Territoriality and breeding biology of the coot (fulica atra (l)) at Attenborough

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ABSTRACT

Territoriality and Breeding Biology of the Coot (*Fulica atra* L.) at Attenborough

Field work was carried out from August 1972 until August 1974 on an area of 119 ha. of the Attenborough Gravel Pits in Nottinghamshire. A total of 135 territorial pairs were monitored with reference to size of territory, length of laying season, clutch size, egg size, hatching and fledging success and relationship with other waterfowl.

Territory size varied from 0.08 ha. to 1.37 ha. with a mean of 0.46 ha. It was not correlated with clutch size or breeding success. Both members of a pair defended the territory. A minimum of 19 pairs are believed to have remained on their territories for the whole of the study period.

In both years the laying season lasted approximately 2.5 months: peak laying occurring from 24 April to 7 May. It is confirmed that *Fulica atra* in Europe is normally single brooded. No correlation was found between egg size and clutch size. In both years eggs laid early in the breeding season were found to be significantly larger than all other eggs. The incubation period was 23/24 days.

The mean clutch size of the 124 completed clutches was 6.1 $\pm$ 0.04 eggs. In Britain as a whole the overall mean clutch size was calculated to be 6.0 $\pm$ 0.08 eggs which is significantly smaller ($d = 23.06$, $P < 0.001$) than the mean clutch size (7.9 $\pm$ 0.03) of the coot in continental Europe.

A hatching rate of 49.3% was recorded and of those chicks that hatched 41.0% fledged at approximately eight weeks. Breeding success averaged 20.2% with a mean of 1.3 young fledged per breeding pair.

Both parents build the nest, incubate the eggs and feed and care for the young. Some young were still on territory, with their parents, at 14 weeks of age.

Intraspecific aggression was noted throughout the year, but interspecific aggression, apart from that towards the moorhen, only occurred in the breeding season. It is concluded that interspecific aggression is unlikely to harm other waterfowl in the area.

TERRITORIALITY AND BREEDING BIOLOGY OF THE COOT (*Fulica atra* (L.)) AT ATTENBOROUGH.

By

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Thesis submitted to the University of Durham for the degree of Master of Science.

September 1978.

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INTRODUCTION AND METHOD

Background, Scope and Problems of the Study

The field research was carried out during the period September 1972 to August 1974 and was aimed at increasing the ecological knowledge available on the coot. A single study area of about 119 ha. was selected at the Attenborough Nature Reserve, approximately 8 km. south-west of Nottingham, within a complex of flooded gravel pits extending over 300 ha. in the alluvial meadowlands of the River Trent (see plate 1). These contain a large number of flat islands and the depth of water varies greatly. At the time of the study the pits were owned by Trent Gravels and 96 ha. was managed as a nature reserve by the Nottinghamshire Trust for Nature Conservation Ltd.

Reasons for choice of the study area included:

a) It was known from personal observations over several years to contain a large population of breeding and wintering coot and had, in addition, been shown (BTO census figures) to carry a large breeding population of moorhen (Gallinula chloropus) and great crested grebe (Podiceps cristatus). In most years the following also breed in sufficient numbers to be of interest with respect to possible inter-specific aggression with the coot; mallard (Anas platyrhynchos), canada goose (Branta canadensis), little grebe (Tachybaptus ruficollis), tufted duck (Aythya fuligula), and the mute swan (Cygnus olor)(pers. obser.).

b) As the whole pit complex was wardened by volunteers it was hoped that there would be little vandalism to affect the research results - this in fact proved to be the case.

c) The pits were one of the most intensively watched area in the county and it is likely that someone may one day carry out

further research there, if not on coot, then on other water birds.

d) A large amount of data on the ecology of the study area had been collected by Bell (1968), Catchpole (1970) and Hornby (1971).

e) The area was very well known to me and was within 5 km. of my home.

f) The study would help to build up knowledge of the biology of the nature reserve: such knowledge possibly being of value for reserve management and for monitoring changes both in habitat and species.

Attention was concentrated on the breeding biology, although limited observations were carried out during the non-breeding season. As male and female coot are alike in plumage and size, it was hoped that observations would be facilitated by marking individual birds with either coloured leg rings or numbered wing tags. However, even with the help of the Attenborough Ringing Group, it proved impracticable to catch any coot. Given the lack of obvious differences between the calls of the sexes, it was only possible to sex birds by their copulatory behaviour. In consequence the sex of individuals could not be determined except in cases where there was overt sexual behaviour in progress. It probably would have been possible to trap adults on the nest while they were incubating but this was not done to avoid adding to the disturbance that my normal nest visits inevitable caused. Behaviour was monitored from the mainland but nearly all visits to a nest necessitated a boat trip.

The time spent at each nest was kept to a minimum but there

were occasions when adults were kept away from the nest for fairly long periods (up to 15 minutes). There is no direct evidence of birds deserting because of nest visits but it is certain that in 1974 the visits directly contributed to the loss of at least one egg and probably some newly fledged young (see page 157).

It proved difficult to cover all the study area in the time available. As data were accumulating on breeding biology, it was decided to concentrate on a more general study covering the whole of the study area rather than on obtaining detailed breeding behaviour on just a few pairs. This decision was based on the fact that two continental studies already existed which covered coot breeding behaviour in some detail (Kornowski 1957; Wagner 1962).

Literature on the Coot

Significant studies on the ecology of the coot in Britain are limited to those of Alley and Boyd (1947; 1950), Boyd and Alley (1948) and Sage (1969). Alley and Boyd (1947; 1950) gave data on hatching and fledging success and parent-young recognition. Their paper of 1948 discussed the problems of head coloration of nestling coots and other nestling Rallidae. Sage (1962) presented data based on observation over eleven years in Hertfordshire, on population structure, nest construction, clutch size, hatching, fledging and breeding success and causes of failure to hatch. He also compared clutch size and hatching success in three different areas of Europe. Cramp (1947) gave information on territorial aspects of the coot in St. James's Park, London. Huxley (1934) provided

information on territorial activity. Other studies include those of Ingram and Salmon (1935), Collinge (1936), Brown (1955), Hinde, Thorpe and Vince (1956) and Kear (1965). Other original publications concerning the coot in Britain are in the form of short notes.

Major studies on the coot in Central Europe include those of Kornowski (1957), Bezzel (1959; 1967; 1970), Wagner (1962), Havlin (1970) and Blūms (1973). Kornowski (1957) and Wagner (1962) presented full descriptions of many aspects of coot behaviour and breeding biology in Germany. Both included data on clutch size, but only Kornowski presented any figures for breeding success. Bezzel's (1959) study, also in Germany, included data accumulated over nine years on clutch size, egg size, laying dates and hatching success. Havlin's (1970) study of coot in Czechoslovakia concerns the length of breeding season and the degree of breeding success over a period of ten years. Blūms (1973) studied the coot in Latvia between 1958 and 1971. His data are extensive and concern observation on 3,009 nests, 1860 clutches and 15,100 eggs of which 1794 were measured. He also dealt with migration, breeding biology, interspecific relations, growth and development of the young, food, mortality, etc. His data account for 61% of all the clutches and 65% of all eggs examined in Europe.

Kornowski (1957) and Wagner (1962) in continental Europe, and Sage (1969) in Britain found that emergent vegetation, used for cover and food, was an essential factor in the breeding success of the coot. Other studies on the breeding biology include Grimeyer (1943), Nylund (1945), Lelek and Havlin (1956), Lelek (1958), Askaner (1959) and Krauz (1968).

A further study of a member of the Rallidae valuable in relation to this thesis is the series of papers by Gullion (1951; 1952; 1953a; 1953b; 1954) on the American Coot (Fulica americana). Four of the five elements Gullion described as forming the basis for the American Coot's display - body posture, wing arching, the ruff and the frontal shield - can all be recognised in the displays of Fulica atra. The fifth element, the under tail coverts, which are white in the American Coot, are black in Fulica atra and, although these feathers are used by Fulica atra in various displays connected with alarm and aggression, their function is not apparent. Gullion (1952), however, suggested that the raising of the tail when alarmed occurs in all Rallidae.

Methods of Study

a. Observations and recording of data

During the months of September to March, visits were made to the study area and a census of the coot present was taken at least once a month. The study area, for the purposes of these counts only, also included pasture land on the opposite side of the River Trent since it was found that coot from Attenborough crossed the river to feed on the grass (see figure 1). If disturbed, they would immediately fly or swim back into the Attenborough pits. Since repeated observations during the breeding season in this area only disclosed two pairs of coot nesting on a small lake approximately 450m from the river, it is apparent that the birds feeding across the river should be regarded as Attenborough-based birds. The data were plotted on a 1: 2500 scale map prepared by the Nottinghamshire Trust for Nature Conservation Ltd. from the most recent Ordnance Survey maps and aerial photographs.

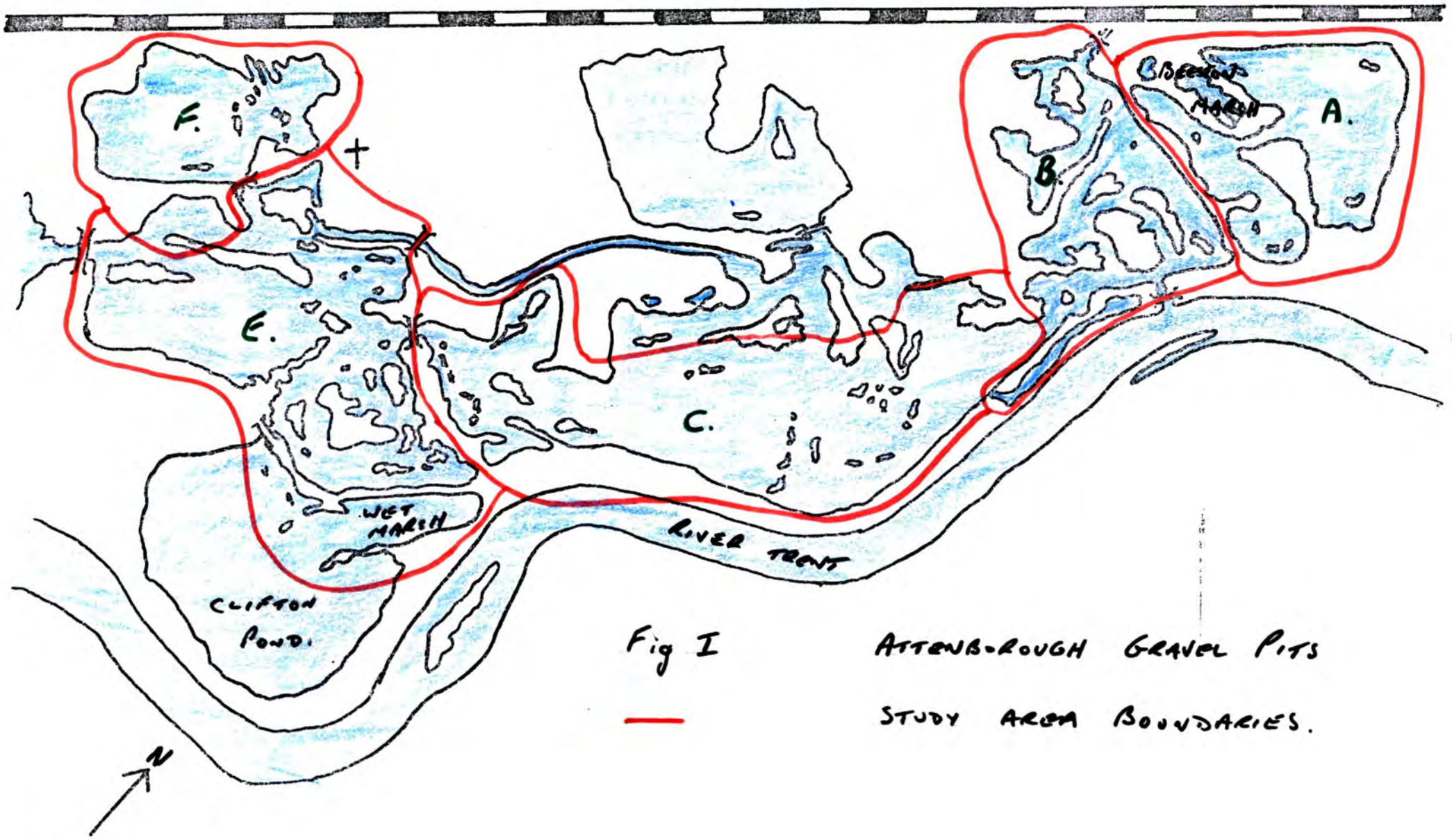


Fig I ATTENBOROUGH GRAVEL PITS

STUDY AREA BOUNDARIES.

The study area was initially divided into six sections, A to F (Figure 1), arbitrarily delineated in size and chosen for convenience of visiting. When the whole of the study area could not be checked at one time, sections A and B were checked together and sections C, D, E and F were checked on the next visit. After the breeding season of 1973 it became apparent that section D was of minor importance, and because it was also difficult to reach it was dropped from the study apart from an occasional visit. Nest sites located in 1973 have been shown on the territorial map (Figure 3) but these and all other data from this area have been omitted from further consideration.

During March to August the area was visited at least once every two days. Particular note was taken of territorial behaviour, inter- and intra- specific aggression, and breeding behaviour. During the two breeding seasons, every territorial coot was checked many times for possible breeding, and itis almost certain that all the nests started in the study area were found.

Every territorial pair was given an individual code based on the section in which it was located. Individually coded 'data sheets' were then filled out in the field at each visit and a copy was kept elsewhere in case of an accident in the field. Information was transferred from the 'data sheets' to a card index system under such headings as 'Description of the Young', 'Mating', 'Food'. During, and at the end of the breeding season, all territories and nests were plotted on a 1 : 2500 scale map.

Visits to nests were made in a two-seater rubber dinghy. This provided a stable platform for recording at the nest and most of the data required were obtained without leaving the dinghy. Nests were generally located by watching from the land with 12 x 40 Ross binoculars. The only area where this method of locating nests was unsuccessful was a small section of Area A known as Beeston Marsh (Figure 1), half of which was open water. The other half consisted of a bed of narrow-leaved reedmace (Typha angustifolia) mixed at its north-east end with broad belts of reedmace (Typha latifolia). Beeston Marsh is a sheltered habitat and in early spring, the Typha latifolia was sufficiently dense to make nest-finding difficult. Later, as the Typha angustifolia developed, this too had to be searched by wading. Fortunately it covered only .07 ha.

As the breeding season progressed, the majority of the time spent in the field was used to obtain data on aspects such as nest size and structure, nest situation, laying dates and sequences, egg size, clutch size, incubation period, hatching and fledging success. These data were also recorded on coded sheets for later analysis. All eggs were marked as they were found and the maximum length and breadth was measured with a vernier caliper to the nearest o.1 mm. Each egg was marked with a number; when more than one egg was present and the sequence could not be determined, then all the eggs marked at the same time were given the same number. Marking was carried out with a red felt-tipped permanent marker "el Marka" manufactured by Paper-Mate. The number was easily seen on the eggs for ten or twelve days and then the eggs were remarked. On one occasion when the eggs of a nest were washed out by heavy floods

one of the eggs marked ten days previously, was subsequently recovered, after two days in the water, some 50m. from the nest site. The number was still clearly visible. Several other methods of marking the eggs were tried but none had the necessary permanency. After marking, the eggs were replaced in the nest with the marked side underneath so that the marking would not disturb the parents on their return to the nest.

In order to assess territory requirements for successful breeding, the vegetation was mapped on a 1 : 2500 scale map. This was mainly the emergent vegetation but also included some Salex spp. Changes in the vegetation were monitored throughout but detailed mapping (Figure 2) was only carried out in late May and early June - the time of peak hatching.

A photographic record was made to illustrate nest site, nest building, hatching sequences, development of the young and breeding and ceremonial behaviour. Photographs were obtained using a 35 mm. camera and 50 mm. and 500 mm. lenses.

b. Analysis of data

The maximum length and breadth of 760 eggs were recorded. Analysis of the data resulting were carried out on a Data General Nova 1220 machine. Most of the remaining statistical work, in relation to clutch size, laying date, laying sequence, territory size etc., was carried out with the aid of a Litton Monroe 1860 calculator.

THE HABITAT

The Attenborough gravel pit complex was designated a Site of Special Scientific Interest by the Nature Conservancy in 1965. Bell (1968), Catchpole (1970) and Hornby (1971) gave extensive descriptions of the physical and dry land vegetational features of the habitat. Bell also described the fauna of the pits and Hornby the methods used to extract the gravel. General accounts of the area (1968; 1975) Plants (1968), Birds (1969) and Invertebrates (1970) have been published by the Nottinghamshire Trust for Nature Conservation Ltd. Plate 1, an aerial photograph dating from 1968, shows the main features of the area. Since this photograph was taken, the section outlined on the Plate 1 overlay has had the gravel extracted and this now forms part of the pit complex.

Figure 2 shows the location of the main plant species or families which were found in the course of the study to be of particular importance to the coot.

Glyceria maxima (reed sweet grass) is the dominant emergent vegetation on the study area. It fringes many islands and it is also found growing in belts one to two metres wide along much of the mainland banks. It is grazed heavily, particularly in early spring, by the coot who seem to use it more as a food source and for nesting material than as nesting cover (Plates 2,3 and 4 illustrate these aspects).

Typha latifolia (reedmace) occurs widely over the study area, but only in a few sheltered habitats does it form extensive beds. It is very important to coot as a food source and for nesting cover and nest material. In sheltered habitats the previous year's emergent

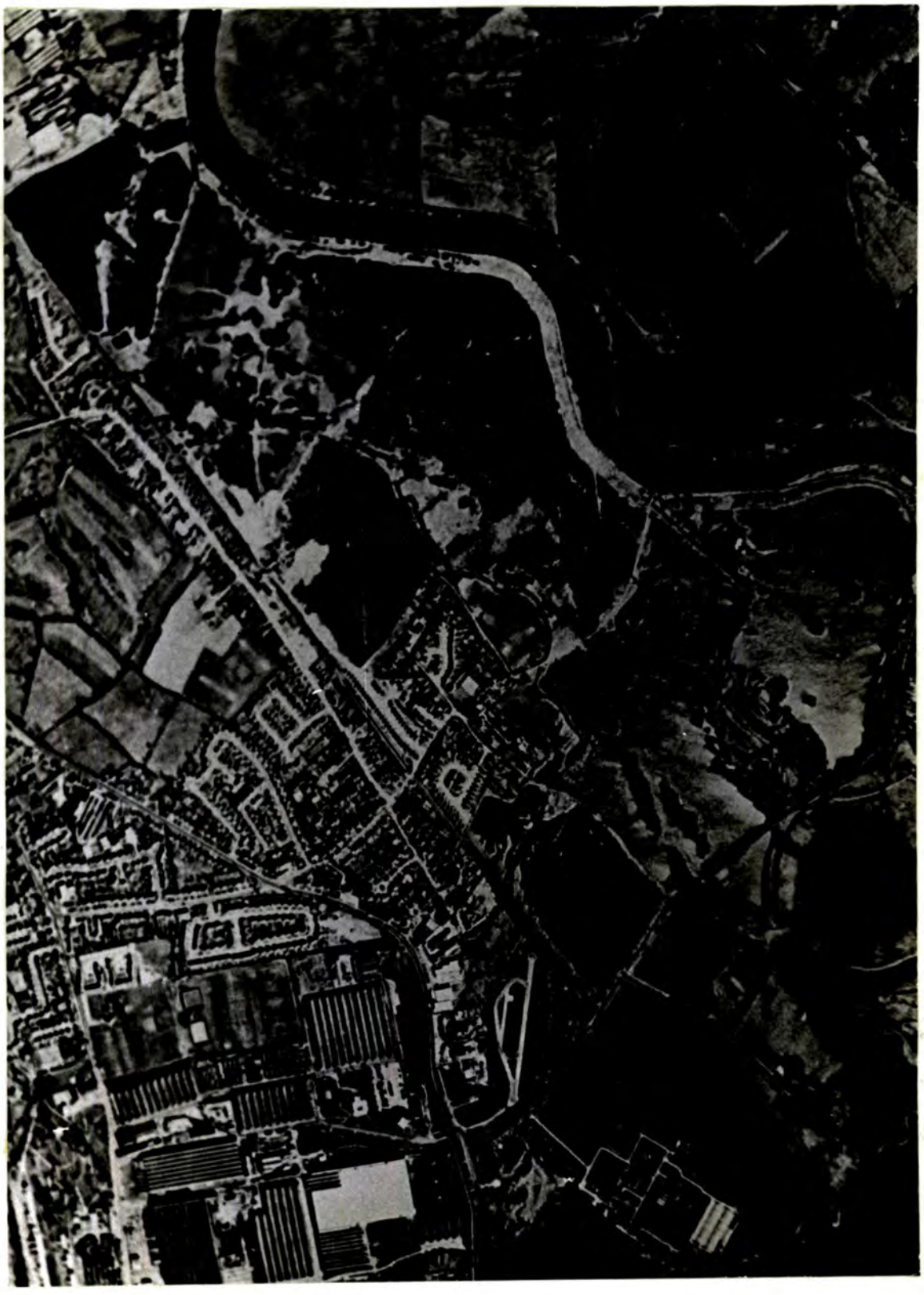


Plate 1 Attenborough Gravel Pits

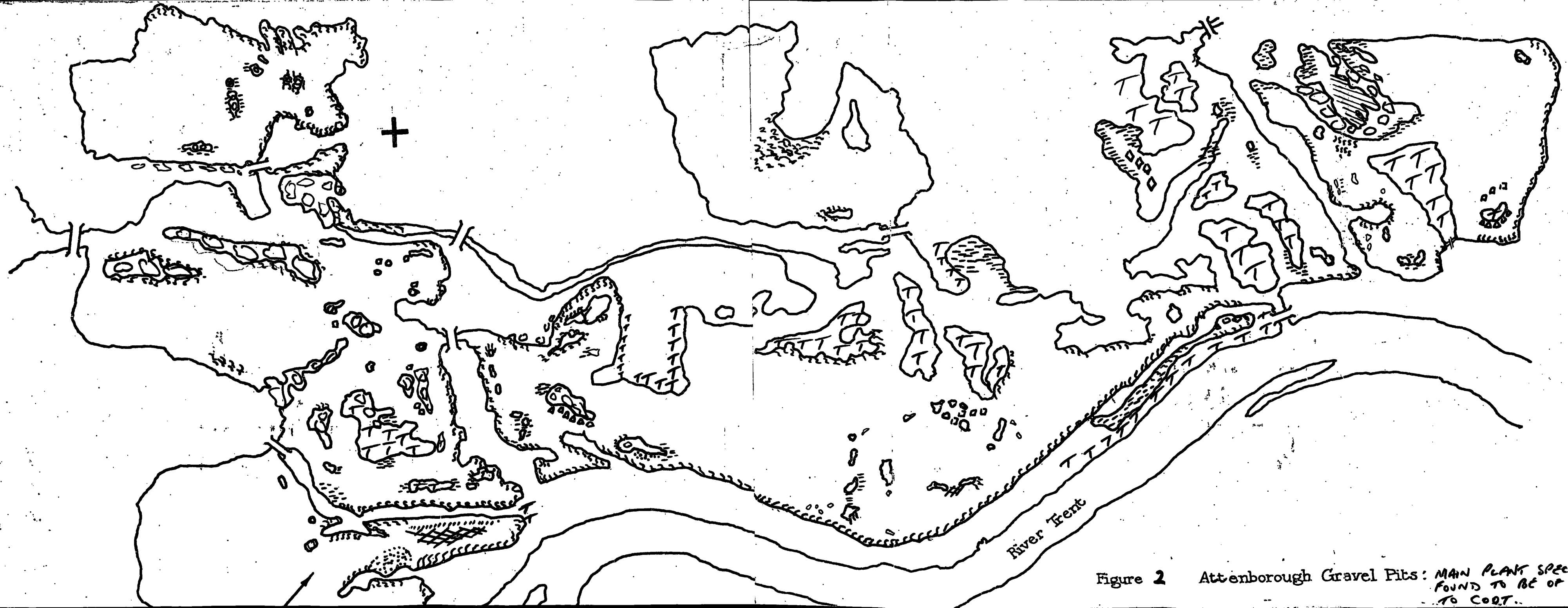


Figure 2 Attenborough Gravel Pits: MAIN PLANT SPECIES FOUND TO BE OF IMPORTANCE TO COOT.

Plate 2 Glyceria maxima fringing an island

Plate 3 G. maxima growing in a belt along the mainland shore

Plate 4 G. maxima showing typical effect of grazing by Coot

growth provides early nesting cover and nest-making material which the coot exploits (Plate 5).

Typha angustifolia (narrow-leaved reedmace) This is found in the study area only in the area known as Beeston Marsh - it is important in that coot use it for food, for nesting material and for nest cover.

Phragmites communis (common reed) is found in several areas of the reserve but in all except the Wet Marsh site (Figure 1), it is found as a 'dry' reed bed. Coot were never found exploiting the latter habitat. The wet Phragmites bed was of importance to coot mainly for nesting purposes.

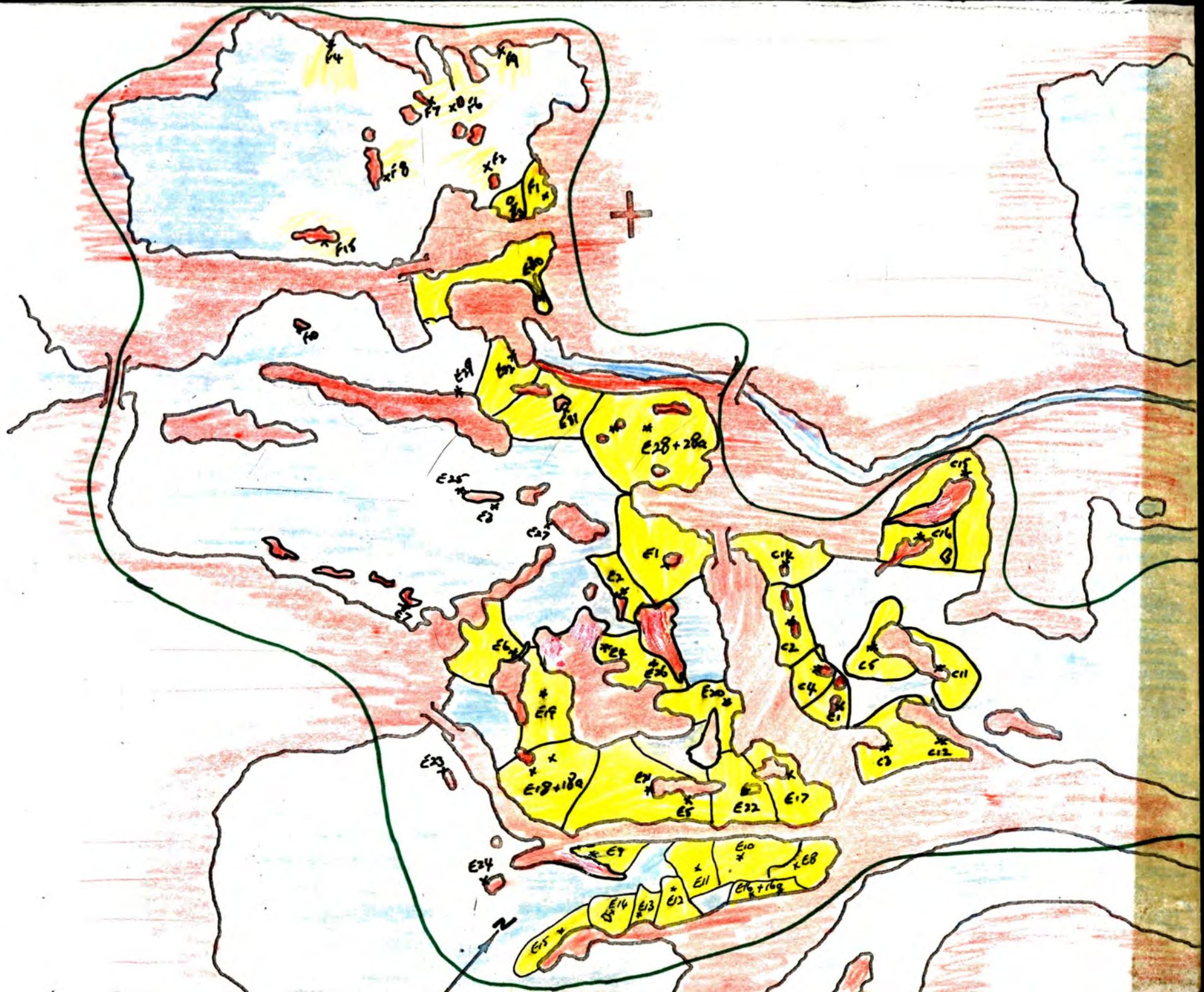
Carex acutiformis (lesser pond sedge) This sedge was only found in any quantity in two small island sites. Both these sites held coot nests.

