <i>Perca fluviatilis</i>
Splav, 11. VII. 1948	adult. ♀	4,20 g	scales of <i>Perca fluviatilis</i> , about 10 cm. long, <i>Gobio gobio</i> , pharyngeal teeth, 3 otoliths, indeterminate bones
Slavníč, 26. VII. 1948	adult. ♂	10,52 g	—
Vytanov, Blatná, 1. VIII. 1948	adult. ♀	6,11 g	—
Vytanov, Blatná, 1. VIII. 1948	adult. ♀	4,60 g	—
Vytanov, Blatná, 1. VIII. 1948	juv. ♀	2,90 g	ribs of very small, indeterminate fish, about 4 cm. long
Slavníč, 15. VIII. 1948	adult. ♂	5,05 g	—
Splav, 21. VIII. 1948	juv. ♂	5,75 g	bones of the head of a perch, about 10 cm long
Slavníč, 21. VIII. 1948	adult. ♀	3,90 g	half-digested remains of two perches 8—9 cm. long, pharyngeal teeth and bones of <i>Gobio gobio</i>
Slavníč, 21. VIII. 1948	adult. ♂	9,42 g	bones and scales of perch
Slavníč, 21. VIII. 1948	adult. ♂	8,00 g	—
Splav, 21. VIII. 1948	adult. ♀	3,53 g	indeterminate remains of a fish, 2.5—5 cm. long
Břehyňský, Doksy, 23. VIII. 1948	juv. ♂ (20 days)	2,21 g	—
? VIII. 1948	adult. ♂	4,57 g	—
Studénka, Slezsko 26. VIII. 1948	adult. ♂	2,65 g	<i>Perca fluviatilis</i> , 7 cm. long
Velký Pálenec, 30. VII. 1948	juv. ♀	7,52 g	remains of a perch, 3 cm. long
Pardubice, VIII. 1948	juv. ♂	3,55 g	—
Břehyňský, Doksy, 4. IX. 1948	adult. ♂	2,87 g	—
Slezsko, Ostrava, IX. 1948	juv.	12,30 g	—
Ostrava, Slezsko, IX. 1948	adult. ♀	7,30 g	—

of stomachs.

Insects	Varia	Hunted down by
—	scales of <i>Perca fluviatilis</i> , about Fish lying against the wall of the stomach. Feathers	Hanzák
indeterminable remains very abundant, fragments	feathers	Hanzák
abundant wing-sheaths of <i>Melolontha</i>	feathers full of remains of chitin	Hanzák
<i>Gyrinus natator</i> , <i>Phyllobius</i> and <i>Carabidae</i> var. <i>Formidae</i>	feathers	Černý
remains of Hymenoptera, <i>Phyllobius</i> sp., <i>Formica</i> sp.	feathers, green contents insects only	Černý
indeterminable remains of Hymenoptera, <i>Formicidae</i> — 2 sp.	feathers, wall of the stomach of the colour of evergreen	Černý
remains of <i>Melolontha</i> very abundant	feathers	Hanzák
—	feathers, yellow mushy substance, down feathers and feathers from the collar	Hanzák
<i>Phyllobius</i> sp. <i>Ottiorhynchus ligustici</i>	strongly ground of feathers, bits of <i>Typha</i>	Hanzák
remains of insects, 1 s. <i>Melolontha</i> vulg.	feathers	Hanzák
fragments of Hymenoptera, <i>Ottiorhynchus</i> sp., <i>Tiphia</i> sp., <i>Myrmica</i> sp.	feathers and three small stones of a diameter of 2 mm.	Hanzák
—	in the glandulous stomach one undisturbed feather. Yellowish mushy substance	Hanzák
several <i>Paravespula vulgaris</i>	feathers, quartz $\frac{1}{2}$ cm. in diameter, two others 2 mm., one 1 mm. and $\frac{1}{2}$ mm.	Šarbort
indeterminable remains of <i>Carabidae</i>	feathers, yellowish mushy substance	?
indeterminable remains	feathers	Svoboda
<i>Harpalini</i> , <i>Phyllobius</i> , <i>Formica</i> sp.	feathers, quartz 4 mm. in diameter	Černý
remains of <i>Melolontha</i> vulg. — 1 sp. Hymenoptera ?	feathers	Strachota
<i>Formica</i> sp., <i>Myrmica</i> sp., <i>Phyllobius</i> sp., <i>Tiphia</i> sp.	feathers, green contents	Šarbort
<i>Phyllobius</i> sp., <i>Tiphia</i> sp., <i>Myrmica</i> sp., indeterminable Hymenoptera	feathers, one flat stone	Skotnica
head of Hymenoptera sp.	feathers	Skotnica

