

## TERRITORY IN THE GREAT CRESTED GREBE.

BY

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### INTRODUCTION.

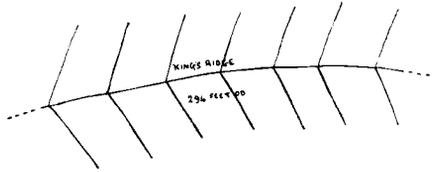
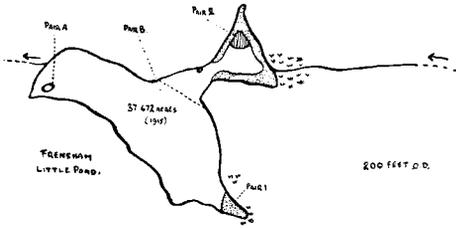
IN their review of territory in bird life, D. and L. Lack (6) consider that the claims for territory have been much exaggerated and that, especially, there is not adequate proof in any species that territorial behaviour has food value. It was further questioned whether territorial behaviour limited the population density at all, irrespective of its possible food value. Subsequently, Huxley (4) has answered the latter question in the affirmative for Coot (*Fulica a. atra*) and Mute Swan (*Cygnus olor*), while Venables (8) has shown that territories, at least food territories, do not limit the population density in the Dartford Warbler (*Sylvia u. dartfordiensis*). The following observations show that in the Great Crested Grebe (*Podiceps c. cristatus*) territorial behaviour at times limits the population density, but that this behaviour bears no direct relation to the food supply. We would record here our grateful thanks to Professor Julian Huxley for reading through the manuscript and supplying some valuable criticisms.

Harrisson and Hollom (1) give a detailed account of the distribution of the Great Crested Grebe and of the great increase in numbers which has occurred since about 1860. The authors (*loc. cit.*, p. 124) take the usual view that "territory acts as a safety valve against over-population and is responsible for spread outwards from populated areas". They do not, however, include observations on territorial behaviour in their paper.

### FIELD OBSERVATIONS.

The following observations were made by Venables in 1932, 1933 and 1934 at the two Frensham Ponds, on the Surrey-Hampshire border. Great Pond has an area of 69½ acres and Little Pond of 37½ acres (1915).

*Great Pond* was colonized in 1899 (Harrisson and Hollom, *loc. cit.*, p. 85). Records of the number of breeding pairs are available for 1907 to 1920 (kindly communicated by H. Bentham), for 1931 (Harrisson and Hollom), and for 1932 to 1934 (Venables) as follows: 1907 seven, 1908 four, 1909 five, 1911 six, 1912 and 1913 four, 1915 five, 1920 seven, 1931 and 1932 six, and 1933 and 1934 eight pairs. There has thus been a small increase in numbers in recent years.



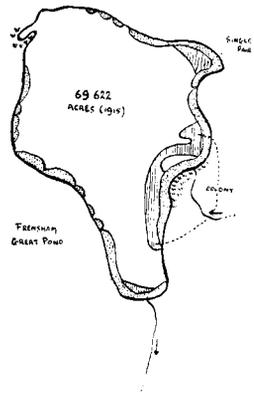
200 FEET  
D.D.

**SKETCH MAP OF  
FRESHM PONDS,  
S.W. SURREY.**



6 INCHES TO 1 MILE.

-  REED-BED
-  POSE-TAIL BED



The Great Crested Grebe is absent in winter. Birds begin to arrive on the pond in mid-February and number about thirty or forty in mid-March, after which they decrease. Most of these are migrants passing through to other breeding grounds; they do not stay for more than a few days and their numbers fluctuate greatly. By early April the last of the passage migrants usually depart. (Their departure cannot be attributed to aggressive behaviour by the remaining pairs which will later nest). Much fighting is observed among the Grebes during March, some at least of which is associated with pairing. This fighting occurs mainly in the open water in the centre of the pond and is quite distinct from the fighting discussed later, which is associated with the nesting sites in the reed-beds.

The later passage migrants are already in pairs before they leave for their nesting grounds; hence pairing often, if not invariably, precedes the taking up of the territory. In this respect the Grebe differs from Passerine birds, the group in which Howard (2) first applied the term territory.

In early May a few pairs commence breeding in the, as yet thin, reed-beds off the south shore, but these nests seem invariably to get robbed, and it has always finished up with six or seven pairs breeding in a colony along the south shore in a horsetail (*Hippuris*) bed. In this colony (six pairs in 1932 and seven pairs in 1933 and 1934) no fighting has been observed except for an occasional squabble in the horsetail near the nests, which probably indicates that the immediate neighbourhood of each nest is kept clear of intruders by the pair in possession. This has also been observed by Huxley (3), who noted, as was the case on Great Pond, that such territories are not food territories. The birds feed amicably together all over the water, and take their young out to the centre of the pond a very few days after they are hatched.