Juncus spp. Where Juncus spp. occurred as clumps surrounded by water, they were often used by coot as nesting sites. Juncus conglomeratus, acutiflorus, inflexus and effusus were all identified as coot nest sites of this type. Very often only a single clump would exist in a territory and this would be used as the nest site. Dry Juncus areas were checked for coot but as with the dry Phragmites areas they never held any birds. (Plate 6).

Rumex hydrolapathum (great water dock) This occurred as a dense floating 'mat' in the Wet Marsh area. Numerous small indentations on the edge of the 'mat' gave a very enlarged edge line. This area in both years held a high density of breeding coot (Figures 3 and 4). Coot were seen to feed on the leaves, but this plant was primarily used for nesting cover at Attenborough.

Plate 5 Typha latifolia growth from the previous year being used for early cover by a nesting Coot

Plate 6 Coot nest in a typical isolated Juncus spp. clump


F4
F9
F7
F6
F8
F2
F1
F5
F10
E30
E29
E31
E11
E28+28a
E25
E3
E27
E1
E2
E7
C14
C16
C15
C2
C4
C5
C11
E1
C3
C12
E6
E4
E26
E30
E19
E18+18a
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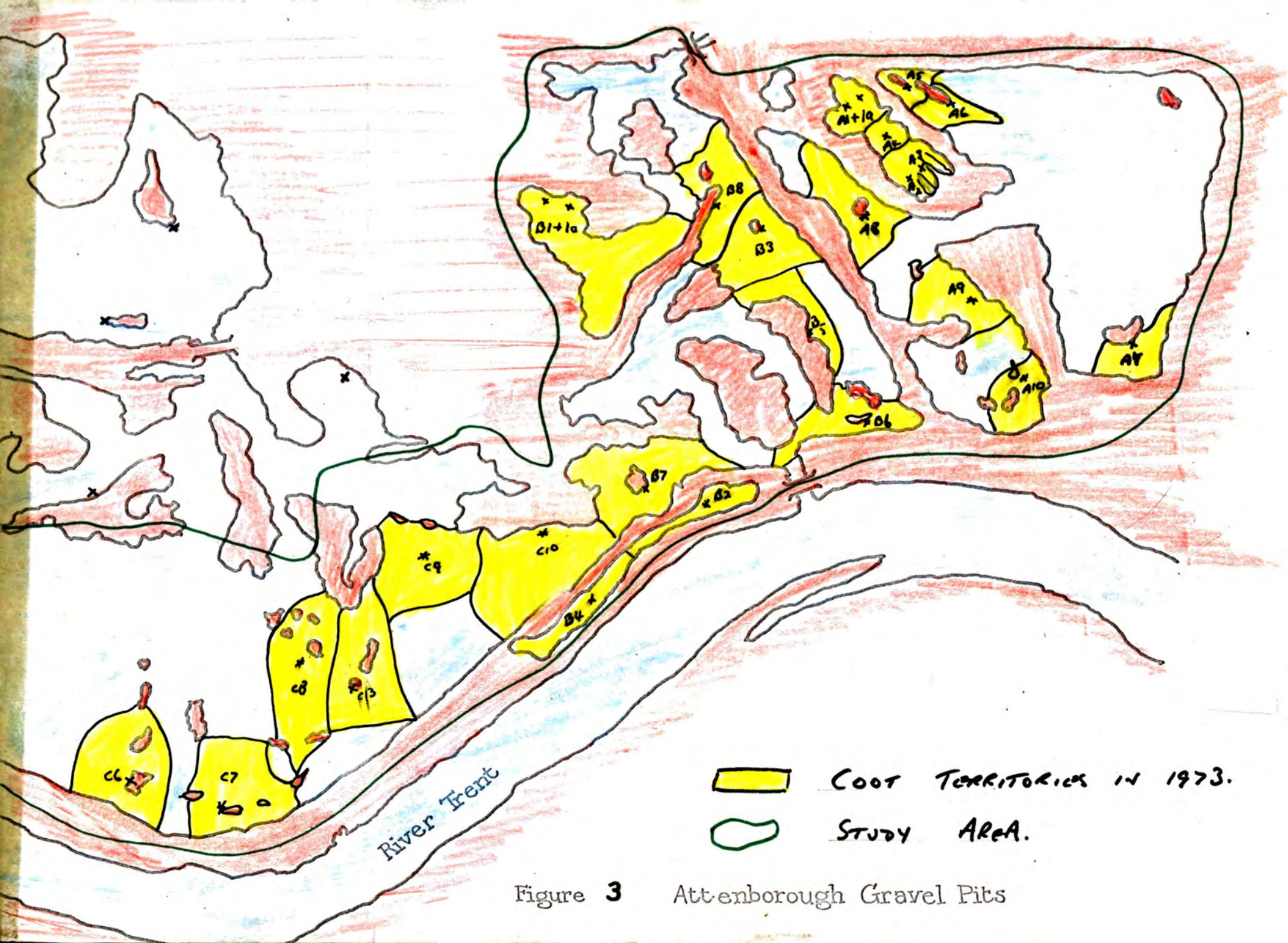

Figure 3 Attenborough Gravel Pits

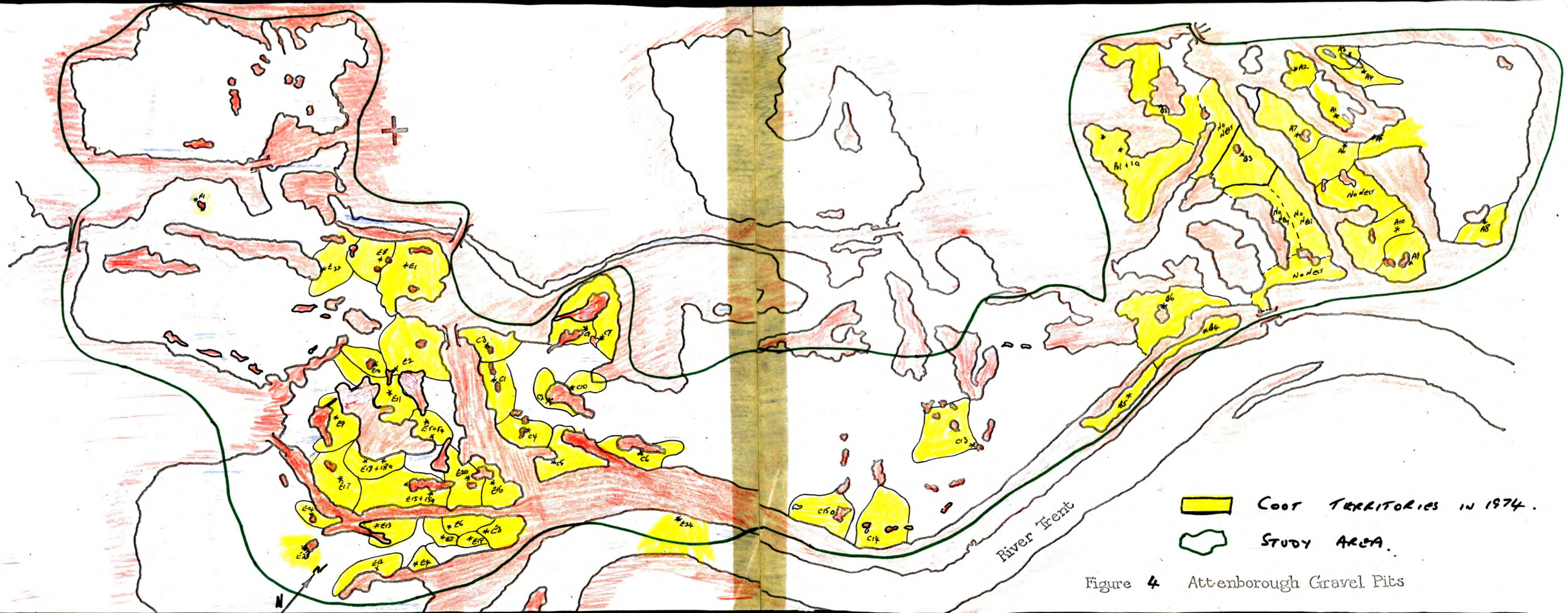

Figure 4 Attenborough Gravel Pits

Polygonum amphibium (amphibious persicaria) This occurs only locally in the study area, but where it does, it is exploited extensively as a food source.

In addition to these emergent species, Salix and Juncus were found to be important as cover and as anchorage points for nests. Coots were, however, never found to breed in areas which did not have some emergent vegetation. Many coot on territory throughout the winter did not attempt to build until after the appearance of a substantial amount of emergent vegetation, even though they had 'safe' Salix sites. This would again indicate the reliance of coot on emergent vegetation for an adequate food supply. Table 1 indicates the nest site choices of coot in the study area.

Recent Changes and Their Effects

The area covered by the pit complex increased from 100 ha. in 1963 (Bell 1963) to approximately 300 ha. in 1972. Although during this time, the size of the reserve remained at 96 ha., the whole gravel pit complex was wardened as if it were a reserve.

The overall ecology of the pits apparently changed little in the period from the end of Hornby's (1971) field work in 1969 until the commencement of this study in the autumn of 1972. One small area within the reserve of importance to the coot, known as Wet Marsh (Figure 1), was however undergoing rapid ecological change. Hornby (1971) mentioned how, since the breaching of the Wet Marsh bank in 1964 and its consequent flooding, the area was gradually becoming wetter and less marshy. This process has continued. Where-as in 1969 Glyceria maxima formed a hover fen growing as a dense floating mat over deep water (Hornby 1971), by the late spring

Table 1

Vegetation at Nest Sites

Vegetation	1973 No. of Nests	1973 % of Nests	1974 No. of Nests	1974 % of Nests
Salix spp.	13	20%	20	44%
Rumex hydrolapathum (great water dock)	4	6%	4	9%
Juncus spp. (rush)	14	21%	6	13%
Typha latifolia (reedmace)	15	23%	5	11%
Typha angustifolia (narrow-leaved reedmace)	1	1.5%	1	2%
Acorus calamus (sweet flag)	1	1.5%	0	0.0%
Carex acutiformis (lesser pond sedge)	1	1.5%	2	4%
Phragmites communis (common reed)	2	3%	3	7%
Glyceria maxima (reed sweet grass)	14	21%	3	7%
Glyceria fluitans (floating sweet grass)	1	1.5%	1	2%
Total emergent vegetation sites	53		25	
Sample size	66		45	

of 1973 this had been largely replaced by a floating mat of R. hydrolapathum with several pure stands of G. maxima remaining around its perimeter. It also contained a small but pure stand of Phragmites and a linear bed of T. latifolia (Plate 7).

Two months after the start of my field work the owners of the pits decided, against the advice of the Nottinghamshire Trust for Nature Conservation Ltd., to breach the River Erewash, south west of the Reserve, in order that they could extract gravel from the other side of this river. The Company had been assured by the Trent River Authority, the predecessor of the Severn-Trent Water Authority, that the waters of the Erewash would continue to flow in the old channel past the breach and would not flow into the gravel pit. Trent Gravels consequently removed some 80 metres of river bank on each side of the river. This enabled the Company's barges to convey the excavated material from the west side of the River Erewash to their processing plant on the east side.

Since the breach was made, water from the Erewash has, in fact, flowed into the gravel pit complex frequently and for prolonged periods. This has caused constant mixing of the Erewash water with that in the pits and substantial flooding has occurred on numerous occasions. It is now admitted by the Severn-Trent River Authority that the water in the Erewash is frequently heavily polluted by the effluent from a local sewage works. A Nature Conservancy Council report of July 1975 stated that, while no catastrophic changes had yet occurred, there was no doubt that ecological alterations had already taken place and that the mixing of Erewash water of the present quality would lead to a progressive impoverishment of the

Plate 7 The Wet Marsh area in winter. In the foreground is the linear bed of Typha latifolia, then the remains of the floating Rumex hydrolapathum and in the background the bed of Phragmites communis

Plate 8 The earth bund; completed in the autumn of 1974 it now effectively divides the reserve into two halves

of the fauna and flora (N. Lewis pers. comm.). It is also suggested that a further consequence is the raising of the ground water level in and around Attenborough.

One remedial measure taken by the Company after consultations with the Nottinghamshire Trust for Nature Conservation Ltd., was to divide the pits by the raising of an earth bund. (Plate 8). The bund, completed in October 1974, has effectively stopped the water flow from the Erewash River and the southern pits into the northern end of the nature reserve. In order to try and control the water level in the southern pits, a new weir was put in a short distance in front of the bund.

The long term effects of these major changes on the coot is hard to predict. The monthly winter counts (Table 2) on the reserve, made on Wildfowl Trust count days, indicates, in spite of the remedial measure taken, an overall drop in the number of wintering coot since the Erewash was breached. This drop in the wintering coot since November 1972 was found to be highly significant. ($d = 4.90$, $P < 0.001$). A possible reason for the drop in winter numbers is the higher water level generally in the pit complex and the heavy sweeping floods which from November 1973 have inundated all the pits periodically. Since the bund was built, these have affected only the southern half of the reserve and pits. The effects of these floods on the breeding coot will depend on changes it causes in the emergent vegetation. It was obvious that the quantity of emergent vegetation which survived the winter was less over much of the area in 1974 than in 1973. The effect of the floods on the coot is complicated by the pollution now entering the

Table 2 : Numbers of coot on the Attenborough Nature Reserve 1968-1978

Data collected on Wildfowl Count Dates

YEAR	SEPT.	OCT.	NOV.	DEC.	JAN.	FEB.	MARCH	SUM OF COUNTS SEPT. TO MARCH	MEANS
1968-69	194	128	68	250+	200+	150	108	1098+	156
1969-70	200+	198	154	202	76	300+	53	1183+	169
1970-71	274	240	162	124	228	128	118	1274	182
1971-72	152	120	151	130	165	95	119	932	133
1972-73	285	235	247	168	158	165	162	1410	201
1973-74	84	78	124	124	109	126	74	719	102
1974-75	56	102	46	62	106	74	45	491	70
1975-76	111	118	128	106	112	195	125	895	128
1976-77	127	93	72	116	148	69	160	785	112
1977-78	68	66	60	86	96	88	81	545	78
Sum of counts 1969-1978	1551+	1378	1212	1368+	1398+	1390+	1045	9332+	
Means	155	138	121	137	140	139	105	932	

pits. Both Wagner (1962) and Büttiker (1949) pointed out that the coot inhabits waters which are rich in nutrients and Wagner agreed with Büttiker who stated that coot are "indirect beneficiaries of eutrophication", and that the species can be regarded as an indicator of polluted waters. If this were so, then the coot should directly benefit from the organic pollution now entering the pits. At the same time, the choice of emergent vegetation nest sites could diminish if the flooding continues and if it reduces the amount of emergent vegetation available appreciably.

The policy of management since the designation of the reserve in 1966 has been to increase the number of ecological niches available in order to increase the diversity of the species present. This policy has in the past probably had little effect on the coot as management efforts have been concentrated on the dry land areas. However, the placement of the bund has allowed the general water level of the pits north of the bund to be controlled artificially by the manipulation of a new weir.

The management policy with respect to this northern area is:

1) to leave uncovered large areas of soft mud to attract wading birds when they are on autumn and spring passage along the River Trent.

2) to plant some wet areas with beds of Phragmites.

The effect on the coot of 1) will be almost certainly detrimental and probably will act by:- a) reducing the amount of aquatic vegetation available in the winter; b) reducing the area of open water in the autumn and the spring; c) possibly reducing the amount of emergent vegetation in the spring. The long term effect of 2) will

depend largely on the nature of the Phragmites beds that are formed. If they stay as wet beds then the coot will almost certainly benefit greatly with respect to both food and nesting cover. If, however, the habitats created are allowed to evolve into dry Phragmites beds then it is unlikely that the coot will try to exploit them.

TERRITORIALITY AND BREEDING

Territorial Behaviour

In the following discussion a territory is defined, using the criterion of Tinbergen (1957) as a 'defended area'.

Territorial Fidelity from Year to Year.

None of the research so far (Ruthke 1939: Kornowski 1957: Blüms 1973) has been able to show conclusively that a pair of coot have over-wintered on their breeding territory. Cramp (1947) reported that a pair which had failed to breed in two successive seasons maintained their territory throughout the winter and were still on territory when his observations ceased in mid-June. He does not, however, give any evidence as to how he identified the individual birds. The abandonment of territory and loss of territorial activity in coot, brought about by ice or flooding was first reported by Huxley (1934). Kornowski (1957) and Wagner (1962) both recorded this type of breakdown of territory accompanied by an absence of territorial strife. Kornowski (1957) like Huxley (1934) also recorded individual coot defending a section of their territory while the majority of their territory was ice-bound. The ability of Rallidae to return to a previously occupied territory has been demonstrated by Gullion (1953a) who found that experimentally removed immature American Coot returned to the territory of their birth from distances of 50 km.

At Attenborough territorial breakdown occurred on only three occasions. Two of these cases occurred in winter when ice covered large areas of water and the only ice-free areas were kept open by the gravel barges. Large numbers of coot were feeding together in

the ice-free channels and on some nearby grassland. The third occurrence was noted in early spring when the whole pit complex was flooded to a depth of over 1 m. The coot deserted the water and spent most of the time feeding communally on nearby grassland. In all three cases the previously held territories were filled again as soon as conditions returned to normal. It is believed, on the basis of observational data, that the territories were re-occupied by the original displaced pairs.

No example was seen where a coot abandoned territory because of intraspecific aggression. Fifteen pairs failed to lay while occupying a territory but observations suggest that this was not caused by intraspecific aggression. The fact that a pair of birds was unable to produce eggs did not apparently cause territory abandonment (see Table 3 and fuller discussion in section on Seasonal Fluctuation in Numbers). The non-laying pairs seemed no more susceptible to domination by successfully breeding pairs than laying birds.

It is believed that, at Attenborough, 19 pairs held their territories over the study period of 24 months. For many of these pairs identical nest sites were used in both years, territorial boundaries appeared to be the same, as did particular spots for preening and roosting. In some cases such as pairs E28, E1 and C14 (1973) even the feeding behaviour was distinctive. For example pair E28 spent many hours scavenging off the food left by fishermen and eating grass on the nearby car park; at the same time pair E1 would be feeding on freshwater mussels they collected by diving in the barge channel (see page 205). Pair C14 seemed particularly adept at feeding in

Table 3 : Abandonment of territory during the breeding season.

1973 Data

Month	No. of Pairs on Terr. at Start of Month	Pairs abandoning territory. which never laid	which lost all eggs	which lost all young	No. of Pairs on Terr. at End of Month
April	75	0	1	0	74
May	74	0	3	0	71
June	71	2	4	0	65
July	65	1	0	0	64
August	64	1	0	0	63

1974 Data

April	60	0	0	0	60
May	60	0	4	0	56
June	56	2	6	7	41
July	41	3	1	1	36
August	36	2	0	0	34

and on Salix bushes. They were seen at various times eating leaves and catkins and were twice seen climbing about in the Salix bushes which fringed part of their territory. Many other coot had the opportunities to exploit similar feeding situations but none were seen to do so at the same intensity as the pairs mentioned.

Some coot, such as pair E15 in 1973 (Figure 3), apparently remained faithful to a territory throughout a winter and then the following breeding season, often constructing nests but apparently never laying any eggs. Pair E15 built three large nest sites, all with substantial ramps and one with a nest cup, between the 20 April and 4 July. The defended the area vigorously, both intra and inter-specifically but never laid any eggs.

The coot for which there is other than behavioural or territorial evidence regarding successful breeding in the same territory for at least two years, is for the female of the territory designated B1 in 1973 and 1974. This female laid a series of exceptionally large eggs (Plate 9) in both seasons and the probability of finding two different birds in successive years on the same territory that laid eggs with mean lengths far greater than normal (see page 116) is so small as to be negligible. It is assumed that this was the same female coot on the same territory in successive breeding seasons.

Observations at Attenborough suggest that in mild winters in England it is possible that many of the coot which are either successful breeders i.e. hatch eggs, or are non-breeders (do not lay eggs) overwinter on their territories. The unsuccessful breeders i.e. those that fail to hatch eggs which have been laid, usually abandon their territories in late May / early June (see page 43).

Plate 9 The clutch of B1 in 1973. Note the two exceptionally large eggs. The egg in the foreground is the largest (65.1 x 39.5 mm) recorded in literature

Plate 10 Some of the 70 adult Coot which were counted at Martin Mere on June 16th 1976

Seasonal Fluctuation in Numbers and Territoriality.

a. In spring and summer.

Höhn (1949) found non-breeding, non-territorial, adults present throughout the breeding season. He did not state when he first noticed them, only that by July 8 at Feltham none had young and at Slough on June 14 fifty coots were without a single young. Sage (1969) in refering to the size of a non-breeding populations at Hilfield Park Reservoir - Hertfordshire, suggests that the flock included failed breeders from elsewhere. Wagner (1962) recorded large flocks of non-breeding, non-territorial coot building up in June and July. He made the statement that a flock of coot "including adult birds" began to congregate in June. (See Discussion regarding the validity of this statement).

At Attenborough in the spring and summer of both 1973 and 1974 all the coot present in the study area were holding territories but not all the territorial pairs finally bred (Table 16). The study area also contained many neutral areas (Figures 3 and 4) which did not form part of a territory. Coot were rarely found here but some areas of the gravel pit complex outside the study area did contain a few non-territorial birds, the maximum count in May 1973, and May 1974 being 9 and 7 birds respectively. There was no increase on these numbers in either June or July.

Although an early build-up of non-breeding coot did not occur at Attenborough, some recent observations I have carried out at the Wildfowl Trust refuge at Martin Mere, Lancashire confirm non-breeding coot arriving during the breeding season. On a 5ha. artificial mere created in 1975, over 70 non-breeding, non-territorial coot were

counted on June 16 th 1976 (Plate 10). On the same date at least five pairs of coot had small young on this water and several other pairs were incubating eggs. The nesting coot were all holding territories and the non-breeding coot were subject to agonistic behaviour whenever they approached an occupied territory.

Analysis of the Attenborough data (Table 3) provides a clue in 1974 to the identity of the birds that make up the summer flocks on non-breeding coot in other areas. Of the 75 pairs in 1973 that held territories at the beginning of April, some 63 pairs were still on their territories at the end of August. The birds that maintained territories but did not lay had at least as strong a territorial fidelity as birds that lay and subsequently lost their eggs or young. Five pairs still had young birds on territory with them at the end of October. During 1974, the rate which territories were abandoned because of failure to breed was much higher. Birds abandoning territories invariably left the gravel pit complex completely, whereas most of the successful coot remained on territory (with their young) until at least late August. This study confirms the findings of Nylund (1945), Wagner (1962) and Blüms (1973) that late August is the time that successful coot start to abandon territory.

The above study suggest that the majority of coot appearing on some waters from middle May onwards, with a rapid increase in numbers in June and July, are failed breeders from elsewhere. Sage (1969) suggested this for some of the birds in these summer flocks but the very early dates for territorial abandonment for failed breeders has not previously been documented.

b. In autumn and winter

The population of coot at Attenborough has fluctuated between 285 birds in September 1973 and 56 birds in September 1974. Whereas previous personal observations from 1964 onward had always indicated a large influx of wintering coot into Attenborough in the autumn, in September 1973 and September 1974 the overall population declined as some territorial pairs and most of the independent immatures moved out and none moved in, leaving only the wintering territorial birds (Table 2). Counts (Table 2) made since November 1972 by the Wildfowl Trust indicate that this reduction is significant (see page 37).

The BTO Common Bird Census figures for territorial coot and the Wildfowl Trust count figures for wintering coot, were checked for any correlation ($r = 0.67$, $P > 0.1$) between numbers of wintering coot and the number of pairs on territory in the spring (Table 4). Although the correlation coefficient (0.67) was high the low probability figure indicates that there was insufficient data available to make the correlation meaningful. Reliable figures on the number of territorial coot in the years preceeding 1972 are not available (K. Corbett - pers. comm.).

Establishment and Defence of Territory

The aggression associated with the establishment and defence of a territory by the coot is the most evident behavioural activity of the species according to Huxley (1934), Boyd and Alley (1948), Kornowski (1957), Bezzel (1959), Wagner (1962) and Blüms (1973). Huxley (1934) and Kornowski (1957) have reported that the European Coot often defend a larger territory in winter than it subsequently utilises for breeding. This is contrary to the conclusion of

Table 4 : Numbers of wintering coot and territorial pairs.

Date	Monthly mean number of wintering coot* (Sept to March)	Territorial pairs (BTO Census figures)
1971/72	133	50
1972/73	201	67
1973/74	102	62
1974/75	70	42
1975/76	128	46
1976/77	112	41
1977/78	78	NO DATA

* Calculated by finding the mean of the sum of the counts from September to March (see Table 2).

Gullion (1953a) on the American Coot which he found defends a winter cone area and then expands its territory as the breeding season approaches.

On the continent many workers (Huber 1934: Ruthke 1939: Nylund 1945: Kornowski 1957: Melde 1959: Wagner 1962) have attempted to ascertain whether or not the coot is paired when it arrives on territory. The only display to be associated so far with pair formation (Kornowski 1957: Wagner 1962) is concerned with mutual preening. Ruthke (1939) believed that the males arrived on territory first but he was unable to distinguish between the sexes. He also failed to observe any behaviour he could place as part of the pairing ceremony. Wagner (1962) found, contrary to Kornowski (1957), no evidence that coot were paired when they arrived on territory. Nylund (1945) stated of the two pairs kept under 'special daily observation' that 'before the nesting season proper, the male and female do not show any interest in one another, although living in the same territory'.

Kornowski (1957) and Wagner (1962) in describing the territorial behaviour of European Coot used the same terminology as that used by Gullion (1952) to describe Fulica americana. I also have used Gullion's adjectives, which are underlined, to describe eight aspects of behaviour of Fulica atra that are similar to that of the American Coot.

The territorial coot at Attenborough regularly patrolled the boundaries of their territories. Boundaries were apparently fixed in relation to points of land, small islands, clumps of, or breaks in the emergent vegetation, and obstacles in the water. These were, in most cases, fairly easy to recognise and map as the birds at

Attenborough patrolled (Plate 11) whenever they were swimming near their boundary.

When a coot charged very rapidly its neck was sometimes awash with water (Plate 12). If the charge alone was unsuccessful in turning aside the violater of the territory, then the coot usually rose into the splattering display in which the bird runs across the water with flapping wings. If the object of the display was another coot then usually it turned and retreated in a similar manner (Plate 13). If this happened the attacking coot usually subsided into the water within a few m.

Paired display (Plate 14) was again easily identified in coot and it proved to be one of the most useful means of identifying territorial boundaries. Two or more rival coot meeting on a territory boundary would go into paired display, the wings are arched high over the back and the birds slowly moved around one another. The display apparently subdued hostility so that fighting did not occur. However, it only reduced hostility levels when it happened on territory boundaries.

My observations on paired display (Plates 15 and 16) on Fulica atra is the same as Gullion's (1952) on Fulica americana. Paired display is aggressive, and not sexual, behaviour.

Fighting was the final act in the establishment and defence of territory. I always found it occurred when the resident coot did not receive a retreat response from another coot which was seen as an intruder. Fighting also occurred (as also noted by Klomp (1972)) when the threat by the resident bird caused the intruding coot to retreat but even in retreat it was closely pursued until it turned to fight. Although fighting appeared to be vicious it

Plate 11 Coot patrolling near its territorial boundary

Plate 12 A pair of Coot charging at a territorial violator

Plate 13 The Coot on the left is splattering at a rival. Note the different positions of the head and neck

Plates 14, 15 and 16 Three photographs illustrating different aspects of paired display

was usually soon over. The vanquished coot was often forced to escape underwater and once, after a particularly violent encounter, the winner pursued the loser under the water, both birds breaking the surface on three separate occasions. Fights usually started with just two birds but as with other coot displays, especially paired display, the respective mates are often pulled into the conflict. One such fight started with both birds charging, going into paired display, and retreating each into their own territory and then one bird charged again and fighting started.