swallow several fish one after the other. One grebe was observed to dive seventeen times within three minutes; it caught 14 small perches in this time. In the Czech literature is found the record of one grebe stomach which contained one *Perca fluviatilis*, 12 cm. long, two *Acerina cernua* of 7 and 8 cm., two *Lucioperca lucioperca* 6 and 9 cm. long. At feeding time the grebe can thus really eat its fill. It is for this reason that its resting time, when it digests the food, is so extraordinarily long. Normally the remains of one or two fish are found in the stomachs.

The size of the fish swallowed varies on an average round 8 cm., the maximum size being 17 cm. Sometimes the grebe feeds also its fledglings with so large fish that after some attempts at swallowing them the fledglings leave them to swim away.

Species of fish determined in stomachs of the Bohemian Great Crested Grebe.

Species	Number of specimens	Length in cm
<i>Perca fluviatilis</i>	22	12, 10, 9, 8, 7, 7, 4, 4,
White weed fish	9	6, 3
<i>Acerina cernua</i>	6	10, 10, 10, 8, 7
<i>Gobio gobio</i>	5	15, 14, 13, 12
<i>Esox lucius</i>	5	10, 10, 8, 4, 3
<i>Cyprinus carpio</i>	3	9, 7, 7
<i>Lucioperca lucioperca</i>	2	9, 6
<i>Alburnoides alburnus</i>	2	
<i>Alburnoides bipunctatus</i>	1	10
<i>Nemachilus barbatus</i>	1	
<i>Misgurnus fossilis</i>	1	
<i>Rutilus rutilus</i>	1	17 (Kadlec)
<i>Leuciscus cephalus</i>	1	
<i>Leuciscus leuciscus</i>	1	

As may be seen from the appended list the great majority—fully 83%—is formed by weed fish and among them *Perca fluviatilis* and *Acerina cernua* take first place. This does not prove any predilection of the grebe for these fish, but is rather due to the fact that these species have relatively the best size for the grebe and are usually present in our ponds in abundant numbers. According to findings made up till now the grebe will catch any fish of a suitable size which lives in the waters it inhabits.

Insects form another important item of the grebe's diet, and were found in almost all stomach contents. Some of them included more especially a great quantity of chitinous remains. A list of the species found in grebes of Bohemian origin (HANZÁK—JIRŠÍK) is given in the table of insects.

List of the species of insects found in the stomachs of Great Crested Grebes

Odonata: Remains of larvae, once three specimens of *Sympetrum sanguinolentum*

Trichoptera: Large quantity of larvae of various Trichoptera.

Coleoptera: *Amara* sp., *Anthrenus scrophulariae*, *Calanthus* sp., *Casida* sp., *Carabidae*, *Chlorophanus* sp., *Donatia semicuprea*, *Dytiscus* sp., *Elatér* sp., *Gyrinus natator*, *Haemonia appendiculata*, *Hylobius* sp., *Harpalus* sp., *Hydrous piceus*, *Hyphydrus ovatus*, *Chrysomela limbata*, *Lema* sp., *Macrolea appendiculata*, *Ottiorhynchus ligustici*, *Phyllobius* sp., *Pterostichus* sp., *Ptinus* sp., *Rantus* sp., *Rhizotrogus* sp., abundant *Melolontha* in the stomachs of my material. Besides often remains of *Donatia*.

Hymenoptera: *Anthophora*, *Apidae*, *Formica* sp., *Myrmica* sp., *Paravespula vulgaris*, *Tiphia* sp.,

Rhynchota: *Notonecta glauca*, *Naucoris cimicoides*, *Corixa*, *Salda*, *Gerris*.

It is not possible to divide the grebes into individuals living on insects and individuals living on fish, as the remains of fish and insects are found together. The grebe collects the insects on the water surface and as it seems also under water, whenever it has an opportunity to do so.

It would be important to know to what an extent the grebe eats fish spawn. So far I have found it only in the remains from the stomachs of two grebes.