In 1933 and 1934 one pair behaved differently. These nested in a horsetail bed in an open bay in the south-east corner. Before nesting they were extremely pugnacious, and kept the whole bay (an area of about  $\frac{3}{4}$  acre) free of other Grebes, any that tried to enter being vigorously attacked and driven off. By the time that the nest was built other Grebes had abandoned this bay. Coots were also violently attacked, but finally bred in the portion of the bay more remote from the Grebes' nest. But the Coots were attacked by the Grebes whenever they entered the Grebes' portion of the bay. Both birds, unless one was incubating, took part

in these fights, and then, on returning and while still excited, would frequently display and almost invariably add a few more reeds to the nest. On the occasions when the female was sitting, the victorious male would frequently carry material back to the nest. As a result, when the eggs hatched out, this nest was much larger than is normal for the species. The Grebes abandoned their aggressive behaviour as soon as the young hatched out and took them to the middle of the pond. Hence their territory was not correlated with food supply for the young.

*Little Pond* was colonized in 1907, and counts of the breeding pairs are available as follows: One pair in 1907, 1908 and 1909, none in 1911 or 1912, one pair in 1913, 1915 and 1920, two pairs in 1932 and 1933 and three pairs in 1934. There is a conspicuous passage migration as on Great Pond. There are only two reed-beds on the pond suitable for a floating Grebe's nest, a small bed in the south-west, and a large one of several acres in extent in a bottle-shaped bay in the south-east. Each of these held one pair of Grebes in 1932, 1933 and 1934.

Pair I. in the south-west corner were territorial in the sense that they both kept to the south-west portion of the pond until their young hatched, when they took the latter to the centre of the pond. No other Grebes frequented this south-west portion, so that one cannot say to what extent pair I. were aggressive against their own species. A few pairs of Coot and Moorhen (*Gallinula ch. chloropus*), which nested in the same reed-bed, were quite unmolested, even when the female Grebe arrived at her nest on one occasion to find her eggs being incubated by a Coot. She waited quietly while the intruder slipped off and then mounted in her place.

Pair II. were extremely aggressive, and successfully kept all others of their species from entering their bottle-shaped bay, patrolling up to a distance some way outside the "neck", thus maintaining an area of  $8\frac{1}{2}$  acres. All passage migrant Grebes which attempted to enter this area were vigorously attacked, and one of the half-grown young of pair I. which once tried to enter would probably have been killed had not the observer distracted the attention of the attacking male (the female was then incubating). As with other Grebes, this pair left their territory and abandoned their aggressive behaviour when the young hatched, the latter being taken to the centre of the pond. Unlike the aggressive pair on Great Pond, pair II. did not attack other species. Coot, Moorhen,

Tufted Duck (*Nyroca fuligula*) and a passage migrant Black-necked Grebe (*Podiceps n. nigricollis*) frequently entered the area, always without molestation, and Tufted Duck, Coot and Moorhen bred there.

In 1934, after the passage migrants had departed, two extra pairs, A and B, remained on Little Pond. For several days these made repeated attempts to enter the bay occupied by pair II., but were always repulsed. Pair A then retired to the centre of the pond, and later frequented the northern part, where there were no reed-beds. Pair B continued to attempt an entrance, and on April 17th were joined by a fresh arrival, and then all three made periodic attempts on the bay. The odd bird left about April 22nd, but pair B continued to fight and to be repulsed until May 2nd, when they also left. But pair A stayed, and finally nested on a small island in the north part of the pond. It is extremely unusual for a Great Crested Grebe to build on dry land.

#### FACTORS AFFECTING THE GREBE POPULATION.

1. *Mortality*.—The mortality of eggs and young is very high, the former being taken by collectors, the latter by large pike (*Esox lucius*). The bird normally lays four eggs in the nest, and, until late in the summer, the pairs always laid again when their eggs were destroyed. But in 1932 and 1933 the average of successfully reared young was only 1.5 per pair. (In 1934, with more adequate protection, this average was 2.5 per pair).

2. *Nesting Site*.—On Great Pond there is much untenanted but suitable reed-bed, and nesting site is ruled out as a factor affecting the population density. On Little Pond there is a small reed-bed occupied by pair I., and one larger reed-bed in which pair II. prevented other Grebes from nesting. Hence it is primarily the aggressiveness of pair II., and only secondarily the nesting-site factor, which limited the population here. Pair B would almost certainly have bred on Little Pond had other reed-beds been available, and pair A nested in spite of this deficiency. (As has previously been pointed out by Lack (5), the restriction of a species to a particular type of nesting site (although it sometimes limits distribution) is often one of behaviour and not of necessity. Pair B successfully reared their young in an unusual site, but pair A were evidently not so adaptable in their behaviour).