There was much calling from both fighting coots, this immediately brought in a third bird and the paired birds started to give the single bird a buffeting. The single bird's loud calls brought in the fourth coot at a splattering run. Just as this bird approached, the three fighting coot broke apart. The incoming bird attacked its own mate, as if it had mistaken it, for several seconds. As fighting ceased all four birds went into paired display before returning to their own territories.

That there has to be a recognisable threat to the bird on territory by the bird that trespasses, was suggested by the behaviour of three territorial pairs towards an injured coot. This bird was seen struggling in some reeds in late April. It was caught very easily, it apparently could not dive, fly or walk. Its legs hung uselessly but there was no obvious injury; when released it moved away across the water using its wings to propel it; the legs trailed like rudders behind it. As it passed through the territories of three pairs of coot they went into the charge position, two pairs actually splattering into the attack. The injured bird attempted

to evade them but it had little control over its direction and it pursued a very erratic course through the territories. All the birds on territory approached closely to the injured bird, one bird actually buffeted it as it dropped out of its splattering run, and appeared to be about to attack. Each coot in turn, however, suddenly ignored the injured coot and returned to normal territorial activities. Paired display was not evident from the territorial birds and I can only assume that the injured bird did not give out the normal threat stimuli and that, therefore, the normal threat response was not evoked from the birds on territory.

During swanning (Plates 17, 18, 19 and 20) the coot arches its wings low over its back, lowers its head and raises its neck feathers. The white stripe down the leading edge of the wing and the white indistinct tips on the trailing edge of the secondaries, help to create the illusion that the bird is larger than it actually is. Swanning was only seen used in interspecific situations, against the brown rat (Rattus norvegicus)once, the canada goose three times, the mallard and the great crested grebe several times. It was also seen in defence of eggs or small young. Plate 7 shows both birds of pair A1 in 1973 defending their eggs against man by swanning. When swanning did not succeed in driving away the intruder, both birds of this pair retreated for about five m. and started displacement feeding.

Plate 21 shows a coot from A1 in 1974 (almost certainly the same bird as was on this territory in 1973 and featured on Plate 17), swanning at a colleague who is checking the nest. Although the male did on occasions help with this defence (Plate 22)

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Plate 17 Typical Coot aggression towards man, in defence of their eggs

Plates 18, 19 and 20 Typical Coot swanning positions

Plate 21 Female Coot from A1 site in 1974 trying to defend her eggs by swanning

Plate 22 Churning used as a nest defence against man by the A1 site pair

it was never as pugnacious as the bird presumed to be the female. The 'female' never attempted to press any attack to the point of making physical contact but she did, on at least three occasions in 1974, start to churn the water as she moved parallel to the nest at a distance of 5 or 6 m. When churning failed, she joined her mate and resumed distraction feeding about 12 to 15 m. away.

Coot have been recorded as pressing home an attack on Man when swanning has failed to drive away an intruder, Hawkins (1932) reported that on three separate visits to a nest, an adult coot frequently struck him on the leg and hand and even climbed up him as he investigated the nest.

Churning (Plate 22) a vigorous pounding of the water with both feet which raises the coots body out of the water as the bird moves backwards, is usually used when swanning fails to displace an interspecific aggressor. It was, however, recorded without swanning when I suddenly came upon a brood of four day old coot feeding with an adult on the bank. The adult immediately jumped into the water and started to churn calling with very high pitched notes to the young. Churning continued while the adult retreated from the bank taking the young with it. After covering about five m. the bird dropped on to the water and led the young away. Churning following swanning was seen in an attempt to defend a nest, of chipping eggs, by the pair A4 in 1974. The nest had been approached across open water in the dinghy and both adults retreated about ten m. behind the nest. As the eggs were checked one of the adults came within 1 m. of the boat and started swanning. Swanning continued for the two minutes it took to check the eggs but as the boat was moved away from the nest, the bird commenced churning the water. Paddling

towards the bird caused it to retreat for at least ten m. by churning, all the time maintaining a constant distance between us. Suddenly the churning bird dropped on to the water; turned and fled in a splattering run. The run lasted some 45 m. and took it across the corner of another territory, the owner of which pursued it for several m.

Churning was also used during interspecific aggression by an F2 adult on 4 June, 1973. Both coots were feeding small young on the edge of the marginal G. maxima when a brown rat swam towards the group. The rat was about 1 m. into the open water and some 3 m. from the young coot when one adult coot suddenly charged at the rat without any previous warning that I could discern. The coot appeared to strike the rat in its back and pushed it under the water, the next moment the rat was on the bank having crossed at least 0.5 m. of G. maxima. The coot pursued it into the vegetation for a short way and then jumped back into the water. As the rat moved along the bank behind the vegetation the coot moved parallel to it in the water stopping to churn the water every few seconds. Again the rat appeared on the water's edge and the coot raced in to churn and then attacked. The rat fled inland but the coot stayed for several minutes calling and patrolling the water's edge before rejoining its mate.

The above observations on churning behaviour do not confirm Gullion's (1952) comment that it is "primarily a displacement activity". It was always recorded as a hostile action aimed at driving away an interspecific intruder.

Although coot defend their territories vigorously against

intraspecific intruders, many large winter territories were compressed (Huxley 1934) as the breeding season progressed. Other large territories were held intact throughout the year.

An example of a compressible territory was that of the pair E8 in 1973. From the start of this study two birds were showing agonistic behaviour towards other coot over half the Wet Marsh area. At this time pair E8 was trying to defend an area that subsequently held four other breeding pairs, as well as a neutral area. During the winter months the two resident coot were seen many times making aggressive runs at other coot that were feeding in the area. These acts of aggression, however, were not continuous and on many occasions other coot would be tolerated throughout the whole area and even within the area that subsequently comprised E8 breeding territory. At other times, both birds would suddenly start to drive other coot from the area. On one occasion (January 1973), one bird was watched for 40 minutes while it drove seven other coot out of the Wet Marsh area into the open water of Clifton Pond (Figure 1). By mid-February, however, aggression was declining and by the middle of March, three other pairs were occupying territories. The female of E8 started to lay at the beginning of April as did E12 while E10 and E11 had eggs by mid-April. A fourth pair E16 then finally 'carved' out a territory and had a complete clutch by 8 May. A similar situation occured in 1974: E8 pair remained on territory throughout the winter of 1973/74 while all the other coot, that held breeding territories in close proximity to E8 apparently gave up defending their territorial boundaries and were mixing freely over the whole area (other than the territory of E8). The E8 pair behaved exactly as in the winter and spring of

1972/73 in that they fought for and held large areas of the Wet Marsh, only to relinquish it again as the breeding season progressed.

Many of the territories which were not compressible were larger than average and were held in bays or 'anchored' to large islands. In most cases this cut down the length of territorial boundary to be defended. The largest territory in both years, E28 in 1973, E1 in 1974, was a territory of this type. Although this territory in 1973 was 1.25 ha. and the overall coot breeding population was high, the resident coot only had to defend a water boundary of approximately 110m. In 1974 when the overall population level was less, they extended their territory by 0.12 ha. (an increase of 8.7%) but to do so they had to defend a water boundary of approx. 170 m. (an increase of 65.0%).

The larger territories were all in more open areas with little emergent vegetation. These territories apparently attracted very little hostility from territory seeking coot. This is thought to be because the birds seeking territories spent more time trying to win territories in the areas with more emergent vegetation. It was in areas with large amounts of emergent vegetation that most aggression was noted and that territories were at their highest densities.

Aggression at Attenborough occured in all seasons but in winter such aggression was always associated with pairs still holding territory and was almost always intraspecific. The only inter-specific aggression seen in winter was towards the moorhen. New territories were established in the spring by both birds of a

pair. During the time the territory is maintained it is defended by both adult coot.

Almost all the distinctive behaviour of the coot is aggressive in character, apart from the behaviour associated with mating and care of the young. The only behaviour which is recognisably not aggressive and which occurs throughout the year is nibbling.

Nibbling (Plates 23 and 24) is usually carried out after the two adults have been apart for some time. It may be only a momentary gesture or it can last for several minutes with each bird taking it in turn to nibble the other around the head and neck. It takes place on land or in the water.

As the paired coots at Attenborough approached one another on the water they normally turned a circle, gradually getting closer; one then usually turned its head on one side, at the same time lowering its bill. The other bird, at this inciting behaviour, usually started to nibble in the feathers of the head and neck of its mate. The bird being nibbled appeared to push its head at the beak of its companion and actually dictated which part was to be dealt with next. When the nibbling bird wanted reciprocal treatment it stopped nibbling and pushed its own neck or face at its companion - it was sometimes several seconds before any notice was taken of this change of behaviour. On several occasions coot were seen to come together, one going into the submissive posture which was used to incite nibbling, only to be ignored by its companion. Normally when one bird broke off they both turned and swam away from one another without any further ceremony.

Nibbling was seen on land on the 16 August 1974 by the E1 pair.

Plates 23 and 24 Two sequence shots showing nibbling in progress. Note how in Plate 24 the bird being nibbled gradually sinks its bill below the water

Both birds were standing on the mud when one lowered its head until the bill pointed directly downwards and the neck feathers became ruffled. It then pushed its head and neck at its mate. But the other coot went through exactly the same process until both birds stood facing each other with lowered head and ruffed out neck feathers. They stood like this for approximately 90 seconds before one bird raised its head and started to nibble the head feathers of its companion, gradually working around to the neck feathers. After about a minute the one being nibbled just stepped away into the water and swam off. The other bird started to preen itself without any sign of further ceremony. (Later in C1 area two moorhens were observed standing on the bank in almost identical positions except that they remained facing one another for several seconds after one bird had nibbled around the face of the other).

Only on two occasions was nibbling seen to be associated with any other recognisable unit of behaviour. On 25 August 1974, the birds from C3 area (Figure 4) were in the abandoned territory of C1 pair. One of the adult coot swam to the base of the ramp of the old nest of C1 pair. It started to preen on the base of the ramp, pulling out a feather it climbed the ramp and placed the feather in the nest - however the wind blew it out. The bird then turned and faced down the ramp towards its mate now swimming at the base of the ramp. The bird on the nest started to stamp (see section on nesting behaviour) in a desultory manner. The swimming coot then came on the ramp, the two birds were facing each other and they started to preen themselves. Both stood fully upright and preened their breast feathers; as they did this they seemed to make an effort to show

their neck feathers to one another. The bird at the base of the ramp climbed up the ramp and offered its head in the bowing attitude to its mate. Both birds then nibbled at each other for 6 minutes working around the face and the back and side of the neck. At last the first bird on the nest stopped nibbling - the other bird immediately pushed in on it, bowing its head and apparently trying to incite it to continue. The bird which had stopped however, sidestepped and walked down the ramp into the water. The bird still on the nest started to preen and remained preening for 25 minutes. (At this time two immature coots which had hatched on the 1 June (89 days old) were still in the territory.)

The other occasion when nibbling with other recognisable behaviour was observed was on the 4 April 1974 in E2 territory. The female (presumed) was sitting on a clump of Juncus spp. when the male came up behind her and attmpted to mount her. The female, however, pecked at him and started to swim away. The male followed closely and the female kept turning her head to nibble him around the head - the male responded by nibbling the female also. They proceeded across the water like this for about 15 m. before the male turned and swam away.

The observations that nibbling occurs throughout the year confirm the findings of Wagner (1962) who recorded that he saw it once in October and also recorded it as a frequent occurrence with some young coot he reared, until by the age of six months, only the male was being nibbled.

Nibbling is carried out infrequently but throughout the year at Attenborough. Observational evidence supports the view that it

is concerned with pair bird maintenance behaviour. It could be involved with pair formation as well, but observations to support this view were not obtained as, by the time they were seen at Attenborough, all the birds seemed paired.

Wagner (1962) suggested that the actual aggression shown by coot in establishing and maintaining a territory could in itself be behaviour associated with pair formation and maintenance. The difficulties of testing this theory under field conditions made it beyond the scope of this study.

Size of Territory

Cramp (1947) mapped eight territories in 1943 in St. James's Park, London; sizes ranged from 0.12 ha. to 0.44 ha. Askaner (1959) mapped 20 territories in Sweden, mean size was 0.25 ha. with a range of 0.08 to 0.47 ha.

Not all the territories at Attenborough were mapped - the most difficult ones to map being those adjoining neutral areas. Because of the neutral area, border conflicts of an intraspecific nature were few and thus the opportunity for plotting agonistic behaviour were much reduced. The main mapping effort in 1974 was on areas that had already been covered in 1973. Mapping covered 56 territories in 1973 and 43 in 1974 (Figure 5). The mean territory size in 1973 was 0.44 ± 0.04 ha. and in 1974 0.48 ± 0.04 ha. Territory size varied widely: the smallest was that of A3 (1973) with an area of 0.09 ha., the largest was some 15 times larger at 1.37 ha. (pair E1 in 1974).

The largest territory (E1 in 1974) had only a very small amount of emergent Glyceria maxima: it did however have 3 small clumps of

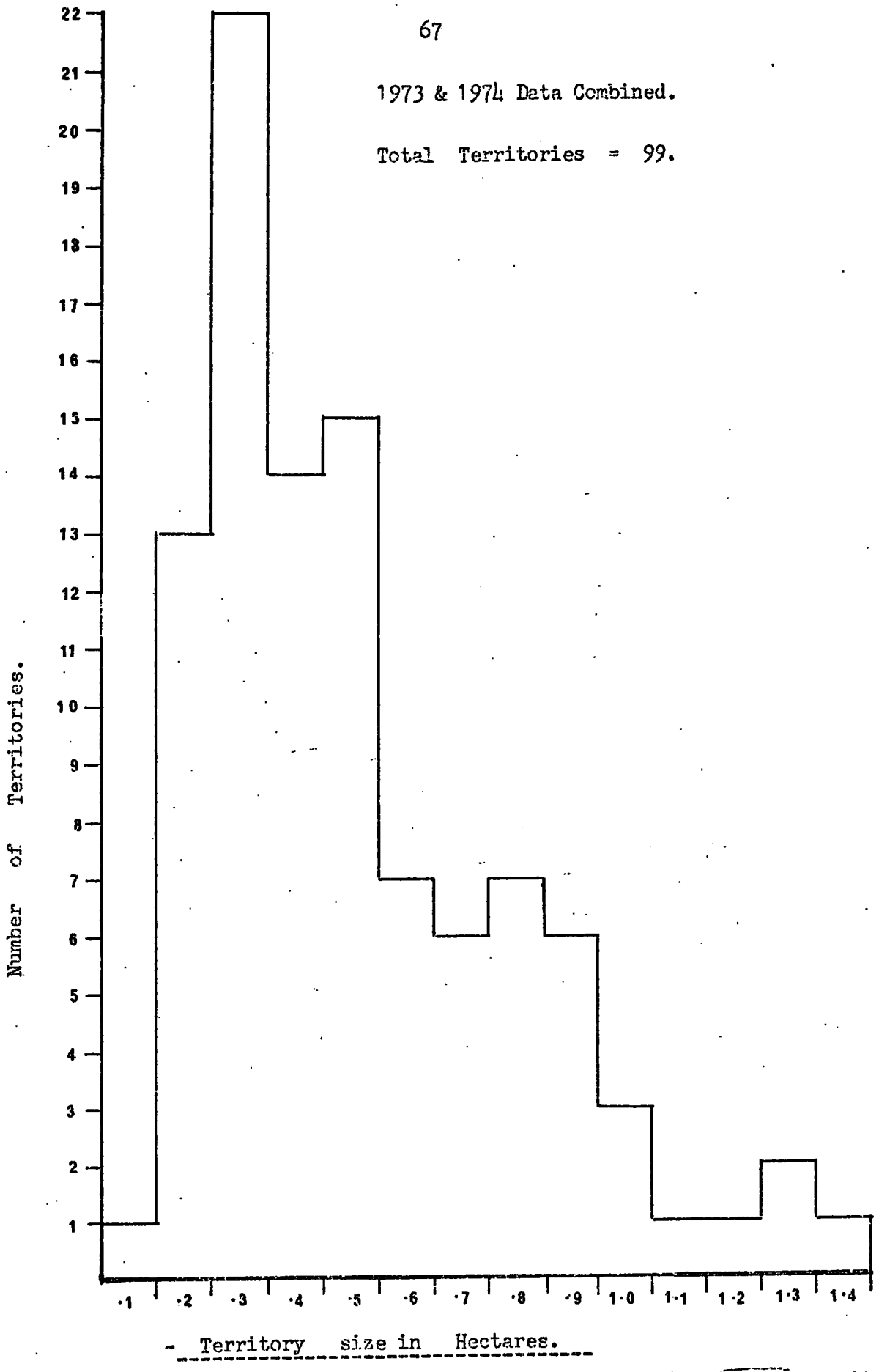

Figure 5 Analysis of all territories according to estimated size.

Juncus, and several small islands. The Juncus and the islands provided the nest sites, but natural food appeared to be in short supply in the winter months and these two birds spent many hours on the bordering car park eating grass. Their territorial area was also a prime location for the visiting fishermen and a first stopping point for the public that visit Attenborough in large numbers. Although it is impossible to quantify the amount of food made available to these coot from the fishermen and the public it must have been considerable throughout the year.

There is evidence that it was this additional food supply, and not the large territory, which was the reason for these birds being one of the most successful pairs over the two breeding seasons. They were the first birds to lay in 1973, rearing two young from eight eggs. In 1973 they also attempted a second brood - a second clutch of seven eggs was incubated for 20/21 days before being lost in a very heavy flood. They defended their territory throughout the winter laying again on 10 April 1974. From seven eggs they reared four young to an age of 56 days - 3 of these young still being on territory with their parents at 90 days.

Cramp (1947) found that an attempt to breed in a territory of 0.12 ha. was unsuccessful. Askaner (1959) recorded successful breeding in territories of 0.08 ha. and 0.09 ha. although these territories were in an area where artificial feeding took place. At Attenborough the smallest territory with successful breeding (Table 5) was 0.09 ha., the clutch size was four eggs with a 100% hatch and 50% fledgling success to at least eight weeks.

Kornowski (1957), Lelek (1958) and Wagner (1962) all believed that a coot's territory size was governed by the amount of food

Table 5 The Relationship Between Territory Size, Clutch Size and Breeding Success.

1973

Area Code	Territory Size	Clutch Size 1st. Complete Clutches only.	% Breeding Success
A3	0.09	4	50
A2	0.12	6	NIL
E14	0.11	5	NIL
E13	0.14	9	22
A5	0.14	8	25
A6	0.16	5	40
E16	0.17	6	NIL
E2	0.20	8	62
A4	0.21	6	NIL
C11	0.21	6	17
E11	0.22	8	37
E12	0.22	6	33
E9	0.22	6	NIL
A1	0.24	6	NIL
B2	0.26	4	50
E6	0.26	4	25
E8	0.26	5	40
E10	0.27	6	NIL
B4	0.27	6	17
C5	0.28	7	NIL
C1	0.29	7	28
E17	0.29	5	20
C7	0.32	5	NIL
E20	0.32	4	75
B5	0.36	9	22
E4	0.36	6	17
A8	0.42	6	17
E31	0.42	4	25
E19	0.44	7	14
E22	0.46	7	43
C14	0.48	7	43
C15	0.48	4	25
A7	0.48	5	40
E32	0.50	7	NIL
B6	0.53	5	40
B3	0.54	7	29
A9	0.54	6	33
B8	0.58	5	20
E30	0.64	6	NIL
C2	0.64	7	57
E18	0.68	7	14
E1	0.70	7	57
A10	0.70	10	50
C8	0.79	5	20
B1	0.81	4	50
B7	0.84	4	25
C9	0.89	7	14
C10	0.98	5	20
E5	1.00	5	NIL
C6	1.14	6	33
E28	1.25	8	25

it produced. This could account for the fact that as the season progresses, and more emergent vegetation becomes available, coot will sometimes relinquish areas of its territory to other territorial seeking coot (see page 60).

a) In relation to egg laying and clutch size.

There was no evidence of any connection between failure to lay and the size of the occupied territory. Coot which did not lay eggs held territories of 0.12, 0.32 and 0.95 ha. in 1973 and 0.32 ha. in 1974, the mean being 0.41 and not materially different from that of the population as a whole. Observational logging did not suggest any factor which could have caused the failure to lay eggs. Neither was there any apparent difference between the vegetation of a territory in which eggs were laid and one in which no eggs were laid. The relationship between territory size and clutch size (Tables 5 and 6) was investigated. The correlation coefficient of 0.04 was not significant ($P > 0.1$) and there was no evident relationship between territory size and clutch size (Figure 6).

b) In relation to breeding success.

Individual breeding success, based on the number of young surviving to the age of eight weeks, as a percentage of the eggs laid, was calculated for each mapped territory in which first full clutches were laid (Tables 5 and 6). The data were then examined to check the relationship between territory size and breeding success. Both years data, 51 territories in 1973, 42 territories in 1974 were examined independently ($r = 0.09$ and 0.23 respectively) and combined ($r = 0.13$, $P > 0.1$). There was thus no apparent correlation between

Table 6 The Relationship Between Territory Size, Clutch Size and Breeding Success.

1974

Area Code	Territory Size	Clutch Size 1st Complete Clutches only	% Breeding Success
A3	0.14	9	56
E19	0.14	6	NIL
A4	0.16	6	17
E6	0.19	9	NIL
E7	0.19	9	22
A1	0.21	5	NIL
C2	0.21	7	NIL
E12	0.22	7	29
E4	0.23	7	29
B4	0.26	6	33
B5	0.27	8	50
E18	0.31	3	NIL
E8	0.32	6	NIL
E3	0.32	8	38
C9	0.32	5	NIL
E13	0.35	7	29
C6	0.36	4	NIL
E22	0.37	5	NIL
E16	0.41	5	NIL
A2	0.45	6	17
A7	0.45	8	25
C4	0.46	7	14
C3	0.48	6	50
C7	0.48	6	17
E5	0.49	6	NIL
A8	0.49	5	20
B3	0.54	7	14
E9	0.57	10	30
C1	0.64	6	NIL
A6	0.65	6	33
E20	0.67	9	11
A9	0.70	6	33
B2	0.70	6	17
C5	0.72	6	NIL
A10	0.78	6	17
B1	0.81	6	NIL
E15	0.83	5	NIL
B6	0.84	5	40
E17	0.94	9	NIL
E2	1.20	9	44
E1	1.37	7	57

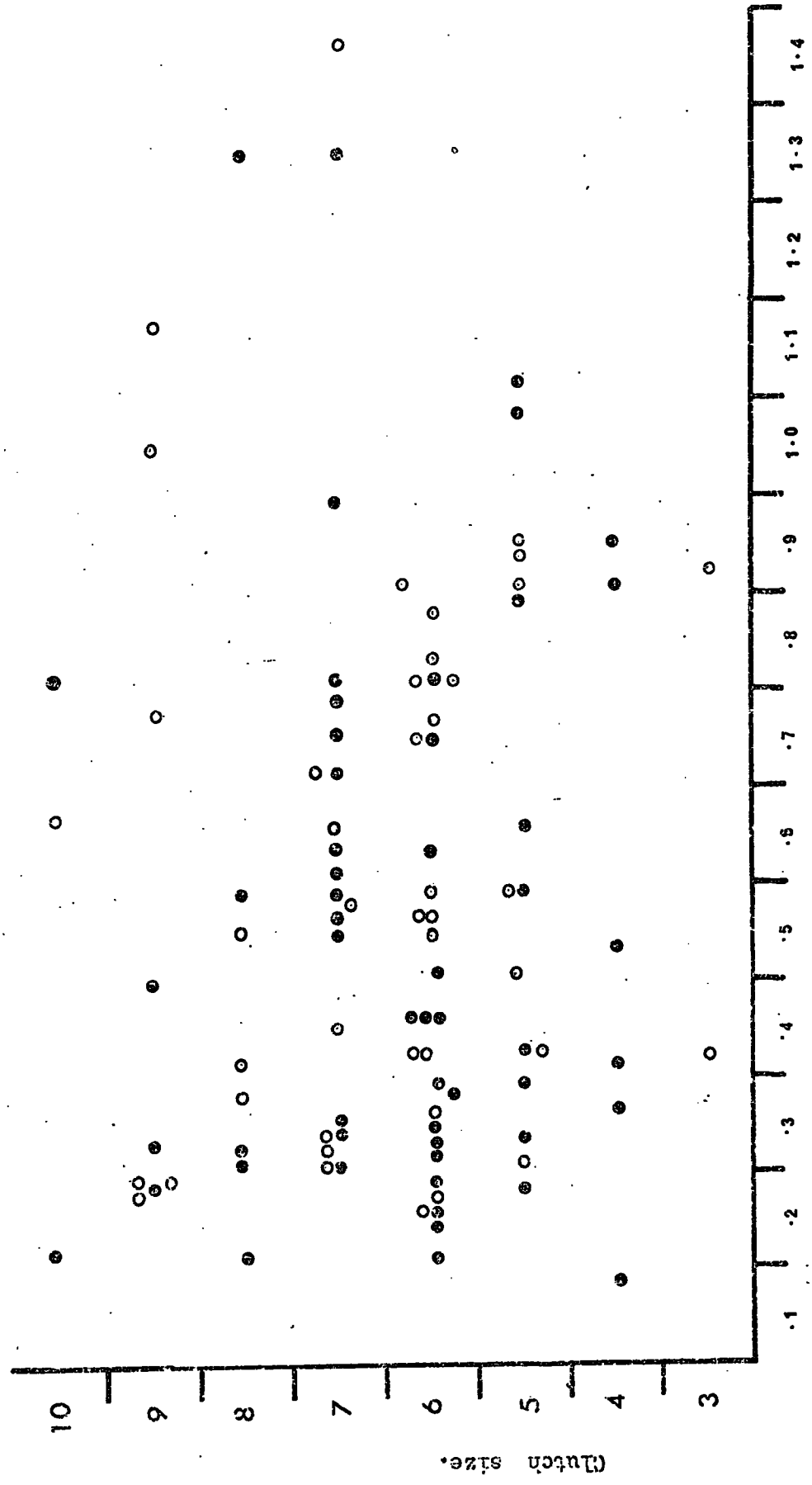

Figure 6 Clutch Size in Relation to Territory Size.

Key :- ● data for 1973.
○ data for 1974.

territory size and breeding success.

Distribution of Territories

Distribution of territories over the study area was very variable. Figure 3 and 4 show the distribution of territories in 1973 and 1974 respectively. If the territory was not accurately mapped then an estimated territorial outline has been included in order to show all the known territories. Nest sites are marked with an asterisk. All the territories at Attenborough gave the birds access to at least some open water. In two territories, B2 and B4 in 1973, this was limited to 30 and 21 sq. m. of open water respectively by the end of their incubation period. All territories had some emergent vegetation. Many areas which did not have territories also contained marginal emergent vegetation, usually G. maxima.

Within the very densely populated Wet Marsh area there were two neutral zones in both 1973 and 1974. There was, however, no obvious difference in the overall vegetation types and quantities between the zones carrying territories and the neutral areas. In each year the neutral areas were of a size similar to many territories. Although no quantitative measurements were made in the Wet Marsh area it was obvious on purely observational evidence that this small section of the study area was the most productive of the vegetational types associated with the coot at Attenborough (Plates 25 and 26 and Figure 2). The area also had open water, the one apparently essential ingredient for a coot territory. If food availability does govern the size of a territory so that the

Plates 25 and 26 Two views of the Wet Marsh area in 1973

more food produced the smaller the territory (Kornowski 1957), the Wet Marsh area with its abundant food should have had smaller territories, as was in fact observed.

Besides the seven pairs of breeding coot, the Wet Marsh area of 2.3 ha. held in 1974 one pair of mute swans, three pairs of moorhen, at least four pairs of great crested grebe, one pair of little grebe, two pairs of mallard and a probable pair of water rail (Rallus aquaticus).