In the analyses of some stomachs their green contents was strikingly large. JIRSIK had such a green contents examined by spectroscopic method, by means of which it was found that the nature of the green colour is really chlorophyll transformed by the action of the gastric acids into chlorophyllan. Its origin is most probably the algae eaten.

In several cases I found in the stomachs also small pieces of reed halms, but only to a trifling extent, and several stones, but at most small, rounded pebbles. These have certainly a mechanical function in the stomach, similarly as in other birds.

For its nesting place the grebe chooses generally larger ponds in which already weighty fish is cultivated. In such waters the grebes may be left in complete peace, but they cannot be allowed on stock ponds in which young carp are set out, of which 100 pieces weigh usually 0.4—3 kg. Also in breeding ponds the grebe may cause considerable damage. Thus the persecution of the grebe has to be restricted to such ponds.

The Significance of the Swallowing of Feathers.

The young grebes receive feathers from the old ones from their earliest youth, in fact soon after leaving the egg. The fledglings begin to swallow their own feathers only at the time when their first contour feathers begin to appear. But this does not mean that they then cease to eat feathers from their parents and feathers collected on the water surface. The old birds swallow their own feathers, which fall out when they preen themselves, or they collect feathers on the water surface. Thus I found in the stomachs of old grebes feathers from all parts of the body, even feathers from the collar. The feathers found in the

stomach are whole, and most of them come from the underside of the body.

Why do the grebes eat feathers? Without having studied this question more in detail different authors arrive at the following conclusions:

1. The swallowing of feathers protects the walls of the stomach from being damaged by sharp fish bones (MEWES, HARRISON).
2. It helps the digestion in a way similar to that of stones in the stomach (BIEDERMANN).
3. It acts as a kind of filter, which prevents the passage of coarser material (bones, chitine) into the intestine so long as this material is not reduced to a certain size (WETMORE, STRESEMANN).
4. The feathers chemically decomposed help their digestive processes (ROWAN).

Ad 1. This point must be excluded, for the fish contained in the stomach lie sometimes directly at its wall, in one of my own cases the sharp dorsal fin of a perch had even pressed against the stomach wall. If the feathers really served as protection they would have to line the stomach. But this is not the case. Further it must be remembered that the walls of the grebe stomach are fairly tough and resistant to damage.

Ad 2. The ball of feathers contained in the stomach is soft so that hard parts of the food prick into it and it does not resist them. Mechanically it is only hard objects which can help the digestive processes, and with grebes stones serve this purpose.

Ad 3. Microscopically I found that there is no trace of bones in the intestines, even in the duodenum. Neither is there here however any trace of feathers. Thus it is clear that neither the feathers nor undigested roughage pass the pyloric stomach. The thorns of feathers regularly found in the pyloric stomach lying close to the pylorus and forming a kind of net can have only a subordinate function in keeping back rough parts of the food. But I consider that this netlike arrangement of the thorns of feathers arises purely by chance.

Ad 4. ROWAN found in the feathers ergosterol which exposed to ultraviolet rays gives vitamin D. HARRISON and HOLLOM (1932) voiced the opinion that in this way the birds obtain vitamin D.

JIRSIK (1929) is of the opinion that the feathers produce a feltlike substance, which envelopes the sharp parts of the food ejected from the stomach. According to my experience this is the correct explanation.

In each opened analysed stomach we find a certain quantity of a special mush-like substance, which under the microscope proves to be composed of fragments of radia and cilia of the swallowed feathers. JIRSIK's finding that the mush-like substance envelopes bones and chitinous remains and thus makes possible their easier ejection I can also confirm. It is often rather difficult to clean bones thus enveloped. The swallowed feathers have thus really the task to help in forming the ejections, but do not take part in this in their whole form; instead, they produce a felt-like substance and only this takes an active part in ejection.

Migration.

(Phenology, Hibernation, Results of Ringing.)

For the period 1914—1949 51 dates of arrival of grebes are recorded for Bohemia and Moravia. They show that the first grebes appear on our waters in March and April. Earliest date 11-III-1937. Of the total number of 51 dates one falls in the first half of March, 23 in the second half of March, 20 in the first half of April, the others are later. It is most interesting to observe that the grebes usually do not appear in our country before the ponds are free of ice. Very often they arrive already paired, and one may say that this is almost the rule. The passage in spring of foreign grebes nesting farther north is not so striking as their passage in autumn.