3. *Food*.—In 1933 and 1934 eight pairs bred on Great Pond, one pair per 8.5 acres. On Little Pond, in 1932 and 1933, the

density was one pair per 18.5 acres. In 1934 four pairs tried to nest there (one pair per 9 acres), but only three succeeded (one pair per 12.5 acres). Tucker (7) found that one pair per 4.5 acres was the usual maximum in Oxfordshire, Berkshire and Buckinghamshire.

There was no evidence that food supply limited the Grebes, but this is extremely hard to determine. The number of pairs breeding on the ponds has been slowly increasing, and there is no reason for supposing that the food maximum has yet been attained. Further, although it is not conclusive to compare one pond with another since the fauna may be different, it is noteworthy that in neither of the Frensham Ponds does the density approach to one pair per 4.5 acres, and Little Pond supports a smaller density than Great Pond. On the latter, at least, it is very unlikely that the food maximum has been attained.

4. *Territorial Behaviour.*—Owing to the situation on Little Pond, territorial behaviour can definitely be considered a factor limiting the Grebe population. On Great Pond an aggressive pair kept one small part free of other Grebes, but there were many other suitable reed-beds, and the total breeding population on the pond was probably unaffected by their behaviour. This aggressive behaviour is not conspicuously developed in all individuals, and seven pairs were sufficiently lacking in it to nest in a colony. Hence its effect on the population density of Grebes in general is most uncertain.

Owing to the variability in its development, one can probably say that territorial behaviour confers no special advantage on the bird. Had it done so, it is remarkable that it should be conspicuous in only two pairs, while seven pairs reared their young in a colony.

Territorial behaviour is clearly not correlated with food supply in this species, as has sometimes been assumed. First, the greatest food pressure presumably occurs when the young have hatched, but territories are at that time abandoned, the young being taken to the centre of the pond. Secondly, on Little Pond, pair II. attacked other individuals solely in their bay. Had food supply been its object, fighting would have been necessary over the whole pond, but when pair A deserted the south-east of the pond and bred in the north, they were unmolested. Thirdly, while pair II. defended  $8\frac{1}{2}$  acres, which is, perhaps, an adequate feeding area, the pair on Great Pond defended only  $\frac{3}{4}$  acre, which was pre-

sumably inadequate as a feeding area. Fourthly, the latter pair attacked not only Grebes, but also Coots, and the latter are not food competitors of the Grebes.

Territorial behaviour is clearly correlated with the position of the nest. Even the colonial pairs sometimes attacked other individuals which came too close to their nests. This habit seems merely to have become greatly exaggerated in the territorial pairs. The effect of this behaviour was to render uninhabitable for other pairs reed-beds which could otherwise have been utilized for nests. On Little Pond, with its scarcity of reed-beds, this resulted in only two pairs inhabiting the pond, although it could provide sufficient food for at least one, and probably several, more pairs. It was only when they modified their normal nest-building habits that a third pair could breed there. Howard (2) claims as a general principle that the "establishment of territories serves so to regulate the distribution of pairs that the maximum number can be accommodated in the minimum area". But on Little Pond, *territorial behaviour, so far from doing this, actually prevented the number of breeding pairs from reaching the maximum which (from both food and nesting sites) the lake could support*). It was therefore adverse, not beneficial, to the species.

Harrison and Hollom (*loc. cit.*, see esp. Tring, p. 75) have shown that at the beginning of an increase in the Grebes, a lake has often held many more pairs than the number which it has fairly steadily supported in later years. The writers assume that there was an initial over-population followed by an adjustment, and the latter is evidently considered by them to have been brought about by territorial behaviour. But the observations at Frensham Ponds, particularly with regard to the great individual variation in aggressiveness and to the existence of colonial pairs, render it almost impossible to believe that territorial behaviour could have effected this adjustment in the population.

#### SUMMARY.

The following conclusions apply to the Great Crested Grebe population in the area studied:—

1. Territorial behaviour must definitely be reckoned as one factor affecting the density of the breeding population.
2. This territorial behaviour centres round the nesting site, and is extremely variable in its development, some individual pairs being very aggressive and others colonial.

3. The territory is not correlated with food supply.
4. Its variability makes it extremely difficult to see how territorial behaviour could effectively regulate the distribution of pairs so that the maximum number could be accommodated in the minimum area, as has sometimes been claimed for it.
5. Extreme territorial (aggressive) behaviour seems of no advantage to the species. In the case where it limited the population density, it tended to prevent the lake from supporting the maximum number of pairs which food and nesting sites would have permitted.

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