Kornowski (1957), Sage (1969) and others found that breeding coot suffer greatly from nests and eggs being destroyed by the action of waves across open water. At Attenborough the areas which were very sparsely populated by coot had few islands and little emergent vegetation and the areas were very prone to wave action. Losses at Attenborough because of swamping by waves were almost negligible, the coot using more sheltered territories for breeding. In the open water areas coot were unable to find sites to build their nests which were safe from possible mammalian predators or disturbance by man. Over the two breeding seasons only five nests were found which could be reached by wading. Three of these nests did lose all their eggs, probably to human predation. Selective pressures on the coot from human disturbance, accidental destruction and vandalism, were severe during the breeding season and probably enough to account for the placing of many of the nests in open but inaccessible sites. Many of the sites actually chosen for nests were more susceptible to predation pressure from the normal predators of the coot, the fox (Vulpes vulpes), carrion crow (Corvus corone), magpie (Pica pica) and pike (Esox lucius) than if the nests had

been placed in the available marginal vegetation of G. maxima. However, the marginal vegetation at Attenborough was rarely over 2 m. wide and human visitor pathways usually ran very close to the edge of this strip of vegetation. Plate 27 shows a typical stretch of the pit banks in the coarse fishing season. As night fishing is allowed at Attenborough and it is possible to have some areas of the pit banks being fished continuously, human pressure make it virtually impossible for any large birds to utilize the marginal emergent vegetation strip for nest sites. Consequently, if an area had no islands or clumps of vegetaion offshore its use by the coot for breeding was severely restricted.

Mating Behaviour and Nest Characteristics.

Mating

Wagner (1962) recorded coition on water on one occasion only. He gave, as has Höhn (1949) a brief description of mating behaviour. Wagner (1962) implied, and Höhn (1949) stated, that the male coot retains his balance on the female's back by wing flapping and that he does not hold onto the feathers of the female's head as ducks do. Nylund (1945), Kornowski (1957) and Lelek (1958) have discussed mating with respect to its timing within the breeding sequence.

I observed mating take place several times on land but only once in the water. A major problem in observing coot mating behaviour was the lack of pre-coition display. However mating was usually preceded by the male following the female closely across water. The female on reaching land submitted by crouching down and the male mounted her from the rear. Balance was maintained by wing flapping and sometimes by the grasping of the female's neck

Plate 27 The pressures on the environment from fisherman was such that the mainland marginal and emergent vegetation was unsuitable for Coot nest sites

or head feathers.

Only on one occasion was the female seen to initiate mating. A female standing on soft mud was joined by her mate; the female immediately walked forward and pushed her breast at the male. The pair stood very close for several seconds before the female turned round and crouched down in front of the male. The male mounted her from the rear.

The mating sequence normally lasted for about 30 to 40 seconds. It was proceded by loud calls on one occasion and soft calls as mating was taking place were heard on several occasions. In all the observed mating attempts, the mounting of the female was from behind her tail.

The observational evidence on mating behaviour did not confirm the findings of Höhn (1949) that the males do not maintain their balance by holding onto the female's head or nape. Mating was observed eight times and on four occasions head or nape grasping by the male was part of the behaviour pattern.

Nest Site Selection

Although Kornowski (1957), Wagner (1962), Sage (1969) and Havlin (1970) gave emergent vegetation as the chief nest site there are also several records of the coot nesting in other sites. Burkill (1933) recorded that he found five coot nests under willows, while Wagner (1962) also mentioned one nest under a willow. Dry land sites have only been recorded infrequently, Oldham (1935) and Ruthke (1951). Wagner (1962) found one nest 30 m. from open water.

Sites selected for nests (Table 1) were very varied within both years and the pattern of selection varied greatly between the

two years. Table 1 shows that the proportion of coot using emergent vegetation for nest sites dropped sharply in the 1974 breeding season while there was an increase in the number of pairs building under or on Salix spp. A 2 x 2 χ^2 test comparing Salix sites with sites in emergent vegetation shows this shift to be highly significant ($P < 0.01$). Reasons for the variations during the two years have been considered in the Habitat section (see pages 33 to40). Further data collected on 31 July 1976 and by personal communication (K. Corbett 1978) are used to augment the data given in Table 1, and to examine in pages 167/171 the vegetational changes occurring at Attenborough and the possible effects on nest site choices and breeding success.

Many nests were placed partly in the open and, because of the island situation, many of these were successful. But only one nest was built completely in the open, this was a floating nest made of the leaves of Acorus calamus. The eggs were almost certainly lost due to vandalism. When found, on May 1973, it contained 3 eggs but it was empty on 28 May when it was found floating against the bank. This nest, the only floating one found, was still afloat on 10 June (Plate 28).

The island nests at Attenborough were generally placed under bushes of Salix spp. These were on small islands and were open as far as viewing by humans was concerned. However, for mammalian predators the sites would in almost all instances have necessitated a swim and the predator would have had to reach the nest contents from the water. Crows and magpies would have had to approach from a low level, as almost all these nests had a dense tree canopy above them.

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Plate 28 Made of Acorus calamus this was the only truly floating nest found

Plate 29 The only dry land site of a Coot's nest on a small island, it was two metres from the water

Thus, while the open sites were probably more attractive propositions for attacking predators if only because the nest sites were so visible, the actual success of these attacks was probably low. Adult coot in the breeding season were seen to defend their nest successfully against both crow and magpie and losses to these two predators were probably confined to very small young when they first left the nest and started to wander away from their parents. The role of the fox as a predator at Attenborough is difficult to assess. At least one pair of foxes bred in the study area, and occasionally they were seen swimming between the islands. The first clutch of eggs of E5 in 1974 were almost certainly lost to a fox (fox footprints being found in the mud leading to the nest) but no other coot eggs are known to have been lost to this mammal.

From observations at Attenborough it appears that coot are able to exploit most types of vegetation as nest sites if it is in, or gives immediate access to, water. Only one site at Attenborough did not fit this category: nest C7 in 1973 was placed on a small island two m. from water (Plate 29).

At Attenborough a prime factor affecting the choice of a nest site appeared to be the availability of some of the previous years emergent vegetation. This preference with respect to nest site selection was also noted by Blums (1973). The success of the open sites at Attenborough is contrary to the findings of Sage (1969) who recorded that nest built in the open "invariably came to grief".

Plates 30 to 36 illustrate various nest sites used at Attenborough over the two years of this study.

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Plate 30 Typical site using some emergent vegetation and a Salix spp. bush

Plate 31 A nest built in the previous year's T. angustifolia

Plate 32 A neat nest in Glyceria maxima

Plate 33 A typical nest of the Coot at Attenborough using the base of a Salix for support

Plate 34 Also under a Salix but this time the branches are being used for support and shelter

Plate 35 The typical bulky structure of a nest made of Phragmites communis in a bed of the same vegetation

Plate 36 Typical site of the early laying Coot is the still standing vegetation of the previous year

Nest Materials

The materials used depended on the vegetation to be found in the territory. Very rarely was only one type of plant used, the exception being the nest of pair E13 in 1973. This was situated in a bed of Phragmites and was constructed entirely of this plant. Even the nest cup lining was made of Phragmites leaves.

Most coot nests have a strong base of thick twigs on top of which is added the predominant vegetation of the territory. The base could be composed of sticks as long as three m. and sticks of two m. are frequent. On top of this might be a base of Typha spp. with a cup of Juncus lined with Typha.

Vegetation for the nest was collected up to 50 m. away, but also from the nest vicinity, the building bird merely reaching out and snapping off a piece of growing vegetation. Coot have little difficulty in collecting growing vegetation. Three times in 90 seconds, the non-incubating bird of pair E19 in 1973 swam about 10 m. and with the bill cut off with a very slight twist of the neck a long leaf from a R. hydrolapqthum plant. The leaf was taken to the nest and passed to the sitting bird who arranged it on the nest side. They were also seen to collect growing T. latifolia with the same ease.

Usually fresh vegetation was added during incubation and on two occasions a completely new lining of fresh green vegetation was added just prior to the hatching of the first young. Sometimes fresh vegetation was brought in after the young have hatched but this was not nearly so common after hatching as during incubation. During periods of heavy rain, almost all the nests had fresh vegetation brought to them and thus nests increased in size

substantially during periods of inclement weather.

Plates 37 to 49 show methods of nest construction and materials used in a range of nest photographed during the 1973/74 breeding seasons.

Nest Construction

Askaner (1959) stated that only the male coot builds the original or first nest. Kornowski (1957) found that only the male builds the nest cup and the female adds the nest lining.

Although the coot builds a very substantial nest structure, it can be assembled in as little as two days. Very rapid construction was noted for several repeat nests. Nests for first clutches were usually constructed over a much longer period of time. On several occasions when the construction of the nest was proceeding at a more leisurely pace, I found an egg deposited on a flat nest structure: a visit the next day invariably found two eggs in a normal cup shaped nest with its lining complete. It is as if the female coot is suddenly overtaken by egg-laying events and deposits her first egg in the incompleted nest. Observations at Attenborough did not confirm Askaner's (1959) findings, on nest construction, as on several occasions both adults were observed collecting and bringing in nest material.

a. The ramp

The ramp was a prominent feature of many coot nests (Plate 52) but was missing in about 30% of nests. Ramps were much more evident in emergent vegetation and in Juncus rush. Kornowski (1957) suggested that a ramp is formed if all building material is brought from the same direction. I was unable to confirm this observation.

Plates 37, 38 and 39 A sequence of photographs which illustrates the development of a Coot's nest in Rumex hydrolapathum

Plate 40 The early foundations of a Coot's nest based on several branches of a Salix

Plate 41 The same nest as Plate 40 photographed two days later

Plate 42 Foundation twigs of Salix being added to a trampled base of T. latifolia

Plate 43 Typical nest structure to which the cup has to be added

Plate 44 A nest made completely of Phragmites communis placed in the open

Plate 45 A Juncus nest in a Juncus clump

Plate 46 A nest in T. latifolia but with Juncus spp. woven into the nest cup

Plate 47 A nest cup made largely out of bents of dead grass

Plate 48 Illustrates a nest sited in Juncus with the cup made of T. latifolia and with some Juncus woven into the cup

Plate 49 The whole nest including the cup lining was made of T. latifolia

Plate 50 A Coot 'platform' taken over by a Water Vole as a feeding post

Plate 51 Taken on the 31st July 1976 this is apparently an example of a second brood attempt by a Coot. The Coot on the nest would be unlikely to tolerate the large young if they were not here from a previous brood

Plate 52 Many Coots build very poor nest cups but very few build them on a slope as did this bird. The egg stayed on the ramp for at least seven days before it disappeared

b. The platform

As well as the nest in which eggs are laid, the coot sometimes builds one or more platforms. These (Boyd & Alley 1948) are constructed exactly like a nest except that a cup is never added. Boyd and Alley (1948) found that platforms were used for brooding small young, very often while the other adult remained on the eggs still being incubated. Kornowski (1957) also remarked on the frequent occurrence of platforms around the nest site. At Attenborough, platforms were only found at a few sites; these were territories without islands but which had emergent vegetation of either T. latifolia, G. maxima or Phragmites. On four occasions, adult coot were seen brooding small young on islands close to the nest while their mates were still incubating. At Attenborough, it seemed that coot only built brooding (or loafing) platforms when there were no suitable dry areas for young birds within the territory. Plate 50 shows a typical coot platform which was taken over by a water vole (Arvicola amphibius) for a feeding post. The mud on the platform is in fact composed of the droppings of the water vole.

Nest Dimensions

Dimensions were taken from 79 completed nests, 38 in 1973 and 41 in 1974, and were recorded to within ± 2.5 mm. Table 7 summarises the collected data. Data for the two years were tested to see if they could be combined. However for both the height of the nest above water ($t = 3.8576$; $P < 0.001$) and the diameter of the nest cup ($t = 3.0140$; $P < 0.01$) the data could not be statistically combined. The data for the depth of nest cup ($t = 1.3660$; $P > 0.1$) could be combined but in view of the results of the two previous 't' tests,

Table 7

Coot Nest Dimensions

Year	No. of Nests Measured	Height of Nest above Water (cm.)	Depth of Nest Cup (cm.)	Diameter of Nest Cup (cm.)
1973	38	10 - 28 Mean = 19.1 ± 0.83	4 - 9 Mean =6.1 ± 0.24	15 - 23 Mean = 20.0 ± 0.41
1974	41	8 - 24 Mean = 15.2 ± 0.6	4 - 10 Mean =6.6 ± 0.27	12 - 24 Mean = 18.4 ± 0.36

this was not tested.

The range of dimensions at Attenborough are similar to those recorded by Kornowski (1957).

	n	Height of Nest above Water	Depth of cup	Diameter of cup
Attenborough	79	8-28 cm	4-10 cm	12-24 cm
Kornowski (1957)	32	8.5-28 cm	3.5-10 cm	19-26 cm

The comparison cannot be analysed statistically as Kornowski (1957) did not provide means or standard deviations for his data.

Probably the most significant Attenborough measurement will relate to the height of the eggs above the water. If the depth of the cup is subtracted from the height of the nest the resultant figure is the height of the eggs above the water. This ranges at Attenborough from 3 to 21 cm. Since many of the nests were not able to rise and fall with the water level, it needed only a slight rise in level for the eggs in nests at the bottom of the range to be wetted and therefore chilled (see section 'Factors affecting breeding success).

The Nest Dome

Both Kornowski (1957) and Lelek and Havlin (1957) commented on a dome of growing vegetation which the sitting coot often formed over the top of the nest. Kornowski (1957) gave precise details as to how the dome is woven from the new green stems growing around the nest. He suggested that it is to disguise the nest "against egg thieves - mostly crows and harriers". Nest domes were never observed at Attenborough. The dangers to

breeding coot in the Trent Valley from harriers has probably been absent for at least 125 years (Sterland and Whitaker 1879), and although various authorities comment on the danger to coot from the crow (Alley and Boyd 1947: Kornowski 1957: Lelek 1958: Lack 1958b), at Attenborough, the crow was only an opportunist predator on the coot, and a risk only during the period before the clutch was complete and the birds started incubation and, again, during the first two to five days after the young hatched. Even during the laying of the clutch, one or more of the adult coot was usually in the vicinity of the nest and, on three occasions, coot were seen to hurry onto the nest as a crow flew overhead. It seems unlikely that the crow offers sufficient danger to cause the coot to continue with a behaviour adaptation against it alone. (see page 81) As there is some doubt about whether the coot which nests in Britain is migratory (Brown 1955: Spencer & Hudson 1972/1974), it does seem possible that, if Kornowski (1957) is correct concerning the function of the dome, the coot in Britain has dispensed with the dome as the need for such protection from the larger flying predators has decreased.

Breeding Biology

Length of Laying Period

Most of the research on date and length of laying season has been carried out on the Continent. Bezzel (1967) had laying starting in early April with peak laying throughout May. He also commented that in years when egg-laying starts late it develops very quickly. Havlin (1970), reviewing all the available data on coot in

Czechoslovakia, gave the earliest egg on 20 March 1967, with laying generally startingin most years between 10 and 20 April. Most Czechoslovakian clutches were started at the end of April and the beginning of May with a mean date of 4/5 May and a latest date for eggs of 22 July when a clutch of five new eggs was found. Similarly Blūms (1973) found that in early years in Latvia egg laying starts about 1 April. Regardless of the date of the first eggs, he found that mass layings occur in the last week in April and the first week in May. The only published date for Britain is that of Sage (1969) who gave the earliest full clutch date in Hertfordshire as 30 April, with the latest full clutch on 13 July.

For the collection of data at Attenborough the criterion of Lack (1950) has been followed and the date of the first egg is used as the basis on which data are recorded and presented.

On the basis of observations (see section on Incubation) and the data of others (Nylund 1945: Kornowski 1957: Lelek 1958: Blūms 1973) it has been assumed as a working hypothesis that the coot lays one egg a day until the clutch is complete and that the incubation period lasts 23 to 24 days. My observations indicate that incubation of first clutches commenced with the 3rd or 4th egg of the clutch. When a clutch was checked during the laying period, the date of first laying was arrived at using the one-egg-a-day criterion. If a clutch was checked after it was complete, then the date of the first egg was calculated by subtracting the incubation period plus four days, i.e. 28 days in total, from the date on which the first chick hatched.

In 1973, the first egg date was 30 March; the estimated date

in 1974 was 9 April. The last recorded date for an egg being laid was 15 June in 1973 and 19 June in 1974. Thus the egg laying season at Attenborough lasted roughly 2.5 months in both years. To check the statistical significance of the difference in the mean date of egg-laying, 30 March (date of the first egg laid in 1973) was termed day one and subsequent days were numbered consecutively until the season ended. For 1974 9 April (the date of the first egg) was termed day eleven. The number of clutches started on any day was then calculated. In 1973, the mean day of starting to lay = 37.90 $\pm$ 2.7 days, day 38 being 6 May: in 1974 the $\bar{x}$ = 35.30 $\pm$ 2.1 days, day 35 being 3 May. There was no significant difference between $\bar{x}$ egg laying dates in 1973 and 1974 ($t = 0.8517$; $P > 0.1$). The numbers of clutches used in these calculations are not the same as the numbers found since only nests where it is known to within $\pm$ 1.5 days when the first egg was laid have been used. Although, in 1974, laying started later than in 1973, the build up of pairs starting to lay was more rapid. This is in accord with the findings of Bezzel (1967) and Blüms (1973) that in seasons when laying starts late it develops very rapidly.

Figure 7 shows that, for first clutches only, peak egg-laying occurred in both 1973 and 1974 during the last few days of April and the first few days of May. Figure 8 combines the data for 1973 and 1974 and confirms that, for Attenborough, April and May are the peak egg-laying months with 68.0% (n = 91) of all first clutches being started between the period 16 April to 20 May. Figures 7 and 8 also include second clutches when an accurate date is known. Apart from one clutch, all the re-nest clutches

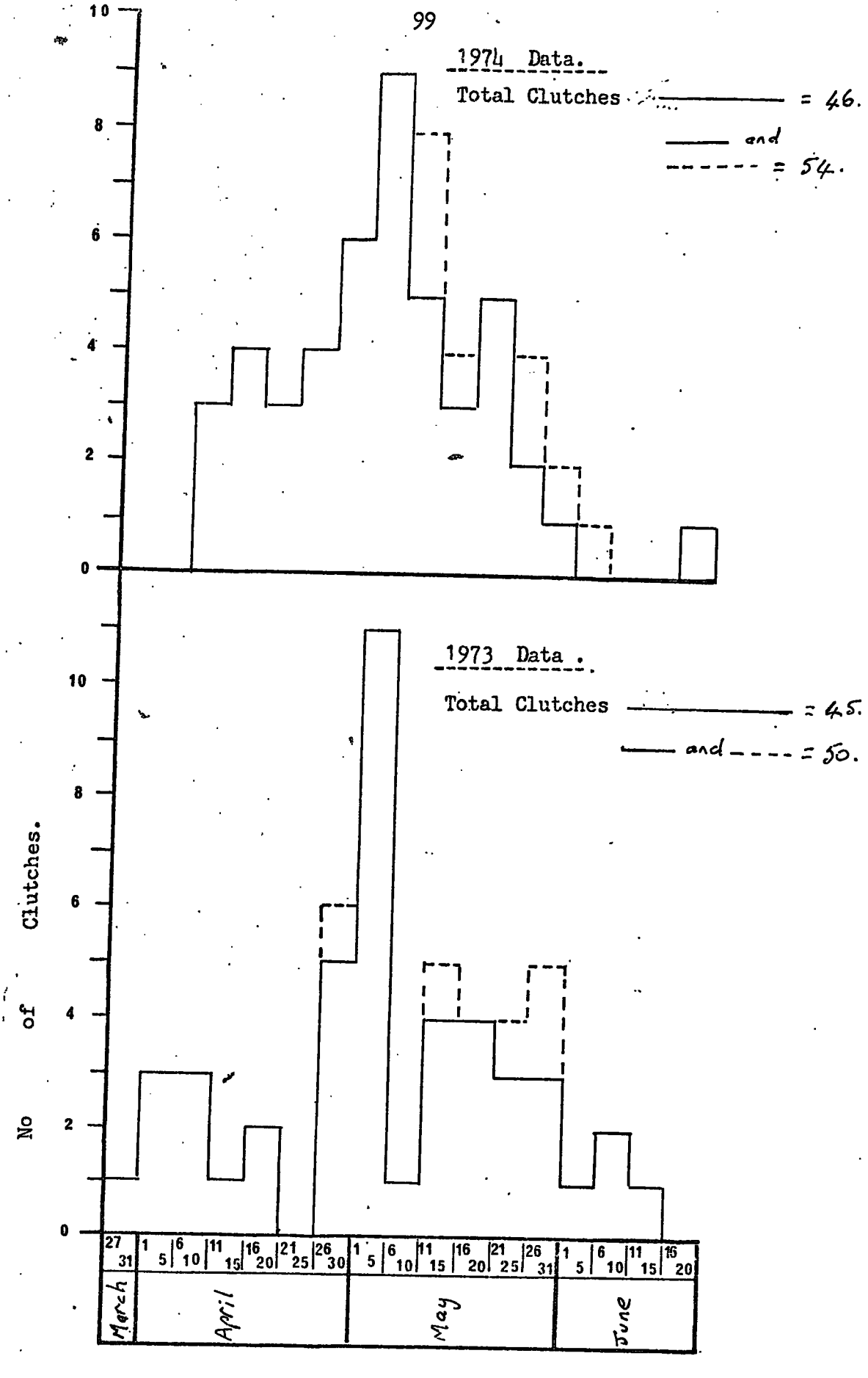


Figure 7. Coot Breeding Seasons 1973 and 1974.
Data limited to clutches where date of the first egg was known or could be estimated within ± 1.5 days.

Area enclosed by solid line includes first clutches only.

Area enclosed by both solid and dotted lines includes all clutches started.

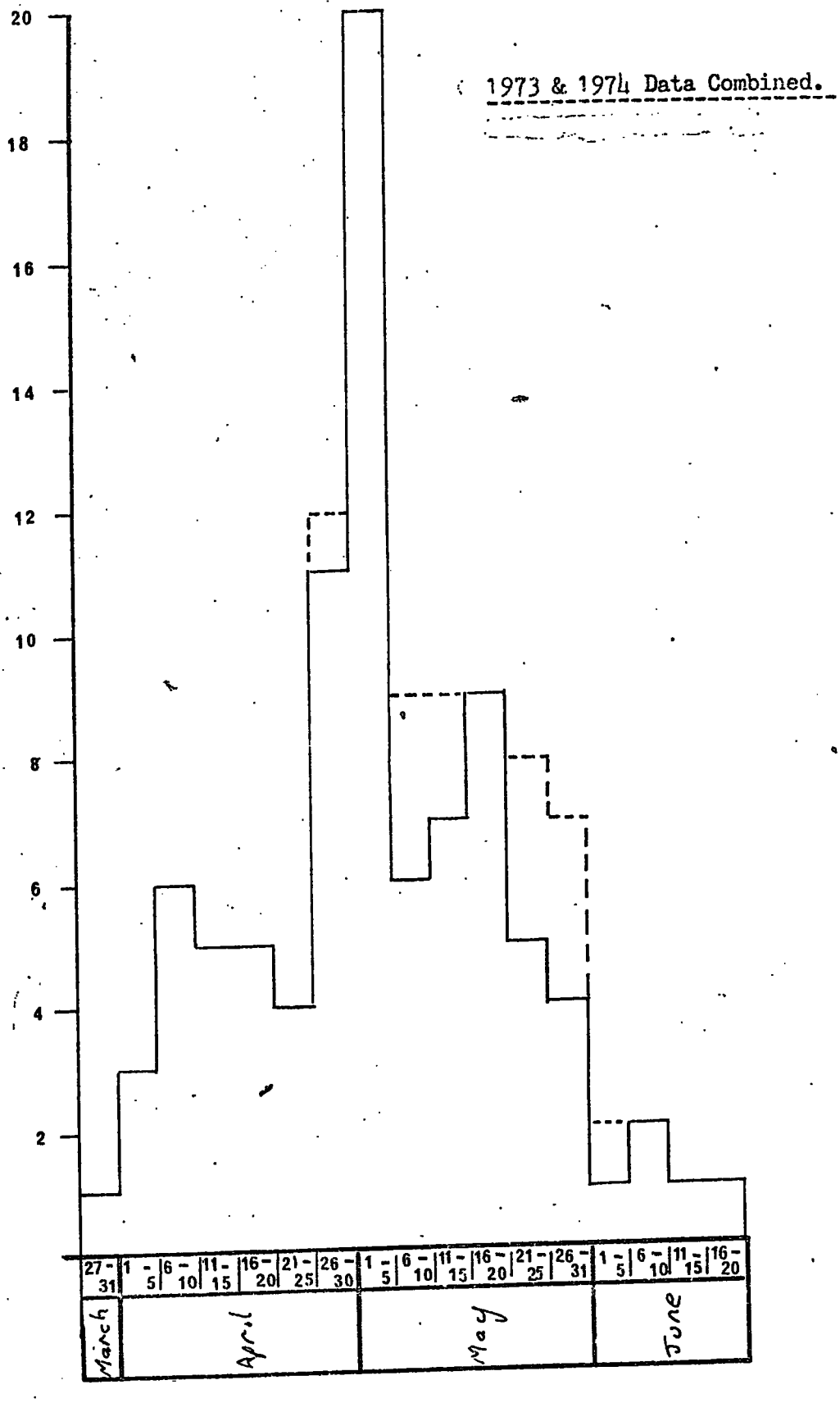


Figure 8 Coot Breeding Seasons 1973 and 1974 Combined.
Data limited to clutches where date of the first egg was known or could be estimated within ± 1.5 days.

Area enclosed by solid line includes first clutches only (n =91 clutches).

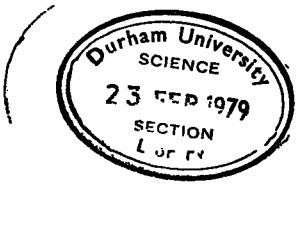
Area enclosed by both solid and dotted lines includes all clutches started (n = 104 clutches).

had been started by the end of May in both years. The re-nest clutches (five in 1973 and eight in 1974) were therefore started earlier than five of the first clutches of late breeders. However, the overall percentage of clutches started in the period 16 April to 20 May dropped to 65% (n = 104) as six re-nests started in the last ten days of May.

A comparison of the Attenborough data with those from the literature shows a very close relationship in respect to peak laying dates. The study confirms that peak egg laying in the coot is during the last week in April and the first week in May.

Second Clutches

Kornowski (1957) recorded that coot only very occasionally used the same nest for repeat layings whereas Bezzel (1959) reported that coot in Bavaria very often used the same nest for second clutches. Lelek (1958) found that two pairs of coot relaid four times before their eggs reached the hatching stage and that the time between the compensation clutches and the preceding clutch became shorter every time a new clutch was attempted. His recorded times range from eight days to one day before relaying occurred. Blümms (1973) reported second clutches starting between two and eighteen days after the loss of the previous clutch, the mean time interval being 7.3 days. Sage (1969) had several pairs that replaced lost clutches once; he also recorded one pair in 1968 that, after having lost an incomplete clutch of two and a complete clutch of seven, laid a third clutch of eleven eggs from which they successfully fledged young.



At Attenborough no pair ever attempted a third clutch. Thirteen pairs in the two years attempted a second clutch after the loss of the first. In 1973 five pairs re-nested of which four pairs hatched and fledged young: the fifth pair abandoned their territory after the loss of their second clutch. In 1974 eight pairs re-nested. Six of these hatched young but only two pairs actually raised them to the fledgling stage. In 1973 two of the five pairs built a second nest for their new clutch and in 1974 six of the eight pairs built a new nest. Exact data on the time interval between the loss of a clutch and relaying was obtained in four cases. This was six days and four days in two instances where the new clutch was laid in the old nest, and nine and thirteen days in the other two where new nests had been built. The size of compensation clutches is discussed in the general section on clutch size (see page 142).

Double Broods

Early literature, such as the Handbook of British Birds (Witherby 1938-41) stated that the coot has several broods in a year. The only specific reference suggesting that coot do in fact rear several broods a year is Burkill(1933) who reported that in 1931 ten nests on the Fetcham Pond, Leatherhead, gave rise to twelve young, "nine of which come from one nest in three broods". He stated that "morning observations never lasted more than a few minutes, just as I passed". Observations were from the mainland and nests were not checked for eggs. This probably accounts for the estimated incubation time of between 33 and 38 days (see page 123 concerning reliability of this estimate) which was arrived at

by checking how long the birds sat on their nests. His notes refering to the chicks of a first brood while parents were feeding a second brood, apparently confirm that at least one second brood was seen but he presented no further evidence for a third brood.