Occupation of the nesting place takes place almost simultaneously in the whole of Europe. This shows how quick the spring migration is effected. But the autumn migration takes place as a rule in such a way that first our birds depart; there is a distinct decrease in grebes and a few days later appear again others, more northerly ones, which only pass through our country. Already in August one can observe a movement of the grebes from pond to pond, but the main time of departure falls in October. In November our nesting places are already deserted.

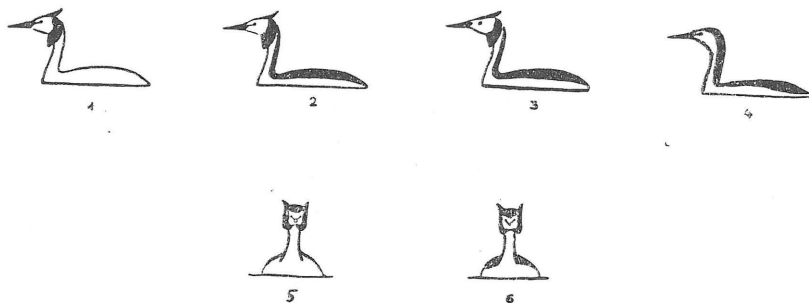
The migration of the Great Crested Grebe is in our country unostentatious. They arrive and disappear all of a sudden, without forming any striking flocks. During the autumn migration foreign birds pass through either sporadically or in small groups. As all representatives of the order Podicipedes the Great Crested Grebe migrates exclusively at night. There are quite a number of cases in which grebes were found in Bohemia in winter.

Only one ringing result is of Bohemian origin. The grebe ringed on 25-V-1935 was found on 23-XII-1935 at the age of 6 months 29 days on the Lago di Lescina in Italy. Thus it had flown 930 km. in a southerly direction. Thus we may express the uncertain opinion that our grebes have not the tendency to eastern migration which is found in the North European grebes.

Tests with Attrappes.

The tests which were designed to elucidate a little the mental capacity of the Great Crested Grebe were made by means of attrappes of the grebe type, frontal and lateral (see pictures).

The use of attrappes and the result of the reaction to them are both connected with the correct visual angle under which the grebe has to look at the attrappe. When the grebe sees the attrappe too much from the side, it pays no attention to it as it is flat. In tests with attrappes it is further necessary to use them for a short time only. When they are shown for long, the grebes get accustomed to them and do not react to them. Thus the greater number of positive reactions fell always at the beginning of the tests.



Kinds of frontal and lateral attrappes used in tests of the mental capacity of the Great Crested Grebe. Attrappes 3 and 6 have a red beak and iris.

The number of tests made was not so great that any far-reaching conclusions could be drawn from them. Upon the whole it may be said that the grebes did not see any difference between different drawings of lateral attrappes. They usually did not react to frontal attrappes. Only once a fairly ambiguous reaction was observed to attrappe no. 5. In the first moment of sighting the attrappe the grebe behaved to it as to a member of its own species, usually therefore suspicious and inimical (position with stretched neck—on guard). Often old birds behave as if to ascertain the identity of a strange intruder in this position. Only in a few cases was it clear that they considered the attrappe a member of their own kind. A distinct proof of this was the attack of a grebe ♂ on the attrappe. This reaction of recognition lasts, however, only a very short time, namely until the grebe discovers that the attrappe is only an immobile object. By a special provocative behaviour the grebe tries to provoke the supposed intruder to move; when it does not succeed and recognizes the immobility of the attrappe, it does not pay any attention to it any longer, on the contrary it is afraid of it. In contradistinction to other birds with which these tests were carried out, the immobility of the attrappe plays a considerable rôle with the grebe.

The knowledge of the individuality of their own parents is probably not inborn in the fledglings judging from a case where the fledgling begged from an old bird of another pair. It is of course highly probable that this reaction was called forth more by the fish carried in the beak than by the appearance of the adult bird. When the fledglings are in the company of their parents they do not react at all to attrappes. When alone they may mistake the attrappes for their parents—of course only for the very short time it takes for them to discover the immobility of the attrappes.



Great Crested Grebe on the nest

Foto Dr J. V. Staněk



Nests of the Great Crested Grebe

Foto Dr J. Hanzák

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