Cramp (1947) reported on double brooding by coot in St. James's Park, London. His observations commenced on 29 June 1943 and by mid-July two of the six pairs were reported as just hatching second broods. Cramp (1947) made no further comments on this aspect of their breeding biology. Alley and Boyd (1947) considered that the coot is normally single brooded. Sage (1969) found no second broods in eleven years.

On the Continent Kornowski (1957) found only two double broods and concluded that double broods in Holstein, Germany occur "only on isolated occasions". Lelek (1958) stated that second broods had not been proved for Czechoslovakia, but Havlin (1970) estimated that as many as 10% of the coot in Czechoslovakia could be double brooded (see Discussion). Bezzel (1959) stated that, while some observations suggest second broods, he had no conclusive proof that they had ever occurred in Bavaria. Blums (1973) also found no reliable data for a second brood.

Kraus (1968) observed a second brood by coots in Nuremberg Zoo. A first clutch of seven eggs, six of which hatched on 30 April, was followed by a second nest from which seven chicks were on the water on 22 June - the first young then being 59 days old. Kraus recorded behavioural aspects which differ from my observations. With the hatching of the second brood, the parent birds behaved in an aggressive manner towards the older young. These did not leave

the territory and, as the second brood developed, the aggression lessened. When the second brood were six to eight weeks old, aggression, from the adults, ceased and the two groups then swam and rested together.

The Attenborough data indicates that second broods were attempted on two occasions in 1973. There were no such attempts in 1974 and, therefore, out of the 135 pairs of birds on territory over the two years (of which 120 pairs laid eggs: Table 17), only two pairs attempted a second brood.

During late March 1973, pair E8 constructed a nest on the Wet Marsh in which five eggs were found on 9 April. Subsequent observations showed this to be the full clutch - unless eggs were laid and lost between visits - and that the first egg was laid on 1 or 2 April (based on an incubation period of 24 days). Only two young were recorded, the first one hatched on 28 April.

On 30 May an adult coot was sitting, as if incubating, on the old nest. Examination disclosed two eggs in a cup relined with fresh reedmace. The first two young were 31 days old and were still being fed frequently by both adults. No further eggs appeared in the nest and, therefore unless eggs were laid and lost without being recorded, the second clutch consisted of two eggs.

The first young remained in the territory and on 24 June, at 1200 hours, a small chick was seen at the base of the nest being fed by an adult. Later two chicks were being fed on the nest. From their appearance, they had probably hatched the previous day. Also in this territory at the same time were two broods of mallard with seven and two young and a moorhen with five young.

No aggression was seen from the adult coot or from the two large young coots that were then 64 days old. Both large young had small shields when they left the territory between 4 and 8 July, aged 91 to 95 ddys. During the time between the hatch of the second brood and the first young leaving, no aggression was seen by the parent coot towards the two older young. Nor were the larger young recorded attempting to feed the smaller chicks. The second brood left their parents' territory between 24 and 26 September aged 92 to 94 days. No aggression was observed by the adults towards these young.

Pair E28 also attempted a second brood. Their first clutch was of eight eggs with an estimated first egg date of 30 March 1973. At least five young hatched on 28 April but all but two of them disappeared in the first five days. The two surviving young were still on territory being fed by the adults when on 10 June one of the adults was found incubating seven eggs in a new nest in a Juncus clump.

The eggs were still being incubated on 2 July when a high flood washed the nest away. On 4 July one of the eggs, in an advanced state of development, was found in shallow water.

Plate 51, taken at Attenborough on 31 July 1976, shows clearly large young coot by an island - which in 1973/74 held nests C14/C3 respectively - with an adult coot apparently sitting on a nest incubating. This bird was watched on the nest for about 20 minutes and its movements indicated that it was on eggs. If this supposition were correct then this too is an example of a second brood.

The evidence shows that under normal circumstances the coot

in Europe is single brooded. Although some coot do raise two broods in one year, this is exceptional. Evidence indicates that double brooding in the coot is linked closely to a high availability of food. The Attenborough records of double brooding come from territories with abnormally large food supplies, one from natual sources the other from artificial feeding. Kraus (1968) mentioned the rich growths of A. calamus available to a double brooded pair in Nuremberg Zoo. That the availability of food could be the inducing factor is suggested by the publication by Siegfried and Frost (1975) of their finding on continuous breeding in another member of the Rallidae, the moorhen. The authors suggested that the rich supply of natural food coupled with the availability of artificially fed protein and some energy conserving behaviour has enabled the two pairs of moorhen under study to produce 40 and 37 clutches of eggs in 48 months.

Dump-Nesting

There are many reports of aberrant egg-laying behaviour by coot: dump nesting by two birds laying in the same nest, odd eggs appearing in a nest in which a clutch is well incubated and compressed egg laying cycles (Alley and Boyd 1947: Kornowski 1957: Wagner 1962: Havlin 1970: Blums 1973). Most workers comment on the difficulty in understanding how a bird so strongly territorial as the coot allows another coot to lay in its nest (see Discussion); however dump-nesting (Wood 1976) is so prevelent that the majority of research workers discount clutches over ten or eleven eggs and eliminate them from consideration when calculating clutch size (Kornowski 1957: Wagner 1962: Bezzel 1969: Havlin 1970: Blums 1973).

Alley & Boyd (1947) presented an example of aberrant egg-laying which they believed was carried out by the resident nesting coot and which they described as a case of a compressed breeding cycle. I observed a similar case but I believe that the new eggs were being laid by a second female.

"Nest site E4 in Wet Marsh

Date 1974		
14 April	3 eggs in nest	(all marked)
15 "	4 " " " " "	
16 "	5 " " " " "	
21 "	3 " " "	2 of them new, i.e. not previously marked. 2 original eggs at the foot of the ramp and 1 just out of the nest. 1 egg missing.
22 "	4 " " "	The egg just out of the nest on the previous day now back in nest.
	(Total of 7 eggs laid so far.)	
4 May	9 eggs in nest.	(Egg No. 2 was still intact under water at bottom of ramp.)
5 "	9 eggs in nest	
8 "	10 " " "	Eggs No. 6 and 7 were pipping.
10 "	7 eggs and 3 young in nest.	Eggs No. 1,6 and 7 hatched.
11 "	8 eggs and 3 young in nest.	The 3 young left nest to join adult.
12 "	8 eggs and 3 young.	Eggs still being incubated
15 "	8 eggs only	" " " "
19 "	nest empty	3 young on water with adult"

The following facts suggest that the eggs were laid as two seperate clutches. The first clutch started on 12 April consisted of eggs marked with numbers 1, 2, 3, 4, 5, 6 and 7. Egg 7 presumably being laid on 18 April. The second clutch started around 30 April consisted of numbers 8, 9, 10, 11, 12, 13 and 14. Note, however, the gaps appearing in the laying sequence of the second clutch. For example, at one-egg-a-day, the nest should have had ten eggs on 5 May - it only had nine, and then a three day gap between eggs on 8 May and 11 May. The possibility must exist that two birds were laying in the same nest and that the first clutch layer went into a genuine compressed cycle and actually laid the eggs that appeared on 8 and 11 May. The loss of the eggs on the ramp was also unusual for Attenborough, although Alley & Boyd (1947) recorded this occuring regularly. Plate No. 52 illustrates an egg lost down a ramp. Note the angle of the nest and the ease with which eggs could in theory roll out.

Two birds laying simultaneously in the same nest also occured at site C1 in 1974. A coot was observed sitting high on the nest on 3 April. The nest was checked regularly but was still empty on 24 April.

"24 April nest empty

27 April 4 eggs - all warm (1 more egg than expected at 1 a day rate)

30 April 9 eggs

1 May 9 eggs

4 May 13 eggs

5 May 13 eggs

8 May 12 eggs - the last egg laid i.e. No. 13 now missing"

The majority of visits to this site occurred between 1200 and 1500 hours so that if eggs are laid at a consistent time, as Kornowski (1957) stated, then the gap in sequence is real and not dependent on the visit schedule.

The eggs started to hatch on 22 May and some eggs were chipping continually until 28 May when the eleventh egg started to chip. All 12 eggs hatched but all the young had disappeared by 10 June. Young were last seen on 5 June when two adults had three young on the water. During observations only two adult coot were seen in the territory.

In 1973, a nest was discovered containing eggs from two females. (Plate 53). From their ground colour and markings the eggs could easily be separated into two clutches of ten and four eggs. The plate shows the four small chalky white eggs on the right. On 17 June, six of the normal coloured eggs had hatched and two were pipping. The remaining eggs showed no signs of hatching nor could any sounds be heard.

At six different nests in 1974, clutches that were well incubated had an egg or eggs added to them. At none of these sites was it certain that the additional egg (eight in all) came from a different bird, the eggs have therefore been treated as part of the clutch in question: this is disucssed further in the section on clutch size.

One other unusual case occurred in 1973. The nest of coot E32 contained five eggs on 25 May. Two days later, the nest contained seven coot eggs plus the egg of a moorhen. Plate 54 shows the location of the morrhen's egg in the centre of the coot clutch. All the eggs were warm. On 31 May, the moorhen's egg had disappeared

Plate 53 An example of two birds laying in one nest. The four chalky white eggs were laid after the ten more normal coloured eggs

Plate 54 The Moorhen's egg which appeared sometime between the 5th and 7th Coot egg. It later disappeared from the nest

Plate 55 This immature Coot died at the age of 79 to 81 days, entangled in discarded fishing line

and the nest contained only the seven coot eggs. The lining of the nest was checked but the moorhen's egg had not been built into the lining, as Wagner (1962) had found some coot doing with strange eggs. Havlin (1970) also recorded a case of a single moorhen's egg in a clutch of five coot eggs.

Variation in Size of Eggs.

Lelek and Havlin (1956) comparing the variability in egg sizes for each of three study years and in the various regions in which they worked in Czechoslavakia, found that egg sizes were "practically equal".

Bezzel (1959) found that the mean length of eggs within a clutch (first clutches only) was correlated with the size of the clutch. His data, extracted from his paper, gave the following:-

Clutch size	No. of Clutches	Mean Egg Size.
7	14	51.39 x 36.32
8	6	52.47 x 36.34
9	8	53.82 x 36.1

The difference he found "statistically very significant" ($t = 2.62$) between clutches of seven and eight and ($t = 4.00$) between clutches of eight and nine. He stated that with other clutch sizes the correlation was too small to be of statistical significance. He suggested that the correlation might be due to the fact that the larger clutches and larger eggs are laid by older birds: Wagner (1962), based on egg dimensions smaller than average from a coot breeding site that had been occupied for the first time, thought that it might be assumed that young coot lay smaller eggs than older coot.

A total of 760 eggs were measured at Attenborough, 403 in 1973, 357 in 1974. Figures 9 and 10 illustrate graphically the variation over the two years in length and breadth respectively. The date for the two years were combined after analysis showed that there was no significant difference ($d = .34$, $P > 0.1$) for the mean egg length for 1973 ($\bar{x}$ 53.75 $\pm$ 0.12 mm) and 1974 ($\bar{x}$ 53.81 $\pm$ 0.14 mm) there was also no significant difference ($d = .31$, $P > 0.1$) for the mean breadth for 1973 ($\bar{x}$ 37.65 $\pm$ 0.17 mm) and 1974 ($\bar{x}$ 37.73 $\pm$ 0.19 mm). The combined means for length and breadth for 1973 and 1974 were $\bar{x}$ 53.78 $\pm$ 0.09 mm and $\bar{x}$ 37.68 $\pm$ 0.13mm. respectively.

The 1973 data from 349 measured eggs in all first completed clutches were analysed for evidence of correlation between egg length and egg breadth. The correlation coefficient ($r = 0.35$, $P > .001$) indicated a considerable degree of correlation between egg lenth and breadth.

To examine the difference, if any, of egg size between areas in 1973 and 1974 an analysis of variance was calculated for both years. Only eggs from first completed clutches were used ($n = 349$ eggs in 1973 and $n = 289$ eggs in 1974). The data indicated a significant difference in 1973 between areas ($P > 0.01$, $F_{(4,344)} = 4.8$) but in 1974 there was none ($F_{(4,284)} = 0.58$). The 1974 data indicate that there was more variation within the groups than between groups.

Table 8 compares the mean egg size and individual maximum and minimum egg sizes of the Attenborough eggs with ten other sets of data from various areas of Europe. The Attenborough mean size

Figure 9 Egg size variation - Length.

1973 / 1974 Data Combined. 760 measured eggs.

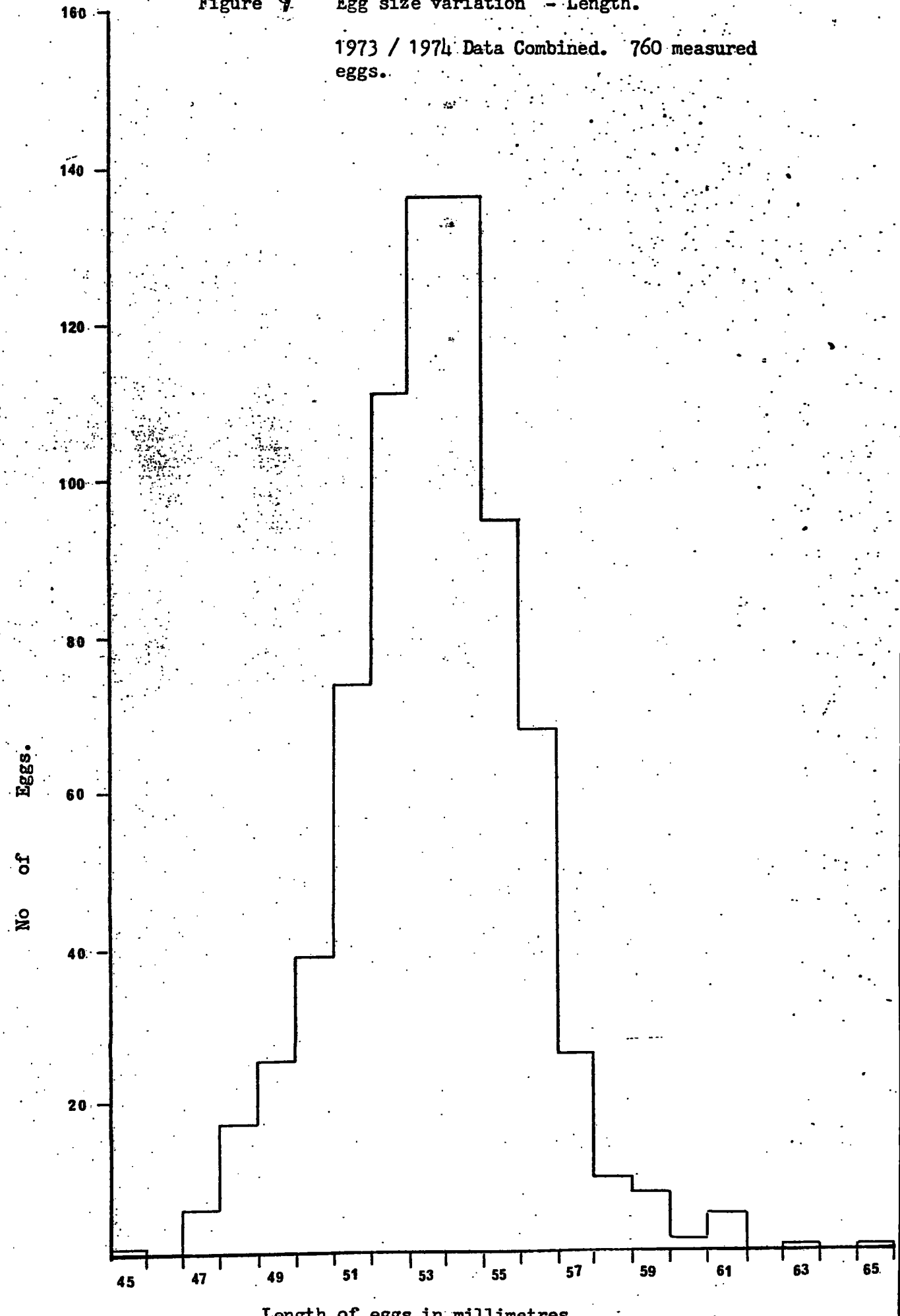


Figure 10. Egg size variation - Breadth.

1973 / 1974 Data Combined.

760 measured eggs.

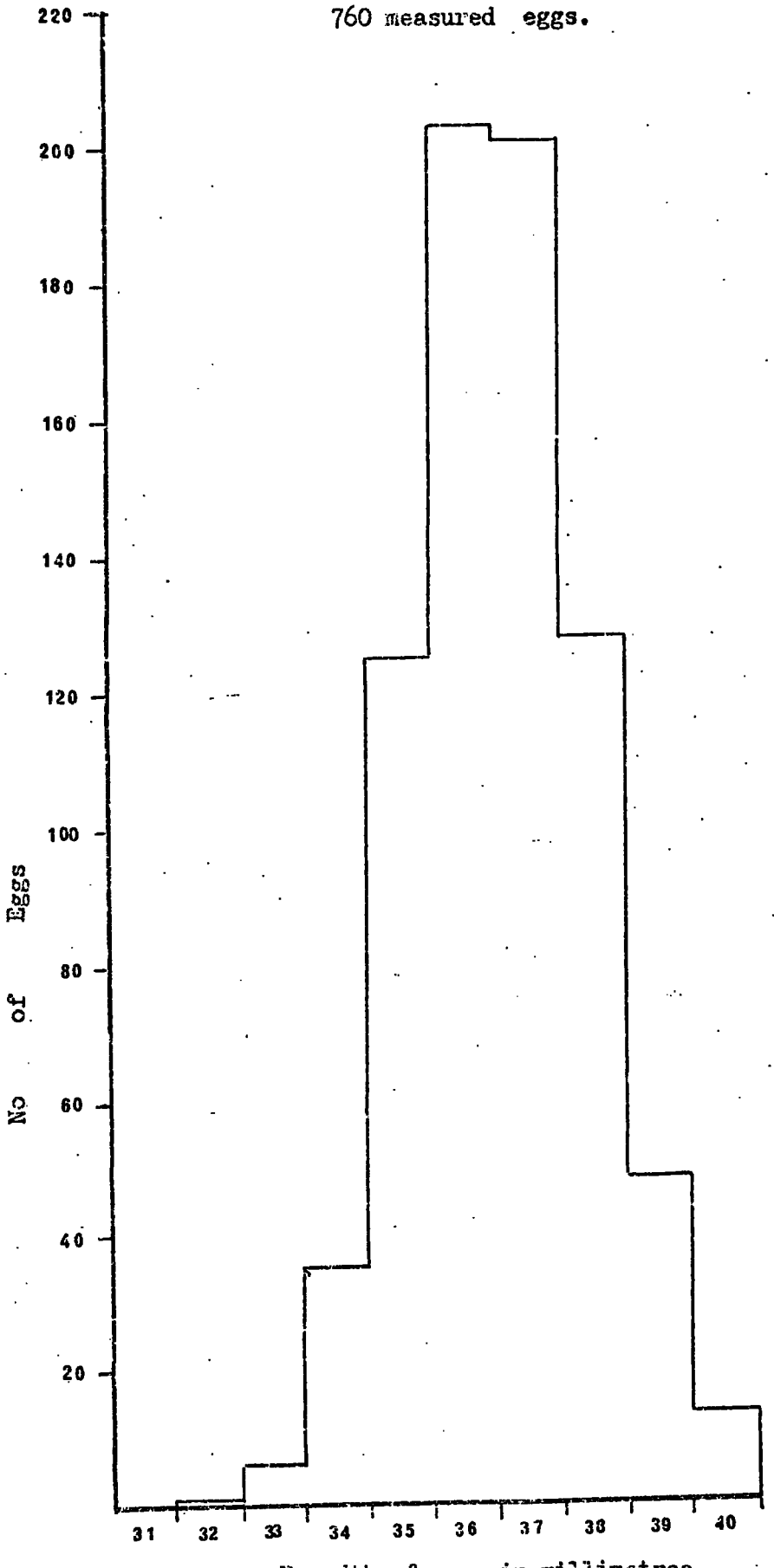


Table 8

Comparisons of Attenborough Coot Egg Sizes with other published figures.

Sizes shown in mms. Data are arranged in reversed chronological date order.

Authority	No. of eggs measured	Mean size of eggs	Max. egg size L	Max. egg size B	Min. egg size L	Min. egg size B	Country	Year of Publication
Gadsby	760	53.78 x 37.10	65.1	40.9	45.6	32.5	England	Present Study
Blüms	1794	53.28 x 36.18	61.8	39.8	42.1	30.7	Latvia	1973
Wagner	278	53.14 x 36.70	59.2	40.1	43.6	32.5	Germany	1961
Wagner	105	52.32 x 35.68	Not given				Germany	1961
Bezzel	449	52.08 x 36.45	59.3	39.2	45.7	30.6	Germany	1959
Kornowski	193	53.2 x 36.7	Not given				Germany	1957
Lelek	328	53.33 x 36.52	61.52	39.20	46.20	30.80	Czech.	1956
Witherby	100	52.57 x 36.17	56.7	39.0	44.2	33.1	England	1948
Niethammer	68	53.3 x 35.4	59.7	40.0	49.7	33.5	Germany	1942
Groebbels	38	51.77 x 35.50	54.5	37.5	48.5	33.7	Germany	1932
Noll	40	50.1 x 34.5	56.2	37.2	43.8	31.6	Switz.	1924
Total	4153							
Means		52.6 x 36.1						

of 53.78 x 37.68 mm is the highest mean value of all for both length and breadth and for both length and breadth new individual maximum sizes have been recorded.

As no standard deviations are provided in other published studies, it has not been possible to test the differences between countries.

An exceptional series of large eggs was laid by the female on territory B1 in 1973 and 1974 (see page 44). In 1973 four eggs were laid, including the largest egg (65.1 x 39.5 mm) recorded in the literature (Table 8 and Plate 9), with a mean size of eggs in the clutch concerned of 58.4 ± 3.1 x 38.3 ± 1.5mm. Two clutches were laid in 1974, the first clutch being deserted after 17/18 days of incubation (see page 159). The mean size of the first clutch was 59.2 ± 2.5 x 40.5 ± 0.2 mm. and that of the second was 59.2 ± 0.7 x 39.9 ± 0.2 mm.

The mean size of the 760 measured Attenborough eggs was 53.8 ± 0.09 x 37.7 ± 0.13 mm. while the mean size of 4,153 eggs taken from literature is 52.6 x 36.1 mm. (Table 8)

The largest previous eggs recorded in literature are those of 61.8 mm. length by Lelek and Havlin (1956) and Blums (1973) and one of 40.1 mm. breadth by Wagner (1962). The female of B1 territory laid five eggs (one in 1973 and four in 1974), equalling or surpassing the greatest length previously recorded and seven eggs (one in 1973, six in 1974) equalling or surpassing the greatest breadth previously recorded. If it is assumed that the length of eggs are normally distributed with a mean of 52.6 mm. (Mean calculated from European literature: n = 4,153 eggs - Table 8)

and a standard error of 0.09 mm. (Attenborough data - page 116) then the eggs laid by this bird in successive years (mean of 58.4 ± 3.1 mm. in 1973; four eggs in the clutch and 59.2 ± 1.2 mm in 1974; eleven eggs in two clutches) were exceptionally large.

The Attenborough data have been examined in order to compare them with the results of Bezzel (1959) (see page111). Table 9 gives the mean egg sizes and standard errors in relation to clutch size. It is known (page112) that there is no significant difference between mean egg length in 1973 and 1974 and it is therefore concluded that there is no significant difference for mean egg length in relation to clutch size over the two years. Regression analysis between clutch size and mean egg length and mean egg breadth was carried out. The analysis showed that there appears to be no correlation between clutch size and egg size (for egg length r - 0.29, $P > 0.1$, for egg breadth r - 0.24, $P > 0.1$). The Attenborough data do not therefore confirm Bezzel's (1959) results that the mean length of eggs within first clutches was correlated with the size of clutch.

Examination to test whether the eggs of re-nest and second brood clutches were smaller than first clutches was carried out. Only re-nest clutches that were laid after the loss of a complete clutch have been considered. The data suggests no evidence of change of size of eggs in second clutches. Thirteen clutches taken from both years give the following results:- on length seven clutches showed a larger mean egg size and six produced a smaller mean. On breadth eight clutches gave a larger mean, five clutches a smaller mean.

Table 9

Mean Egg size in relation to clutch size.

Only first complete clutches counted.

1973/1974 Data Combined

Clutch Size	No. of Clutches	Mean Egg Sizes	
		Length	Breadth
2	1	53.73 ± 1.06 mm.	36.47 ± 0.74 mm.
3	0		
4	11	53.23 ± 0.49 mm.	36.48 ± 0.24 mm.
5	21	53.68 ± 0.19 mm.	37.12 ± 0.19 mm.
6	34	53.86 ± 0.20 mm.	37.24 ± 0.11 mm.
7	18	53.53 ± 0.21 mm.	37.19 ± 0.10 mm.
8	10	53.75 ± 0.21 mm.	36.91 ± 0.13 mm.
9	8	53.05 ± 0.24 mm.	37.16 ± 0.10 mm.
10	3	54.62 ± 0.45 mm.	36.43 ± 0.24 mm.
Total	106		

The Attenborough data were examined to see if there was any variability between the length of eggs that were laid early and the rest of the eggs. The total clutches were divided by taking the first and last 20% of all completed clutches (see page 174). Table 10 gives the mathematical data on which the statistical analysis is based. The data do confirm that the eggs of the early nests are significantly larger in length than the eggs from all other nests. In 1973, the mean length of early eggs was 55.0 ± 0.25 mm. while the mean of the late eggs was 52.4 ± 0.26 mm, ($d = 7.15$, $P \leq 0.001$) while the combined mean of all the eggs other than the early eggs was 53.5 ± 0.13 mm. ($d = 5.35$, $P \leq 0.001$). Similarly in 1974, the mean length of the early eggs was 54.7 ± 0.32 mm the mean of the late eggs 53.0 ± 0.33 mm. and the mean of all the eggs other than the early eggs was 53.5 ± 0.14 mm. ($d = 3.72$, $P \leq 0.001$ and $d = 3.53$, $P \leq 0.001$ respectively).

Bezzel (1959) and Blüms (1973) both reported that eggs of June clutches were slightly smaller in length than eggs of early clutches. These findings were not checked directly with the Attenborough data as only six June clutches were found at Attenborough. However as indicated above the eggs of late clutches are significantly smaller than early clutches and, therefore, it would be expected that the very late clutches i.e. June clutches, would have smaller sized eggs.

Accuracy of Breeding Figures

Kornowski (1957), Bezzel (1959), Wagner (1962) and Havlin (1970) all found it difficult to assess the number of coot which hatched and even more difficult to monitor those reaching the fledging age

Table 10

Mean and standard error of egg length in relation to date of laying.

Completed clutches only.

1973	No. of Clutches	Mean Length in mm.
First 20% of all completed clutches	14	54.98 ± 0.25
Last 20% of all completed clutches	14	52.39 ± 0.26
All clutches except the first 20%	56	53.46 ± 0.13
1974		
First 20% of all completed clutches	11	54.72 ± 0.32
Last 20% of all completed clutches	11	53.00 ± 0.33
All clutches except the first 20%	44	53.47 ± 0.14

of six to eight weeks.

At Attenborough the figures concerning the number of clutches started, the eggs laid and young fledged are thought to be highly accurate. However, it was sometimes difficult to determine the number of eggs which hatched. The coot lays as many as ten eggs, which it incubates from the third or fourth egg (see page 123); nests need to be checked every day during the hatching period, but even if this were possible in the time available, the desirability of such disturbance at a critical time in the breeding cycle would be questionable. Many of the figures given for the number of eggs hatched are therefore determined on the maximum number of young seen on a visit after hatching had started. Probably many more eggs hatched than were actually recorded. Losses of young were very heavy in the first ten days - particularly from day three when the young first start to follow their parents.

Because of the type of territory and vegetation it was possible to census accurately the number of coot fledging from each territorial pair. Even after eight weeks, some losses were known to occur; for example, the one young of pair A2 in 1974 still on territory with them was found dead entangled in fishing line on 1 August 1974 (Plate 55). This bird had hatched on 11 or 12 May and was thus between 79 and 81 days old when it died. The same fate befell one of the young of A10 pair in 1974. This was found freshly dead on 21 August - having hatched on 24/25 May. It was therefore approximately 89 days old when it died and it was still in the territory of its parents.

Incubation and Hatching

Nylund (1945) found for coot in Finland that the incubation period was 23-24 days and that incubation started with the first egg. Kornowski (1957) calculated an incubation period of 23/24 days by finding the difference between the date of the last egg laid and the last egg hatched. He recorded incubation of the first clutch from the fourth egg, general incubation from the fifth or sixth egg with an incubation start in extreme cases from the seventh egg. He found that second clutches were always incubated from the first egg. Lelek (1958) also found an incubation period of 24 days with an occasional 23 days recorded. He recorded incubation as "starting regularly with the second egg laid". Blums (1973) calculated the incubation period using the method of Kornowski (1957). The range, using this method, was 21 to 26 days (n = 26 nests) with a mean of 24 days. He found that with the first clutch, incubation started with the third or fourth egg but for second clutches incubation always commenced with the first egg.

At Attenborough the criteria for judging incubation to have started were:-

(1) that all the eggs in a nest had to feel warm on contact with the hand. (Wood (1974) also used this method for checking the commencement of incubation in the Moorhen).

(2) observing coot sitting close on the eggs. On many occasions at the start of a clutch coot were seen sitting on nests containing eggs but on close inspection the sitting bird was found to be high on the nest and could not have been applying heat (Tucker (1944)).

Thirteen nests were used for calculating the incubation periods; in each case the actual laying date of the first egg was known, as was the laying sequence for many of the eggs in the clutch. The date that the first chick emerged from the shell was termed the hatching date of the clutch. For all 13 nests the actual date this occurred is known. Hatching started for 11 clutches on day 24 and for two clutches on day 23. Incubation of the clutch commenced on the fourth egg day for five clutches, on the third egg day for five clutches and on the second egg day for three clutches. One of the clutches in which incubation started on the second day was a re-nest clutch.

The number of eggs laid before incubation commenced normally decided the hatching sequence. At Attenborough most clutches started to hatch in groups of either three or four eggs. On two occasions, however, five eggs were found to be chipping simultaneously. At nest B3 in 1974, the eggs were marked in laying sequence from the second egg. Eight eggs were laid, but two disappeared during incubation. The first egg was laid on 11 April, the sixth on 16 April; on 21 April the nest contained two new eggs, presumably laid on 17 and 18 April. However the nest only contained seven eggs as egg number three was missing. Egg number five disappeared between 24 and 27 April. The sequence of eggs in the nest on 8 May was No. 1, 2, 4, 6, 7 and 8. On this date all the eggs but number eight were found to be pipping.

Incubation at this nest commenced sometimes between a visit on 13 April when three eggs were in the nest and 14 April when the nest held four eggs. Therefore eggs No. 1, 2 and possibly 4 were

incubated for 24/25 days before chipping, egg 6 for 23 days, egg 7 for 22 days only. Hatching synchronisation of the eggs in an individual clutch in the Moorhen is discussed by Wood (1974). He recorded that three eggs laid "24, 48 and 72 hours after incubation commenced hatched at 13, 33¼ and 40 hours respectively after the hatching of the first three eggs." Vince (1966; 1968) provided experimental data that suggested that both retardation and acceleration of individual embryos can occur in some nidifugous species so that hatching periods are reduced.

Although it is generally considered that the coot is an asynchronous hatching bird, and literature has not been traced which suggests otherwise; evidence suggests that synchronisation of embryonic development within an individual clutch must be considered a possibility.

Plates 56 to 60 illustrate various stages in the hatching of several clutches of eggs. In all cases the eggs when checked had the chipping cracks and holes underneath and they were turned uppermost for photographic purposes. Plates 56 and 57 illustrate clutches starting to chip. Plate 58 shows four young (all dry) with six other eggs none of which had started to pip at the time of the photograph. Plate 59 illustrates a hatching sequence not often seen in coot at Attenborough; two young left the nest at my approach, one young was just about dry while one young was halfway out of the egg. The other egg, although not shown clearly in the photograph, had just started chipping. The egg with the young half hatched was the fourth laid and the pipping egg was number five. This was a re-nest clutch with incubation from the second egg.

Plates 56, 57 and 58 Coot eggs were normally found to hatch in groups

Plate 59 An unusual hatching sequence for the Coot at Attenborough. Two young have left the nest, one further young is drying and its sibling is just about to leave the egg. The other egg is just starting to pip

Plate 60 One hatched chick with three other unpipped eggs

Nylund (1945) and Kornowski (1957) commented on the fear response of young coot and at what stage the young are able to leave the nest. Nylund (1945) put this at six hours old but Kornowski (1957) stated that the young are not able to climb out of the nest until they are 10 to 15 hours old. The young at Attenborough could leave some nests within two hours of being dry, the timing of this possibly being dependent on the depth of the nest cup and steepness of its sides. They were, however, very reluctant to do so at this stage; probably under normal circumstances they would not try to leave the nest for several hours after hatching. Plate 60 shows a young chick with its plumage dry with three other eggs, not one of which was pipped. As the chick did not attempt to leave the nest it was probably less than twelve hours old.

The shortest time recorded by Kornowski (1957) for an individual egg to hatch was 14.5 hours and the longest 39 hours, the mean being 28 hours. He recorded two to five days as normal for a complete clutch hatch. Blums (1973) recorded from two to nine days, for a complete clutch hatch, with a normal time of four to six days (n =174).

At Attenborough the actual time taken for an individual egg to hatch was found to vary greatly. Eggs could hatch from first pipping to young in the nest in less than 24 hours while others in the same clutch had only progressed from first pipping to a one cm. hole in the shell in the same period. The longest recorded time for an individual egg to hatch was 46 hours. Whole clutch hatching times varied from two to nine days, the majority taking from two to five days.

Both Kornowski (1957) and Blums (1973) recorded male and female coot incubating. This research confirmed that both sexes incubate

although the proportion of a day that each spent incubating was not determined. It also confirmed the findings of Fredrickson (1969) that the number of eggs in the nest did not apparently affect the hatching ability of the eggs. While the mean clutch size was 6.1 eggs the nest of C1 in 1974 contained 12 eggs (the product of two females - see section on Dump Nesting) all of which hatched. The second clutch of E8 in 1973 consisted of two eggs, both of which hatched.

A changeover of the incubating adult was observed on several occasions. The sitting bird would be approached by its mate and while the bird approaching was still some 15 to 20 metres away the incubating bird would leave the eggs and swim away from the nest. Changeover of the incubating bird was carried out without any apparent ceremony, neither were any calls exchanged by the birds during a changeover. The incoming bird usually preened at the top of the ramp or on the nest rim before settling on the eggs.

The coot incubating was observed being fed while on the nest by its mate on several occasions at various sites. Kornowski (1957) commented that he has seen this behaviour on film but that he never witnessed it himself.

During a period of observation at C1 site in 1974 the following unusual behaviour was noticed. The bird at the time (6 May 1974) was sitting on 13 eggs - the product of two females (see section on Dump nesting) and the observational period lasted for 108 minutes.

"11.45 am Observation commenced. Coot sitting deep in the nest.

12.06 pm Changeover of adults. The bird starting to incubate, arranges the eggs underneath it.

12.15 pm Incubating bird stands up and rearranges the eggs with its bill. It then settles down in a new position, having made a slight turn to its left.

12.20 pm Incubating bird pulls in some loose T. latifolia which it places around rim of nest.

12.22 pm Mate brings in some T. latifolia which it deposits halfway up the ramp. Incubating bird pulls about half of it into nest structure.

12.25 pm Mate brings some T. latifolia which is ignored.

12.29 pm Incubating bird stands up and rearranges eggs with its bill. Settles down after again having turned further to the left.

12.33 pm More T. latifolia brought in by non-incubating bird. Both birds arrange it in structure. Incubating bird also rearranges position turning once more to the left. The amount of turn since incubation started is now approximately 135° from its original starting point.

12.46 pm Incubating bird stands - rearranges eggs with bill and turns back ie. to the right, about 45°.

01.15 pm Incubating bird stands, rearranges eggs and settles, turning again to the left.

01.20 pm Mate brings in more T. latifolia which is ignored by bird in nest.

01.30 pm T. latifolia again brought in - this time it is incorporated into the nest structure.

01.31 pm Incubating bird stands - rearranges eggs with bill and resettles after having turned once more to the

left. Turn now approximately 280° altogether.

01.33 pm Observation ends".

The incubating bird arranged the eggs and moved its position six times in the 108 minutes of observation i.e. once every 18 minutes on average. Of the 13 eggs being incubated, one, the last to be laid, was missing on 8 May. The other 12 all hatched.

Observations for short periods were made, on several other nests, but the regular turning movements were not seen as a part of the movements associated with incubation. The turning movement made by the incubating coot was possibly an adaption to the extra large number of eggs the bird was covering. A similar turning movement was reported by Siegfried and Frost (1975) for moorhens.

Clutch Size

There is little published regarding the clutch size of coot in Britain. Witherby (1938 - 41; 1948) gave the clutch size as six to nine eggs. Sage (1969) reported a mean of 5.9 eggs in 54 completed clutches. In comparing his mean with two other sets of European data he considered it possible that his mean was reduced because the coot he studied were colonising a new habitat. He thought this unlikely, however, as his mean for the years of 1966-68 when his population appeared to be stable was even lower at 5.8.

Deciding which eggs should be counted in a complete clutch for the coot is sometimes complicated by the addition of late eggs in a nest (see section on Dump Nesting). Therefore at Attenborough, in cases where real doubt existed regarding the number of eggs laid by one female in the nest, all the eggs in such a nest are counted in the clutch. Thus the odd late eggs laid in 1974 have been counted as part

of the clutch of the nest in which they were found. Where two females are thought to have laid in the same nest these have been counted as two clutches.

Figure 11 illustrates the clutch size data for all completed clutches at Attenborough including first completed clutches, completed re-nest clutches and second broods. Figure 12 illustrates clutch size data for all first complete clutches. The increased mean clutch sizes for first complete clutches (Figure 12) indicate that re-nest clutches were smaller than first clutches. This proved to be so, with the mean clutch size for the re-nest complete clutches very much smaller at 4.5 and 4.9 eggs per clutch for 1973 and 1974 respectively.

The number of eggs in the completed clutches varied from two to ten. The most frequent clutch size was six eggs, followed by five and seven eggs. 69.1% of all completed first clutches were found in these three classes and 89.1% of all the first completed clutches were within the range of four to eight eggs.

The mean clutch size for years 1973 and 1974 for all completed clutches was 6.1 $\pm$ 0.14 eggs (n = 124 clutches) and for all first completed clutches 6.2 $\pm$ 0.14 eggs (n = 110 clutches).

In order to examine clutch size further an examination of the BTO Coot Nest Record Cards for the years 1970, 1971 and 1972 was carried out. Unpublished research data on the coot, carried out by D. Rogers and R. Harrison at the Rostherne Mere National Reserve in Cheshire during 1972, 1973 and 1974 was also analysed.

a. <u>British Trust for Ornithology Nest Record Cards</u>

Of the 1,132 nest record cards received from the BTO 184 were

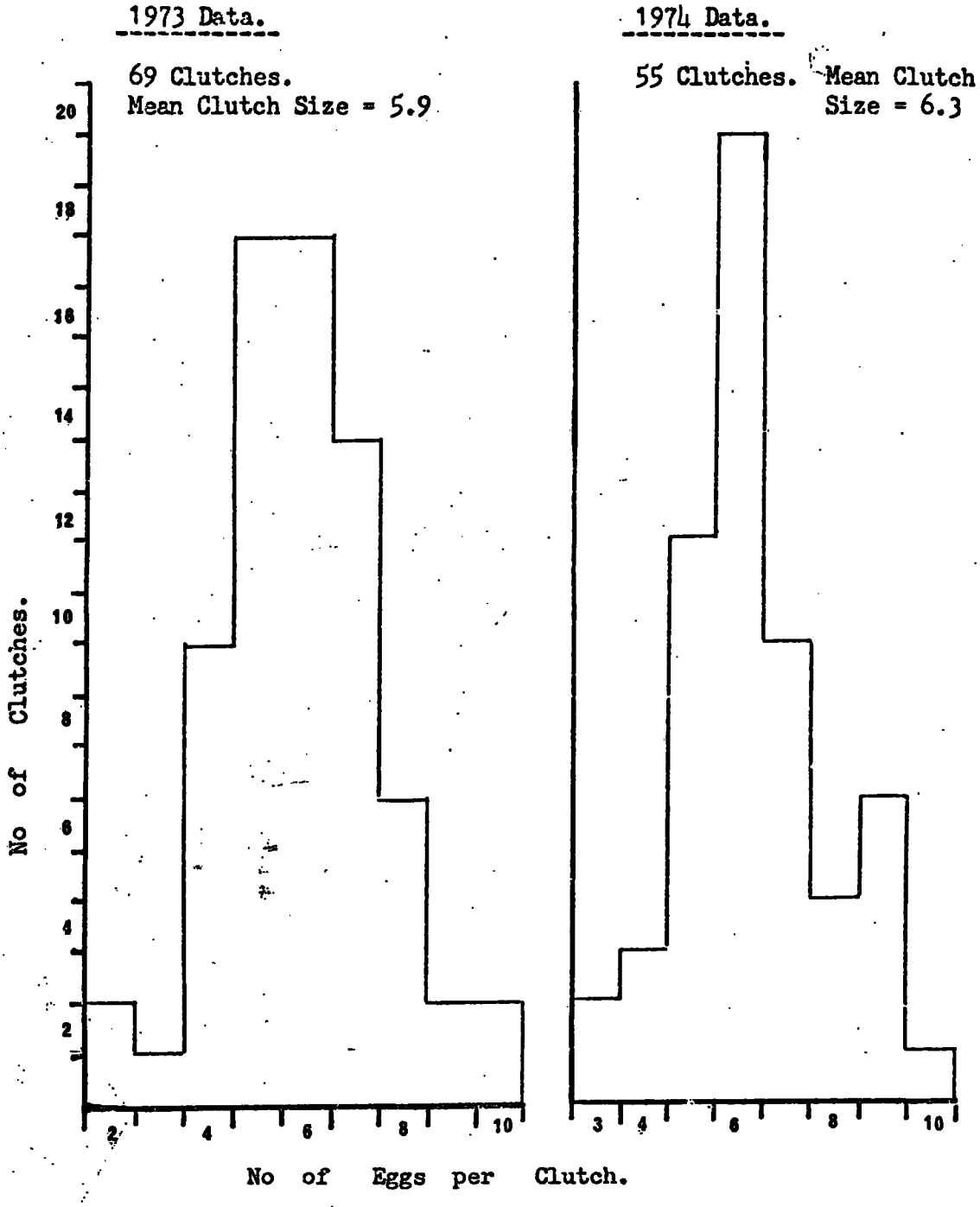


Figure 11 The number of eggs in all completed clutches.

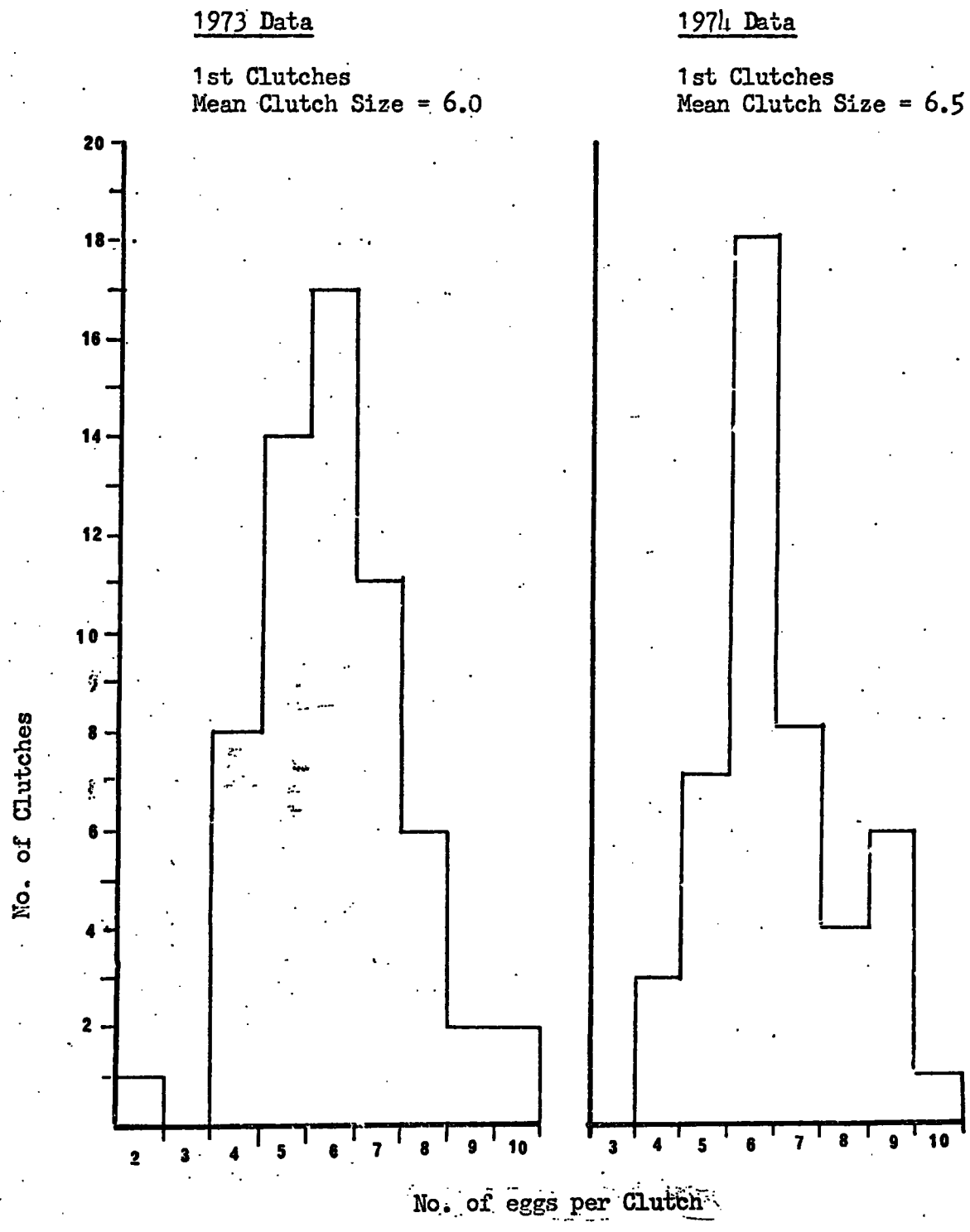


Figure 12. The number of eggs in all first complete clutches

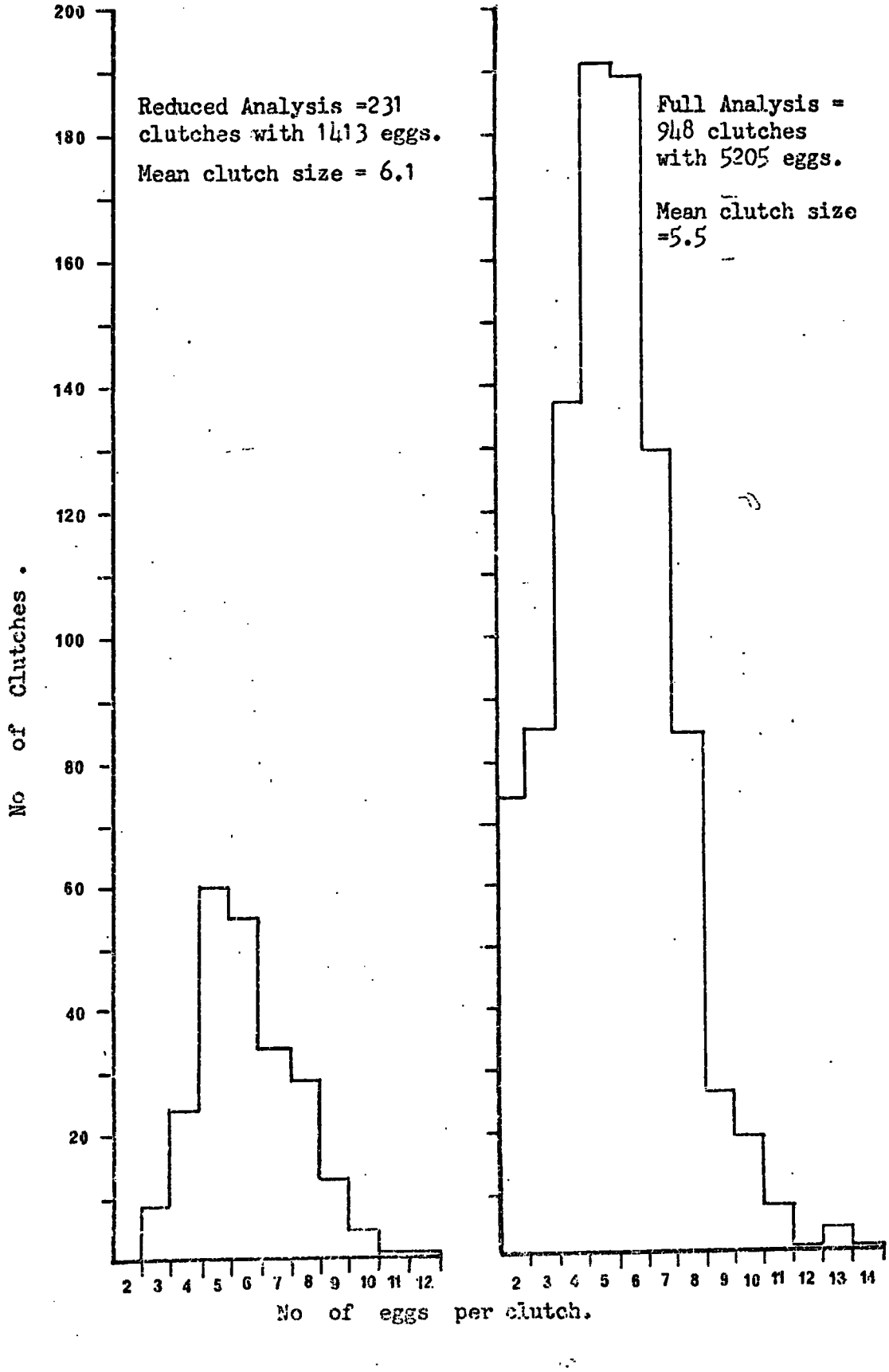
rejected as they do not list more than one egg. (The rejection of cards listing only one egg is based on the data in Table 11. Of the 2820 clutches from Europe (excluding the BTO clutches) only one is recorded as a one egg complete clutch). The remainder, 948 cards, were further checked and analysed for clutch size. The biases of nest record cards have been explored by Snow (1955), Newton (1964), Murton (1968) and Huxley and Wood (1976).

For the purpose of the analysis all the eggs recorded as being in a nest, whether they were laid late or not, were included in the clutch size of the nest. Figure 13 summarises the data extracted from the cards.

231 cards were analysed separately as the data indicated that these were complete clutches; these were also included in an analysis covering all the cards showing more than one egg in the nest. The cards were treated separately when two consecutive counts gave the same number of eggs and later counts did not increase the total by more than one or two eggs. Nests with young and eggs were added together to produce a clutch total. Some cards indicated that clutches were complete without having consecutive egg counts, for example a clutch with six eggs on a visit on 3 May may have seven eggs on 7 May. Even if no further visits on this nest are recorded the clutch would still be counted as a complete clutch of seven eggs as in the time available between the visits on the 3 and 7 May, if the eggs were still being laid in the nest, the clutch would have been ten eggs and not seven eggs.

The 231 cards gave a mean size for all completed clutches of

F igure 13. Analysis of British Trust for Ornithology Nest Record Cards for the Coot. Data from years 1970 ,1971 and 1972used.
Reduced Analysis - NRC only used if at least two counts of eggs showed same number or counts indicated clutch complete when nest data taken.
Full Analysis - all NRC showing more than one egg used in analysis.



6.1 eggs. The analysis of all 948 cards gave a mean clutch size of 5.5. As it seems likely some of the smaller clutches were not complete, there being a far greater chance of finding a nest before the clutch is complete of after the loss of some eggs than there is of finding a complete clutch. (Newton 1964: Murton 1968: Huxley and Wood 1976), an analysis of the Attenborough data was carried out to arrive at a realistic figure for the likely number of two and three egg clutches which would occur in a total of 948 clutches. The Attenborough data for all complete clutches include 1.5% and 2.4% of two and three egg clutches respectfully. 1.5% and 2.4% of the 948 BTO clutches are 14 and 23 clutches respectfully. D. Rogers and R. Harrison (pers. comm.) however, recorded 12% of their total clutches (n = 81) as completed clutches of two and three eggs. The actual number of BTO two and three egg clutches included in the clutch mean of 5.5 is 74 (7.8%) and 85 (9.0%) respectively. (Figure 13) Based on the Attenborough data the removal of 60 x 2 and 62 x 3 egg clutches from the BTO figures reduces the number of clutches to 826 and eggs to 4,899 and produces a corrected mean clutch size of 5.9 eggs with a modal clutch size of five eggs followed by six and seven eggs.

b. Rostherne Mere National Nature Reserve data

The data received from D. Rogers and R. Harrison (pers. comm.) gave 81 completed clutches with a mean clutch size of 5.7 eggs. The clutch size breakdown is given in Table 11 along with all the data on clutch sizes for Europe. D. Rogers commenting on the accuracy of his data stated:-

Nests. "Number of nests containing eggs at any time virtually 100% accurate."

Eggs. "Total number laid. Probably a slight underestimate, as eggs may be laid and lost between visits."

c. Clutch size in Britain

The data of the present study are presented in Table 11 along with the data of Sage (1969), the BTO nest record card figures and the records of D. Rogers and R. Harrison. In Table 11, the first line across in red figures (or underlined in black) gives a summary for the British data. A total of 490 completed clutches resulted in 2,948 eggs with a mean clutch size of 6.0 ± 0.08 eggs. The lowest mean clutch size is the 5.7 of D. Rogers and R. Harrison (pers. comm.), the highest is 6.1 recorded at Attenborough and also from the BTO data. The most frequent clutch size is six eggs (n = 130), followed by five (n = 119) and seven (n = 72).

On the basis of the data presented above the normal expected coot clutch lies between four and eight eggs, some 86.5% of all the British clutches analysed lying within this range. The three most frequent clutch sizes of six, five and seven eggs account for 65.5% of all recorded clutches. For Britain the very large clutches sometimes reported for coot are probably the work of one (or more!) females laying parasitically. The data from Sage (1969), D. Rogers and R. Harrison (pers. comm.), the BTO nest record cards and the present study indicate that six eggs is the common clutch size for the coot in Britain.

Table: II Comparison of Clutch Size of the Coot in Different Areas of Europe

Locality	Authority	Clutch Size 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	Total Clutches	No. of Eggs	Mean Clutch Size	Approx. Latitude and Longitude of Study Areas Lat.	Long
Notting-ham	Present Study	-	2	3	12	28	36	22	10	8	3	-	-	-	-	-	-	-	124	753	6.1	52.57N	1.10W
Hertford-shire	Sage	-	-	2	8	11	19	7	5	-	1	1	-	-	-	-	-	-	54	317	5.9	51.51N	.05W
Cheshire	Rogers & Harrison	-	2	8	9	20	20	9	6	4	-	2	1	-	-	-	-	-	81	465	5.7	53.12N	2.53W
England	B.T.O.	-	-	9	24	60	55	34	29	13	5	1	1	-	-	-	-	-	231	1413	6.1	50.0N/ 55.45N	14.0E/ 5.40W
British Data		-	4	22	53	119	130	72	50	25	9	4	2	-	-	-	-	-	490	2948	6.0		
Czech	Lelek	-	-	-	-	5	3	10	9	8	6	1	1	-	-	-	-	-	43	340	7.9	49.20N	15.00E
"	Havlin	-	-	1	16	37	72	74	68	30	6	6	6	1	-	1	1	-	319	2258	7.1	49.20N	15.00E
		-	-	1	16	42	75	84	77	38	12	7	7	1	-	1	1	-	362	2598	7.2		
Sweden	Askaner	-	-	-	-	2	2	5	5	2	-	-	-	-	-	-	-	-	16	115	7.2	55.33N	13.08E
Germany	Wagner	-	-	1	-	2	1	2	3	3	1	1	-	-	-	-	-	-	14	105	7.5	54.6N	13.23E
"	Kornowski	-	-	-	-	-	8	19	23	18	-	1	1	-	-	-	-	-	70	550	7.9	54.0N	10.0E
"	Bezzel	1	3	-	1	8	19	62	59	58	18	7	3	-	-	-	-	-	239	1886	7.9	48.8N	11.35E
		1	3	1	1	10	28	83	85	79	19	9	4	-	-	-	-	-	323	2541	7.9		
Latvia	Blums	-	-	-	18	85	171	368	515	384	183	75	39	13	4	4	-	1	1860	15100	8.1	57.20N	23.00E
Continental European Data		1	3	2	35	739	276	540	682	503	214	91	50	14	4	5	1	1	2561	20354	7.9 ± 0.01		

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Comparison of Attenborough Clutch Data with Data from European Literature

Table 11 attempts to collate all the modern data from Europe on the clutch size of the coot. Summaries are given for the British data (four studies: Present study, Sage (1969), D. Rogers and R. Harrison (pers. comm.) and BTO), Czechoslovakia (two studies: Lelek 1958 and Havlin 1970) and Germany (three studies: Kornowski 1957, Wagner 1962, Bezzel 1967). The data for all the studies, other than the British, have been added so that comparisons with the British data can be made (Figure 14).

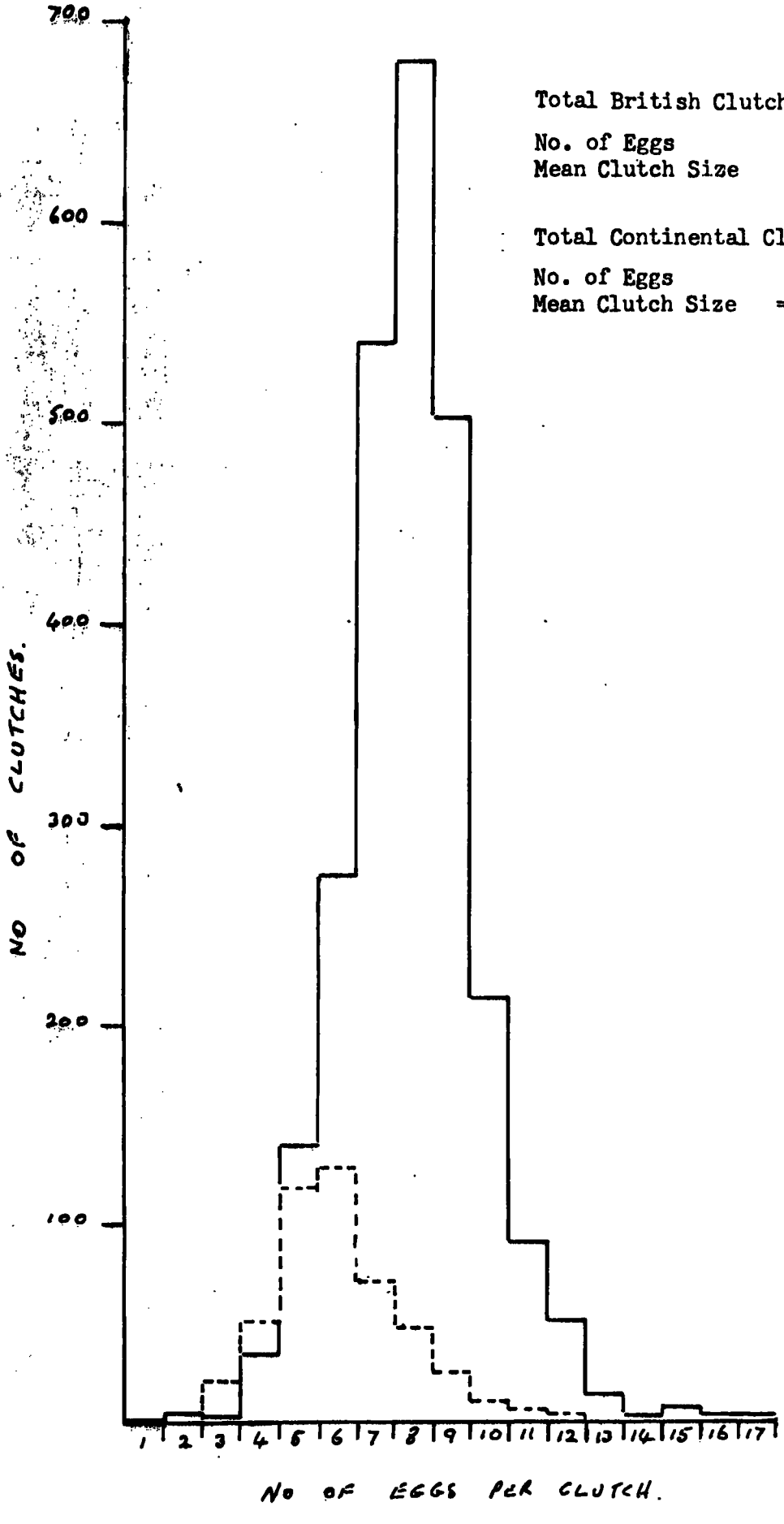
The size of the coot's clutch in Europe ranges from one egg to 17 eggs. However, some 90.0% of all the recorded clutches occur in the range of five to ten eggs. Within the shortened range of six to nine eggs are found some 74.6% of all clutches. Havlin (1970) and Blums (1963) both believed their clutches of over 15 eggs could be the work of two or more females laying in one nest.

The Continental European mean clutch size of 7.9 eggs is significantly higher than the British mean size of 6.0 eggs. ($d = 23.06$, $P < 0.001$)

Clutch Size Variation with Latitude and Longitude

The data in Table 11 have also been used to test the hypothesis that the clutch size of a bird is related to the latitude and longitude at which it breeds (Lack 1947; 1948a, Wagner 1957; Skutch 1967).

The approximate latitude and longitude of each of the



Total British Clutches = 490

No. of Eggs = 2948
Mean Clutch Size = 6.0 ± 0.03 eggs.

Total Continental Clutches = 2561

No. of Eggs = 20354
Mean Clutch Size = 7.9 ± 0.01 eggs.

Figure 14. Analysis of Clutch Size

——— = Continental European data.

------ = British data.

studies is shown in the last two columns of Table 11. The data indicate no apparent correlation of clutch size with either latitude or longitude (Rank Correlation Coefficent =-0.02; $P > 0.1$ and 0.46; $P > 0.1$ respectively).

Clutch Size in Relation to Date of Egg-Laying

An examination of the research on the coot in Europe suggests that it is a bird in which a reduction of the number of eggs per clutch occurs as the season progresses. Bezzel (1967), Havlin (1970) and Blums (1973) all report a measurable decrease in clutch size as the season progresses. Bezzel (1967) gives mean clutch size figures for three periods:- April to middle May - mean 8.4 eggs (n =43), middle May/end June - mean 7.8 eggs (n = 52) and July - mean 6.7 eggs (n = 33). Havlin (1970) reviewing 1,131 clutches from Czechoslovakia records as follows:-

Month	Mean clutch size	size of sample (clutches)
March 10-20	7.75	4
" 21-30	8.8	27
April 1-10	8.5	86
" 11-20	8.1	153
" 21-30	7.6	293
May 1-10	7.5	239
" 11-20	6.9	165
" 21-30	6.6	88
June 1-10	6.1	29
" 11-20	5.9	23
" 21-30	5.9	19
July 1-10	5.0	4"

Havlin's (1970) data apparently confirms the trend of a decreasing clutch size with the advancement of the breeding season. His data could not be analysed statistically as his paper did not show individual clutch sizes.

Blums (1973) analysing 821 clutches in Latvia found that the mean clutch size fell from 9.1 eggs in the first week of egg-laying to a mean of 6.0 eggs in the sixth week.

There is no British data published on this topic for the coot. However, Huxley and Wood (1976) in their study of the moorhen reported a rise in mean clutch size through March and early April with a peak occurring in late April before a steady decrease throughout May and June.

Tables 12 and 13 and Figures 15 and 16 examine clutch size in relation to the date of egg-laying for 90 Attenborough clutches and for data extracted from 231 British Trust for Ornithology Nest Record Cards. A regression analysis was carried out for both sets of data. At Attenborough (Table 12 and Figure 15) there was no significant correlation ($r = -0.16$, $P > 0.1$) between clutch size and laying date. The BTO data (Table 13 and Figure 16), however, indicated a significant correlation ($r = -0.28$, $P < 0.01$) with a decrease in clutch size as the breeding season progressed.

The problem of how these data may be affected by re-nest clutches is discussed in the following section.

a. Re-nest clutches

Lelek (1958), Sage (1969) and Blums (1973) found that coot will relay several times if the previous nests are lost before incubation is complete. In order to make a discussion of clutch

Table 12: Clutch Size in Relation to Laying Date

Complete clutches only used

Date		No. of Clutches 1973/74	No. of Eggs 1973/74	Mean Clutch Size 1973/74
March		1	8	8
April	1 - 5	3	19	6.33
	6 - 10	5	32	6.4
	11 - 15	5	34	6.8
	16 - 20	5	36	7.2
	21 - 25	4	27	6.75
	26 - 30	12	83	6.92
May	1 - 5	20	132	6.6
	6 - 10	9	51	5.67
	11 - 15	9	51	5.67
	16 - 20	7	46	6.57
	21 - 25	6	32	5.33
	26 - 31	7	30	4.29
June	1 - 5	1	3	3.0
	6 - 10	1	6	6.0
	11 - 15	1	7	7.0
	16 - 20	1	6	6.0
	21 - 26	-	-	-

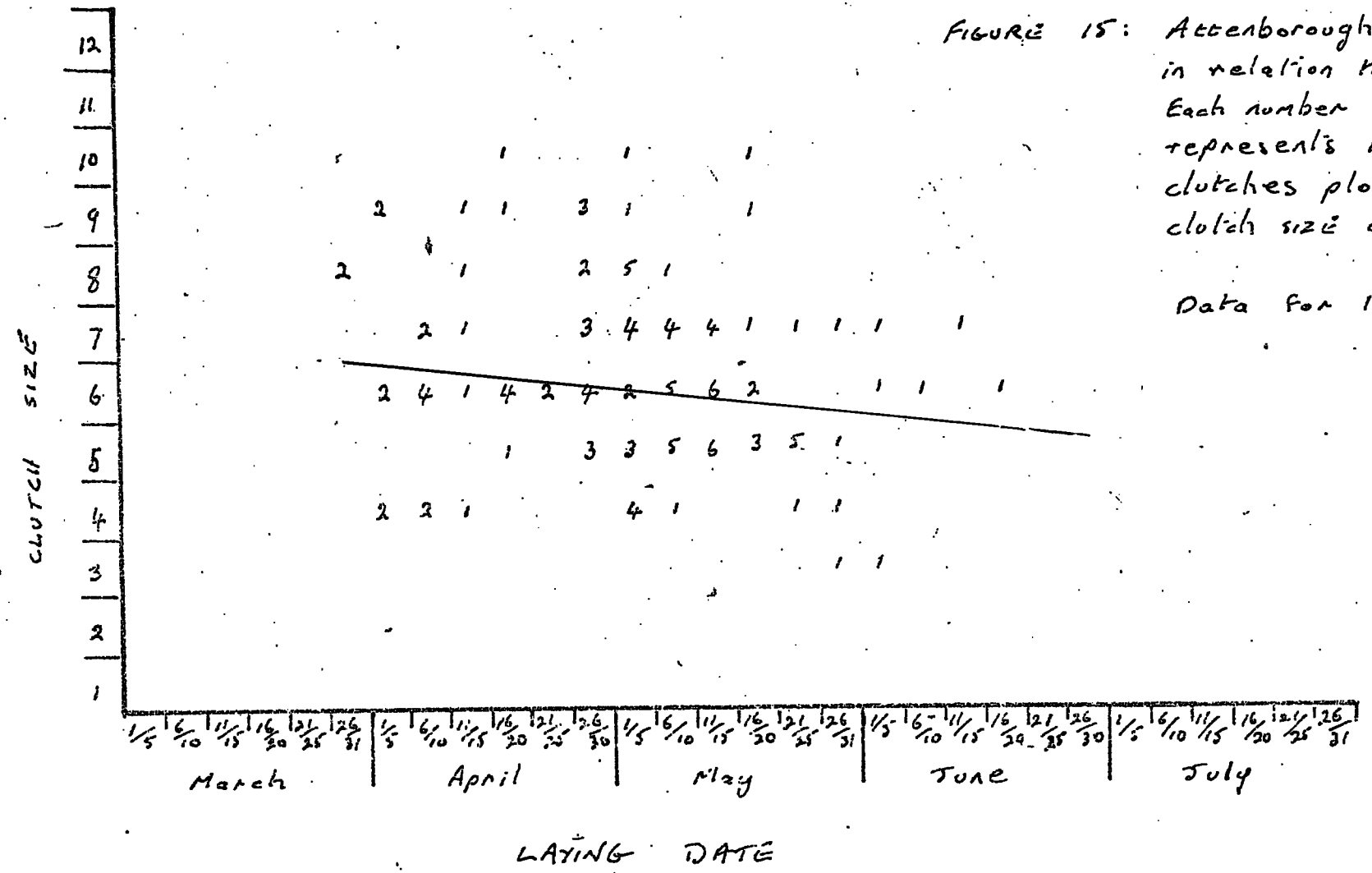


FIGURE 15: Attenborough clutch size in relation to laying date. Each number in the graph represents the number of clutches plotted against clutch size and laying date.

Data for 1973/1974 combined.

Table 13: Clutch size in relation to laying date. 1970/71/72 BTO data: Only clutches thought to be complete have been used.

Date		No. of Clutches	No. of Eggs	Mean Clutch Size
March		1	5	5.0
April	1 - 5	1	7	7.0
	6 - 10	10	76	7.6
	11 - 15	13	80	6.2
	16 - 20	13	81	6.2
	21 - 25	10	61	6.1
	26 - 30	7	47	6.7
May	1 - 5	51	355	7.0
	6 - 10	41	262	6.4
	11 - 15	12	73	6.1
	16 - 20	11	60	5.6
	21 - 25	15	88	5.9
	26 - 31	13	63	4.8
June	1 - 5	3	18	6.0
	6 - 10	5	26	5.2
	11 - 15	4	20	5.0
	16 - 20	2	11	5.5
	21 - 25	5	25	5.0
	26 - 30	1	5	5.0
July	1 - 15	8	42	5.3
	16 - 31	5	28	5.6

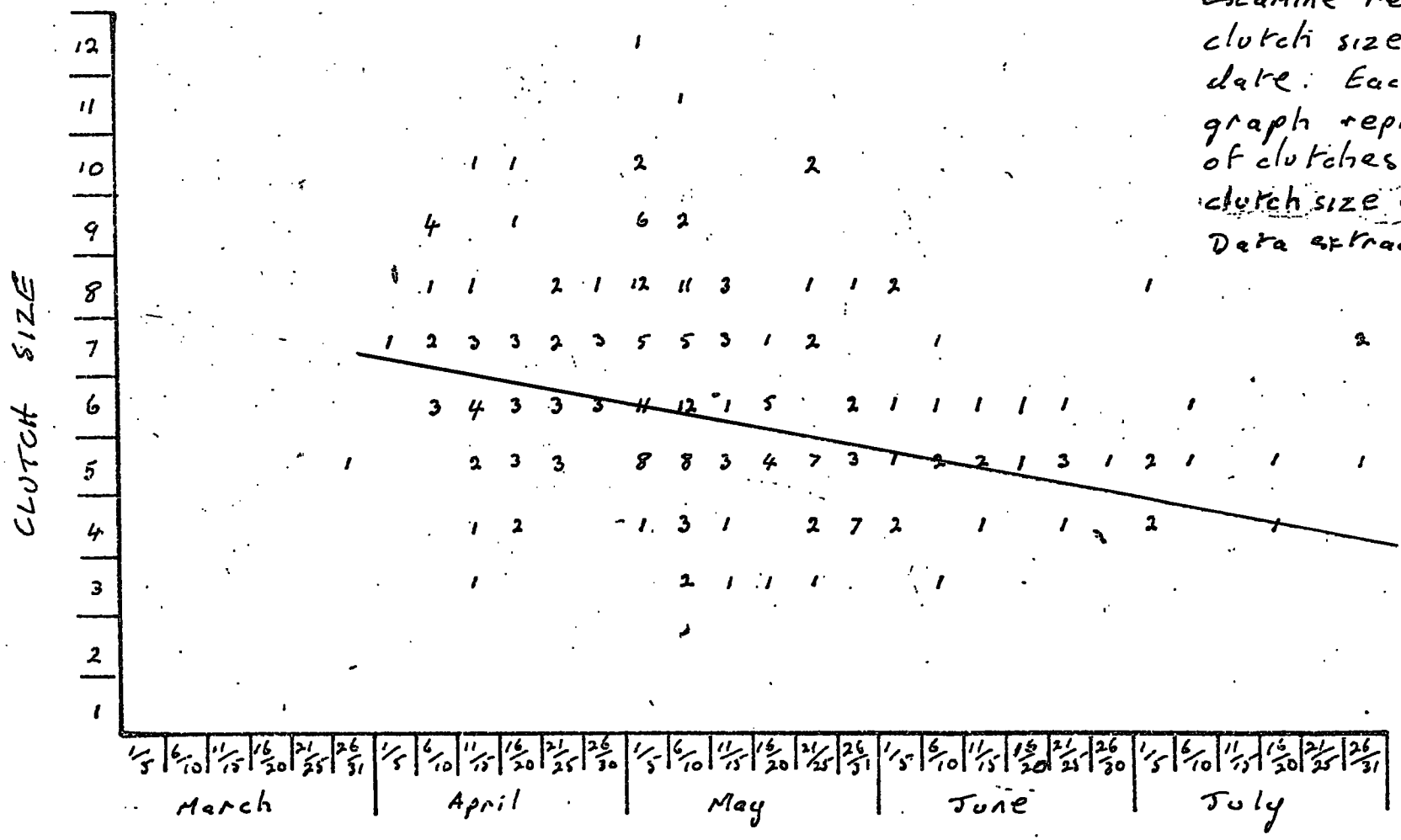


FIGURE 16 BTO data analysed to examine relation between clutch size and laying date. Each number in the graph represents the number of clutches plotted against clutch size and laying date. Data extracted from Table 13.

size in relation to laying date meaningful, the size of the re-nest clutches needs to be known so that their effect, if any, on the overall clutch size can be identified.

Lelek (1958) found coot attempting to re-nest up to three times. For first clutches he records a mean of 8.85 eggs, first re-nest 6.92 eggs, second re-nest 7.25 eggs and for two third re-nest attempts clutches of nine and six eggs were laid. Lelek (1958) concluded that it is not rare for "the coot to lay more eggs in a compensation than in the original (first) clutch." Sage (1969) recorded a clutch of 11 eggs for a third re-nesting attempt, after an incomplete clutch and a complete clutch of seven eggs had been lost. Havlin (1970) in his review of data from Europe concluded that "repeat clutches are smaller than the original ones as a rule". Blüms (1973) recorded that for 34 nests there was a mean decrease of 1.2 eggs per clutch for re-nest clutches. In 32% of the clutches, the number of eggs in the re-nest and first clutch was the same but he never found a re-nest clutch larger than the original clutch.

The mean clutch size of the Attenborough re-nest and second broods was very much smaller than the mean of all first clutches. i.e. mean of 4.7 eggs for re-nests, mean of 6.2 for all complete clutches. However, if a comparison is made between re-nest/second brood clutches and first completed clutches laid by the same birds, the mean difference is slightly smaller with a first complete clutch of 5.8 eggs and a re-nest mean of 4.8 eggs. Of the twelve nest examined, eight had smaller second clutches, three had equal eggs in both clutches and one had a larger re-nest clutch (by one egg) than the first clutch.

The part re-nest clutches play, if any, in depressing clutch size as the season progresses is not clear from the above data. Although re-nest clutches, on average, do appear to contain fewer eggs than first clutches and would apparently be a factor in reducing clutch size as the season progresses it has been shown (see page 98) that at Attenborough all 13 re-nest clutches had been started earlier than five of the first clutches of late breeders.

Clutch Size and Breeding Success

The only data located which relates coot clutch size to breeding success is that of Blums (1973) who reported that the percentage survival rate of young coot is higher for broods from clutches of eight to eleven eggs (mean clutch and modal clutch size eight eggs) than from clutches of below average size.

Tables 14 and 15 and Figure 17 examine the breeding statistics of the coot at Attenborough, in relation to the size of all first completed clutches. The data for 1973 and 1974 differ considerable in respect of percentage breeding success. In 1973 (Table 14) the re-nest clutches were almost as successful as the first clutches in fledging young. The most successful first clutch size in 1973 was four eggs (n = 9 clutches), with a percentage breeding success of 36.1%; this was followed by clutch size eight eggs (n =6) with 29.2%. The least successful clutch size with respect to percentage breeding success was the modal clutch of six eggs (n =17 clutches) at only 13.7%. The percentage breeding success in 1974 (Table 15) for first clutches was 18.2%: re-nest clutches

Table 14: Breeding information in Relation to Clutch Size for 1973
Complete Clutches Only Used in Analysis.

1st Clutches

No. of eggs in clutch	No. of clutches	No. of eggs laid	No. of eggs hatched	% of eggs hatched	No. of young fledged	% of young fledged	% Breeding Success
2	1	2	0	-	-	-	0.0
3	0	-	-	-	-	-	-
4	9	36	25	69.4	13	52.0	36.1
5	14	70	35	50.0	14	40.0	20.0
6	17	102	28	27.5	14	50.0	13.7
7	12	84	44	52.4	23	52.3	27.4
8	6	48	21	43.8	14	66.7	29.2
9	2	18	15	83.3	44	26.7	22.2
10	2	20	14	70.0	5	35.7	25.0
Total	63	380	182		87		
Means				47.9%		47.8%	22.9%

2nd Clutches and 2nd Broods

2	1	2	2	100.0	2	100.0	100.0
3	1	3	3	100.0	1	33.3	33.3
4	0	-	-	-	-	-	-
5	3	15	8	53.3	3	37.5	20.0
6	0	-	-	-	-	-	-
7	1	7	0	-	-	-	0.0
Total	6	27	13		6		
Means				48.1%		46.2%	22.2%

Table 15: Breeding information in Relation to Clutch Size for 1974 Complete Clutches Only Used in Analysis.

1st Clutches Data

No. of eggs in clutch	No. of clutches	No. of eggs laid	No. of eggs hatched	% of eggs hatched	No. of young fledged	% of young fledged	% Breeding Success
2	0	-	-	-	-	-	-
3	0	-	-	-	-	-	-
4	3	12	2	16.7	1	50.0	8.3
5	7	35	6	17.1	3	50.0	8.6
6	18	108	62	57.4	16	25.8	14.8
7	8	56	30	53.6	12	40.0	21.4
8	4	32	16	50.0	9	56.3	28.1
9	6	54	27	50.0	12	44.4	22.2
10	1	10	9	90.0	3	33.3	30.0
Total	47	307	152		56		
Means				49.5%		36.8%	18.2%

2nd Clutches and 2nd Broods

2	0	-	-	-	-	-	-
3	2	6	2	33.3	0	-	0.0
4	0	-	-	-	-	-	-
5	4	20	17	85.0	3	17.7	15.0
6	1	6	5	83.3	0	-	0.0
7	1	7	0	-	-	-	0.0
Total	8	39	24		3		
Means				61.5%		12.5%	7.7%

dropped to 7.7%. The modal class of six eggs per clutch again had a low percentage breeding success at 14.8%.

In 1973, there was no correlation ($r = 0.18$, $P > 0.1$) between clutch size and breeding success. The 1974 data, however, show a high correlation ($r = 0.93$, $P < 0.01$) between clutch size and breeding success with the larger clutch sizes having higher levels of breeding success (Figure 17).

The results indicate that in one of the two years larger clutch sizes gave rise to a higher breeding success rate.

Breeding Success of the Coot at Attenborough

In calculating breeding success only pairs that produced eggs have been included in the data. In 1973 and 1974 there were eight and seven pairs respectively holding territories in which no eggs were laid. Table 16 examines coot breeding data for all completed clutches recorded during 1973 and 1974. Table 17 shows these data combined. The data have been divided into the five sub-areas which comprised the total area. The total number of of clutches has been shown as first and second clutches: this distinction has been maintained throughout the tables in order to clarify the relative contributions of both types of clutches to the overall breeding success.

The number of eggs hatched as a percentage of the number of eggs laid was slightly higher, for all complete clutches, in 1974 than in 1973 (50.9% as against 47.9% respectively) with a mean of 49.3%. The percentage of hatched young which finally fledged was significantly lower in 1974 than in 1973 (34.5% as

Figure 17. Comparison of clutch size frequency with percentage breeding success. First complete clutches only.

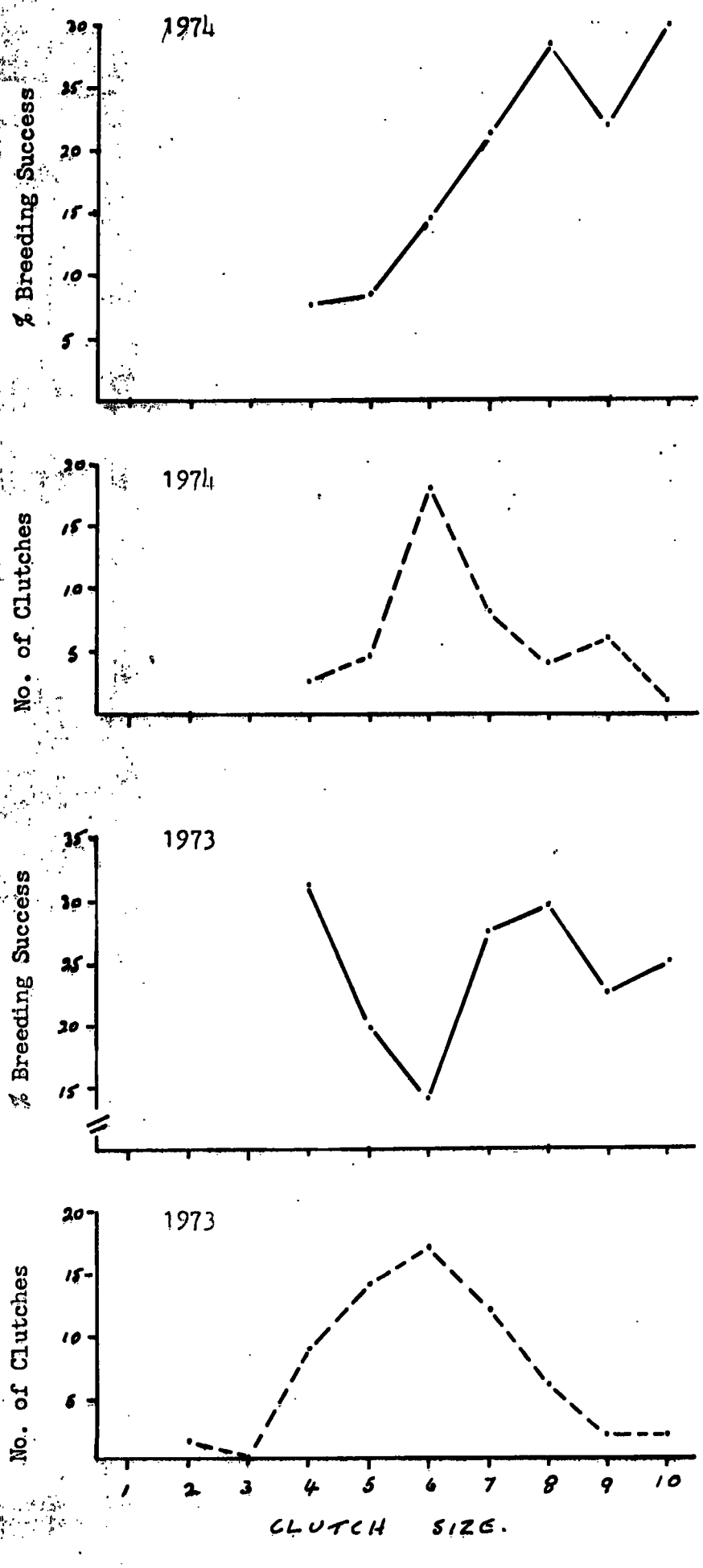


Table 16. Breeding information of Coot (Fulica atra) at Attenborough during 1973-74 according to Area Code. Completed clutches only used for data analysis.

1973 First clutches shown separately. Repeat clutches and second broods added together and shown as second clutches.

Area Code	Pairs on Territory	Pairs laying	No. of completed clutches		No. of eggs laid		No. of eggs hatched		% eggs hatched		No. of young fledged		% young fledged		%Breeding success		No. of young fledged per pair laying
			1st	2nd	1st	2nd	1st	2nd	1st	2nd	1st	2nd	1st	2nd	1st	2nd	
A	10	10	10	1	62	5	30	3	40.4	60	16	1	53.3	33.3	26.0	20.0	1.7
B	8	8	8	0	44	-	30	-	75.0	-	13	-	43.3	-	29.5	-	1.6
C	15	12	12	0	68	-	35	-	51.5	-	16	-	45.7	-	23.5	-	1.3
E	32	29	28	5	171	22	72	10	42.1	45.5	38	5	52.7	50.0	22.2	22.7	1.5
F	10	8	5	0	35	-	15	-	42.9	-	4	-	26.7	-	11.4	-	0.5
	75	67	63	6	380	27	182	13	47.9	48.1	87	6	47.8	46.1	22.9	22.2	
			69		407		195		47.9 %		93		47.7 %		22.8 %		1.4

1974

			1st	2nd	1st	2nd	1st	2nd	1st	2nd	1st	2nd	1st	2nd	1st	2nd	
A	11	10	9	1	57	5	34	4	59.6	80.0	15	2	44.1	50.0	26.3	40.0	1.7
B	10	6	6	1	38	5	20	5	52.6	100.0	10	1	50.0	20.0	26.3	20.0	1.8
C	13	11	9	2	51	12	27	4	52.9	33.3	6	-	22.2	-	11.8	-	0.5
E	25	25	22	4	153	17	71	11	46.4	64.7	25	-	35.2	-	16.3	-	1.0
F	1	1	1	0	8	-	0	-	-		-	-	-	-	-	-	0.0
	60	53	47	8	307	39	152	24	49.5	61.5	56	3	36.8	12.5	18.2	7.7	
			55		346		171		50.9 %		59		34.5 %		17.0 %		1.1

Table 17. Breeding information of Coot (Fulica atra) at Attenborough during 1973/74 according to Area Code. Completed clutches only used for data analysis.

1973/74 First clutches shown separately. Repeat clutches and second broods added together and shown as second clutches.

Area Code	Pairs on Territory	Pairs laying	No. of completed clutches		No. of eggs laid		No. of eggs hatched		% eggs hatched		No. of young fledged		% young fledged		%Breeding success		No. of young fledged per pair laying
			1st	2nd	1st	2nd	1st	2nd	1st	2nd	1st	2nd	1st	2nd	1st	2nd	
A	21	20	19	2	119	10	64	7	53.8	20.0	31	3	48.4	42.9	26.0	30.0	1.7
B	18	14	14	1	82	5	50	5	61.0	100.0	23	1	46.0	20.0	28.0	20.0	1.7
C	28	23	21	2	119	12	62	4	52.1	33.3	22	0	35.5	-	18.5	-	1.0
E	57	54	50	9	324	39	143	21	44.1	53.8	63	5	44.0	23.8	19.4	12.8	1.3
F	11	9	6	0	43	-	15	-	34.9	-	4	-	26.7	-	9.3	-	0.4
	135	120	110	14	687	66	324	37	48.6	56.1	143	9	42.8	24.3	20.8	13.6	
			124		753		371		49.3 %		152		41.0 %		20.2 %		1.3

against 47.7% (d = 2.56, $P < 0.02$) with a mean of 41.5%. The percentage breeding success, i.e. the number of young fledged as a percentage of the number of eggs laid, was higher in 1973 (22.8%) than in 1974 (17.0%) with a mean of 20.2% (Tables 16 and 17).

The overall drop in breeding success in 1974 was largely caused by the failure of the second clutches to fledge young. After a hatching rate of 61.5%, the highest rate recorded during the two breeding seasons, the percentage of young fledged from the second clutches was only 12.5%. This is very low when compared with the percentage of young fledged from the first and second clutches of 1973 and the first clutches of 1974 - respective rates recorded as 47.8%, 46.1% and 36.8%. The drop in the number of young fledging from second clutches in 1974 was significant (d = 2.35, $P < 0.02$).

a. Factors affecting breeding success

At Attenborough of the 753 eggs laid in completed clutches only 371 hatched (Table 17): thus 50.7% of all eggs failed to hatch. Alley & Boyd (1947) with 65.3%. Lelek (1958) 56.4%, Askaner (1959) 60.5% and Sage (1969) 66.2% all recorded higher egg losses. Bezzel (1959) 33.0%, Blums (1963) 25.0% and Havlin (1970) 13.4% quoted much lower egg losses.

Various facts are quoted by research workers as affecting breeding success.

Lelek (1958) mentioned that the hooded crow (Corvus cornix) used to watch while coot nests were checked and that such nests were often attacked before the adult coot returned.

McCartan and Simmons (1956) recorded that at Theale Gravel Pits an incubating great crested grebe killed several young coot as they left their nest. They also reported that the pike was the chief predator on the young of the great crested grebe on the Burghfield Gravel Pits in Berkshire.

Alley & Boyd (1947) considered that other territorial coot contributed greatly to the mortality of the young: they saw one adult coot drown a young bird from another nest. They recorded that the period up to three weeks was the time when most young die: very often the "young would disappear without trace."

A factor which is thought to cause heavy egg losses in coot is the loss of whole clutches through wave action (Sage 1969) swamping nests or rising water chilling eggs.

Hendrickson (1936) investigated mortality in the American Coot after 6.4 cm. (2.5 inches) of rain fell over two days found that where the nests were free to rise and fall with the water level, nest cups were dry and the young survived. In three nests, however, he found one, three and five dead young. These were in soaked nests that were only 25 mm (one inch) above the water level and had not risen steadily with the rising water. Hendrickson (1936) suggested that the young birds "drowned in the nests or died of chilling either with or without a brooding parent at the nest." Macdonald (1962) and Fredrickson (1969) believe that chilling causes heavy losses in some nidifugous young because of the inability of the parents to find enough food for the young and/or to brood them properly in adverse weather conditions.

Havlin (1970) concluded that the very high egg losses found in coot by all but himself, Bezzel (1959) and Blums (1963), were

attributable to "extraordinary local conditions and directly to the method of investigation."

It is difficult to disprove that losses are caused by the investigator and some were certainly caused by the nest checking activities at Attenborough. For example an incomplete clutch of two eggs was lost to crows because of nest investigations. Crows were noticed early in 1974 to be following me around areas C and E as nests were checked from the boat. Normally on my approach the adult coot would leave the nest area, sometimes going around the back of an island or out of sight in the vegetation - after noting the behaviour of the crows the precaution was taken or remaining within sight of the nest being investigated until the resident coot had returned to the immediate nest vicinity. On several occasions crows had to be flushed away from a recently visited nest; the crow usually alighted in a nearby tree and then moved slowly down through the branches until just over the nest. On one occasion a crow flew down to the mud shore and walked slowly towards the nest. Usually the presence of a crow in the territory immediately caused one of the adult coots to hurry towards the nest site - whether it contained eggs or not and it would drive the crow away.

It is also possible that I contributed to some of the losses of the young, as once they could leave the nest the young tended to scatter from the nest on my approach. However only on one occasion was it necessary to rescue a chick and return it to the nest site. Normally the young keep up a constant 'peeping' which is used by the parent for location purposes. It would however be

unwise to discount the possible losses the presence of an observer might have on such small young purely by driving them away from the comparative safety of the nest site.

In order to clarify the causes of egg and chick loss particular attention was paid to this aspect in 1974. Odd eggs were only infrequently lost from a nest, usually because of the activities of the parent coot in nest which had tilted nest cups so that the eggs could roll out fairly easily, as is illustrated in Plate 52. A few eggs were abandoned after failing to hatch. I did not collect figures for the loss of odd and abandoned eggs but they were very few when compared with those recorded by Alley & Boyd (1947). They record 6% and 4% of the 79 lost eggs as due to knocking out and abandonment respectively.

The total number of clutches started in 1974 was 61; of these six clutches were never completed and 16 of the completed clutches were lost before they hatched any young. In spite of the effort made to discover the reasons for egg loss, in eight cases no definite cause could be found. The possibility must exist that some of the unexplained losses were caused by rising water chilling the eggs, which were then deserted with the eggs subsequently being taken by crows.

The coot's apparent ability to recognise a chilled egg was shown by the action of a bird at E20 site in 1974. On 28 May the coot were incubating nine eggs. One of the eggs previously marked on 22 May was cold and was lying underneath the rest of the eggs in its own depression in the bottom of the nest. The depression in the cup base was filled by me and the chilled egg mixed with the other eight eggs. On the next visit, on 11 June,

this egg was again found in the base of the nest and was cold: the other eight eggs were all warm. The first young were seen on 15 June but the nest was not visited until 18 June. The only egg remaining in the nest was the chilled one. At least four young were with their parents in some nearby Carex spp.

It proved impossible to verify any losses of young coot by chilling but they can sometimes be some distance from a parent, especially on the island nest sites, and they could easily be chilled in a sudden storm before they are able to reach their parents. Adult coot were seen on two occasions in heavy rain merely to sit and call the young to them. The young were then brooded until the rain stopped.

The quickly rising water, coupled with strong winds, definitely caused five nests to be flooded and the clutches were lost. One nest under a Salix was lost when a gale blew over the tree and crushed the eggs. Full clutches from two nests were almost certainly taken by children and one incomplete clutch was deserted because of disturbance by fishermen. A full clutch was taken by a fox and it is believed that four nests were annexed by other species. Of these four nests one was taken over by a female mallard after the coot had incubated for 18 days.

The mallard was deliberately disturbed; the eggs were just warm but were not being incubated. The eggs were left in the nest which was very much flattened; the nest cup had been crushed and the eggs were virtually lying on a platform only. The next day a female mallard was again on the nest; investigation proved the eggs were intact and slightly warm. (The coot which had laid these eggs were found on the same date some 15 m. away with an

almost complete new nest. They subsequently laid and hatched five eggs from which one young fledged). The mallard never returned to the site and the eggs remained intact for a further five days before they were removed for examination.

Two other clutches were found in similarly crushed nests with intact clutches; eggs from these later disappeared and were probably taken by crow or magpie. Observations failed to ascertain whether the clutches were deserted by the coot before the nests were appropriated by the other species or if the coot were forced to relinquish their nests in the face of interspecific aggression.

Almost all the recorded chick losses at Attenborough occured while the young were three to ten days old (confirming the findings of Alley and Boyd 1947).

For the first two or three days, the young stay in or on the nest and are fed by the parents bringing food to the nest. Usually one adult stays brooding the young on the nest while the other forages for food. From about the age of three days the young spend most of their time out of the nest while they follow their parents for; unlike most nidifugous species, the young appeared to be totally dependent on their parents for food for about the first three weeks (See section on Development and Care of the Young).

Over the two years five newly hatched young were found dead. One was found floating in the water and was at least 100 m. from any known nest, the other four were found dead in the nest. Three of these had apparently hatched normally and then at some early date (one to three days) they had been crushed to death. The other

was extremely small and it had apparently died immediately after hatching and before its feathers had dried out.

Crows might account for some losses as the young tend to stray long distances along any shore-line within their territory. Such losses at Attenborough are considered slight. Crows were never seen to be attempting to take young coot, possibly the crows had an abundance of more easily obtained food at this time.

Attacks by other territorial coot on the chicks of rival pairs did occur. Mild attacks were recorded on several occasions, and a severe attack once on young birds wandering outside their own territory but this behaviour was seen so infrequently that it is doubtful that it could have more than a minor effect on fledging results overall at Attenborough.

Great crested grebe often nested in very close proximity to the coot (see page 182) and there must have been many occasions when the behaviour as reported by McCarton/Simmons (1956) and noted on page 156 could have occured although such behaviour was not recorded.

Probably the main predator on waterfowl at Attenborough is the pike. Although young birds were never seen to be taken by this animal several fishermen stated that they had seen young swimming birds disappear from the surface of the water in a sudden swirl. One fisherman spoke of seeing five young duckling (out of seven) disappear in one rush by a large pike. The description fitted the tufted duck, a small number of which breed at Attenborough. Pike are common over the pit complex and very many are caught each year (per. comm. with the Water Bailiff) and I have personally seen pike of over one m. in length spawning in the Wet Marsh area. Many areas of the pits hold large numbers of small or

jack pike and it is these which are thought to be the main predators on small surface swimming animals when they are close inshore.

b. Breeding success in relation to habitat

No studies have been located on Fulica atra which quote breeding success rates in relation to the varying habitats found within one study area.

At Attenborough one part of area 'E' known as Wet Marsh (Figure 1) held breeding coot at a much higher density in both 1973 and 1974 (Figure 3 and 4) than any other part of the study area. Using the terminology of Brown (1969) this has been called the preferred area. Area data were examined to see if the area of highest breeding density gave rise to greater productivity with respect to clutch size and overall breeding success.

Within the preferred area there was an increase in mean clutch size, first complete clutch only, for both 1973 and 1974 when compared with all the other areas (Table 18).

Table 18.

Clutch size in preferred area compared with the rest of the study area.

Year	$\bar{x}$ clutch size in preferred area	No. of clutches	$\bar{x}$ clutch size over rest of area	No. of clutches
1973	6.6 ± 0.21	7	5.9 ± 0.09	56
1974	7.6 ± 0.16	7	6.4 ± 0.09	40

This difference in mean clutch size between the preferred and

the nest of the area was examined statistically for both 1973 and 1974. The results for 1973 ($t = 0.98$, $P > 0.1$) were not significant whereas for 1974 ($t = 2.02$, $P < 0.05$) the results were significant. The results indicate that in 1974 the areas with higher breeding densities (higher breeding densities have been shown to be correlated with the richness of food supply (Lack 1958)) gave rise to larger clutches.

In the preferred area the number of pairs on territory producing first complete clutches in 1973 and 1974 was seven (Table 18). In both the preferred and the rest of the area the mean clutch size increased in 1974. Over all the areas (excluding the preferred area) the number of birds completing first clutches decreased from 60 pairs in 1973 to 46 pairs in 1974 (Table 19). This apparent relationship between clutch size and breeding density, between the years was examined statistically, ($t = 1.37$, $P > 0.1$) the difference not being significant.

Although the data indicated no statistical significance in the increase in clutch size with a decrease in breeding density (Table 18), Blums (1973) recorded that as the density of nesting coot, in Latvia, increased the mean clutch size decreased by as much as 0.8 eggs. Similar findings (Lack 1958) have been reported for birds such as the blue tit (Parus caeruleus) and the great tit (Parus major).

The overall production rate using the criterion of the number of young fledged per laying pair as a measure of breeding success gives:-

Table 19

Relationship between number of pairs laying and number of young fledged from first clutches only.

Area	No. of Pairs Laying		No. of Young Fledged		No. of Young Fledged per Pair Laying	
	1973	1974	1973	1974	1973	1974
A	10	10	17	17	1.7	1.7
B	8	6	13	11	1.6	1.8
C	12	11	16	6	1.3	0.5
E	22	18	29	14	1.3	0.8
F	8	1	4	0	0.5	0.0
Wet Marsh (Preferred area)	7	7	14	11	2.0	1.6
	67	53	93	59	1.4	1.1

Thus although the preferred area apparently gave rise to larger clutches (Table 18) the overall production of fledged young from first clutches was no greater for the preferred area than for areas 'a' and 'b'.

One of the reasons for the production rate dropping (in relation to eggs laid) in the preferred area is thought to be because of predation by pike. The preferred area besides providing a rich habitat for birds also apparently provided an ideal habitat for pike (pers. obser.) and it was the shallow water which the pike seemed to favour which also provided the young coot with its first environment after leaving the nest. Milne (1974) observed that when pike appeared after the flooding of a newly excavated gravel pit the number of young wildfowl reaching maturity fell dramatically.

Huxley and Wood (1976) studying the moorhen suggested that the steady increase in breeding success as the season progressed was due to increased cover, being available from the growth in vegetation, which enabled the young moorhens to avoid predators. In the Attenborough preferred area the success of second clutches and a double brood, raised in 1973, the number of fledged young from 1.3 to 2.0 young per laying pair. In the preferred area the additional vegetational growth - especially from R. hydrolapathum was extremely substantial and must have provided late hatching young coot with substantial extra cover.

c. Breeding success in relation to habitat change

The changing habitat (page 33) and the consequent loss of emergent vegetation which was used as a food source, for nesting cover and for cover for the young, is thought to account for the lower overall breeding success rates in 1974 when compared with 1973.

The areas affected most by the habitat change were the open areas of C, parts of E and area F. Area F lost seven breeding pairs, area E (excluding the Wet Marsh) lost 4 breeding pairs and area C lost one breeding pair. If area F and parts of area E and C are considered as buffer zones (Kluyver and Tinbergen 1953)[1].

"Note 1"

The buffer effect (Kluyver and Tinbergen 1953) states that in an area with a high density population where the food supply is superior to contiguous areas the year to year variation in density will be small and will not be proportional to the variation in the total population in the study area. For the buffer effect to operate 'good' habitats must be contiguous with 'poor' habitats.

then this could account for the fact that in 1974 when the whole study area 'lost' 15 territorial pairs nine pairs and seven pairs were lost from areas F and E respectively. (Areas A and B increased by three territorial pairs but suffered a two pair decrease in breeding coot).

Table 19 shows that Areas A, B and Wet Marsh (Preferred area) were all consistently more successful over the two years at fledging young than other areas.

The buffer effect, if operating on the coot at Attenborough, could account for the consistency of the results for areas A, B and the Wet Marsh over the two years and the variability of the results for areas C, E and F (The areas were identical in size in 1973 and 1974). Brown (1969) stated that probably the critical factor for the buffer effect to operate is that there must be a choice of 'rich' and 'poor' habitats within the area in which the species could be expected to search for a territory. Based on observational evidence, this critical requirement was met at Attenborough and some habitats were more suitable for coot than others even though both types of habitat contained territories.

I consider that:-

1. The environment at Attenborough consisted of both poor and rich habitats with respect to the requirements of the coot.
2. In 1973, the poor habitats held territories because the

high density of territories overall meant all the rich territories were occupied and marginal territories had also to be utilised.

3. Some of the poor habitats in areas C, E and F were only marginally capable of supporting breeding territories and with the detrimental habitat change previously discussed on page 37 these became non-viable as breeding territories.

4. The number of coot on territory in 1974 fell because the coot abandoned territories which had become non-viable as the habitat deteriorated.

5. The detrimental habitat change affected the poor habitats first or

   i) the poor habitats were affected more than the rich

   or

   ii) the rich habitats were so rich that even though they suffered equal deterioration they still contained sufficient food and space to support extra territorial coot even though the extra pairs did not lay.

Based on the above, and the data in Table 19 I would offer the hypothesis that the buffer effect was operating at Attenborough over the two years 1973/1974 and that the areas A, B and Wet Marsh were 'better' habitats for territorial coot than the contiguent but 'poorer' habitats of areas C, E and F.

A short follow-up visit was made to areas C, E and F on 31 July 1976 to monitor the changes, if any, in the number of coot and in the vegetation.

The Wet Marsh area, which was the 'preferred area' in 1973

and 1974, holding the highest breeding density of coot (Figures 3 and 4) as well as many other breeding water-birds, had changed dramatically with respect to its vegetation. The R. hydrolopathum had been almost completely eliminated leaving an expanse of open water with some muddy patches. The linear bed of G. maxima had completely disappeared as had most of the large bed of this species on the river side of the area. The linear bed of T. latifolia had been reduced in length and thickness. Only the Phragmites appeared to be surviving over its previous range. The results of these changes were to leave the area as a large pond of open water (Plate 60a), with the areas which held the R. hydrolapathum and the G. maxima as patches of water and soft mud (Plate 60b). Only one pair of coot with two large young in the area previously occupied by E8/E3 in 1973/1974, were seen, plus one other adult coot.

The general level of emergent vegetation over the study area was very much less than in 1973 and 1974. Plates 60c, 60d and 60e illustrate clearly the change occurring around some of the small islands. The same island is featured in each case and the photographs were taken from approximately the same angle. Plate 60c (1973) illustrates the thick growth of T. latifolia in which the nest of C14 was placed. Plate 60d (1974) shows the nest of C3 in what had become a thin growth of T. latifolia. Plate 60e (1976) shows that the T. latifolia had been eliminated completely and the coot (on the left of the photograph) on territory was nesting under a Salix

The BTO common Bird Census count for 1976 was 46 territorial pairs. On a visit on 31 July 76 only seven adults on areas C,

Plate 60a Formerly the Wet Marsh, but by 31.7.76 merely another open piece of water

Plate 60b Soft mud and open water, where formerly Glyceria maxima and Rumex hydrolapathum grew

Plates 60c, 60d and 60e Three photographs taken of the same nest site in 1973, 1974 and 1976 respectively. Note the progressive loss in the quantity of the T. latifolia until in 1976 it had been eliminated and the coot's nest was sited under a Salix spp.

E and F were seen. If the majority of the 46 pairs were still on territory then they would have had to have been in areas A and B. As this seems unlikely it is probable that the majority of the pairs had failed at breeding and then abandoned territory as failed breeders had done in 1974 (see page 43).

Recent data (K. Corbett pers. comm. May 1978) confirms that the River Erewash continues to flow into the southern pits causing heavy flooding. The Wet Marsh area (Figure 1) is now an open pond. The mud and the T. latifolia (Plate 92) have disappeared; the Phragmites has been reduced greatly and the only other emergent vegetation still to be found in the area is the G. maxima fringing the pond. One pair of coot still have a territory in the area. The BTO count for territorial coot in 1977 was 41 pairs; a further drop in numbers.

d. Success rates of early and late nests

In order to test the hypothesis that young birds hatched early in the year have the greatest chance of survival, for instance (Lack 1954: Perrins 1970), the Attenborough data have been analysed under two headings: Table 20 presents the breeding data of the coot based on the laying of the first egg. Tables 21 to 24 have been compiled by taking the first and last 20% of the 1973 and 1974 completed clutches and calling these early nests and late nests respectively.

d. i. Success rate based on the first egg date

Table 20 includes all the complete clutches of known date grouped into half-monthly periods. The percentage of eggs that

Table 20: Breeding information for 1973/1974 according to the date of laying of the 1st egg. Only complete clutches have been used in the analysis. The data has been grouped into half-monthly periods.
(Only includes clutches where the exact laying date of the 1st egg is known or has been estimated within ± 1.5 days).

1973 DATA

Date		No. of clutches	No. of eggs laid	No. of eggs hatched	% of eggs hatched	No. of young fledged	% of young fledged	% Breeding Success
March		1	8	5	62.5	2	40.0	25.0
April	1-15	7	42	24	57.1	10	41.7	23.8
	16-30	8	54	23	42.6	12	52.2	22.2
May	1-15	17	101	64	63.4	35	54.7	34.7
	16-31	12	64	39	60.9	14	35.9	21.9
June	1-15	2	13	7	53.8	4	57.1	30.8
	16-30	0	-	-	-	-	-	-
TOTALS		47	282	162	57.4%	77	47.5%	27.3%

1974 DATA

March		-	-	-	-	-	-	-
April	1-15	6	43	25	58.1	14	56.0	32.6
	16-30	13	92	51	55.4	17	33.3	18.5
May	1-15	21	133	74	55.6	20	27.0	15.0
	16-31	8	44	20	45.5	4	20.0	9.1
June	1-15	1	3	0	0	0	0	0
	16-30	1	6	4	66.6	2	50.0	33.3
TOTALS		50	321	174	54.2	57	32.8	17.8

hatched in both 1973 and 1974 is remarkably similar i.e. 57.4% in 1973 and 54.2% in 1974. The percentage of young that fledged (this indicates the number of young reaching eight weeks old as a proportion of eggs that hatched) is however higher in 1973 at 47.5% than in 1974 when it was 32.8%. Consequently the percentage Breeding Success (the proportion of young fledging from the number of eggs laid) is also higher in 1973 (27.3%) than in 1974 (17.8%).

Examination of the 1973 data (Table 20) do not suggest that there is any advantage in breeding at a particular part of the season. The 1974 data, however, indicates that the earlier clutches were more successful. In 1974 there was a marked drop in the percentage breeding success for completed clutches with a known laying date, after April. Although the percentage of eggs hatched was very similar, at 56.3% in April and 53.1% in May, the percentage of young fledged declines from 40.8% in April to only 25.5% in May. This drop was found to be statistically significant ($d = 2.12$, $P < 0.05$).

Good breeding success was found for three of the last four clutches in June. These three nests started on 8 and 15 June 1973 and on 19 June 1974 had clutches of six, seven and six eggs respectively. Huxley and Wood (1976) analysing BTO Nest Record Cards for the moorhen, found a steady increase in breeding success as the season progressed. If they are correct in suggesting the increased success is due to reduced predation because of additional protection from growing vegetation, then it is likely that this also affects coot with respect to pike predation. This could be one of the factors involved in the

increased success of the three very late clutches. It is also possible that the decrease in emergent vegetation overall (see pages 33 to 40) in 1974 could be a contributing factor in the increase in the number of hatched young which failed to fledge. The percentage of young fledging from those which hatched dropping from 47.5% in 1973 to 32.8% in 1974 (Table 20). This decrease in fledging success was found to be highly significant ($d = 2.78$, $P < 0.01$).

d. ii. Success rate based on the first and last 20% of completed clutches.

Tables 21 to 24 analyse the first 20% and last 20% of all completed clutches to see if there is any difference in the success of early and late nests. Percentage breeding success is based on survival of the young up to the age of eight weeks. The 20% figure, for early and late nesting, was arrived at after considering the spread of egg-laying. For instance, in 1973 there was a seven day gap and in 1974 a three day gap after the first 20% of all clutches were started. The 20% late nests were selected purely for mathematical convenience i.e. there was no apparent gaps in laying sequence (apart from the three very late clutches) during the latter part of the laying sequence. The total number of nests from which the 20% have been caluclated is 69 in 1973 and 55 in 1974. Only nests for which there is a known first egg date, within $\pm$ 2.5 days, have been used to compile these tables.

The 14 early clutches in 1973 all had their first egg by 17 April; the late clutches for 1973 had their first egg after 20 May. The early nests were all first clutches but the 14 late

Table 21.

Success of nests started before 20 April, 1973

Clutch Size	No. of Clutches	No. of Eggs	No. of Eggs Hatched	% of Eggs Hatched	No. of Young Fledged	% of Young Fledged	% Breeding Success
4	3	12	10	83.3	6	60.0	50.0
5	2	10	2	20.0	2	100.0	20.0
6	6	36	7	19.4	3	42.9	8.3
7	1	7	5	71.4	2	40.0	28.6
8	1	8	5	62.5	2	40.0	25.0
9	1	9	7	77.8	2	28.6	22.2
Total	14	82	36	43.9	17	47.2	20.7

Table 22.

Success of nests started before 15 April, 1974

6	5	30	11	36.7	5	45.5	16.7
7	2	14	10	71.4	6	60.0	42.9
8	1	8	5	62.5	3	60.0	37.5
9	2	18	13	72.2	9	69.2	50.0
10	1	10	9	90.0	3	33.3	30.0
Total	11	80	48	60.0	26	54.2	32.5

Table 23

Success of nests started after 20 May, 1973

Clutch Size	No. of Clutches	No. of Eggs	No. of Eggs Hatched	% of Eggs Hatched	No. of Young Fledged	% of Young Fledged	% Breeding Success
2	2	4	2	50.0	2	100.0	50.0
3	0	-	-	-	-	-	-
4	2	8	5	62.5	4	80.0	50.0
5	5	25	15	60.0	5	33.3	20.0
6	2	12	3	25.0	2	66.6	17.0
7	3	21	7	33.3	2	28.6	9.5
Total	14	70	32	45.0	15	47.0	21.0

Table 24

Success of nests started after 14 May, 1974

3	2	6	2	33.3	0	-	-
4	0	-	-	-	-	-	-
5	3	15	8	53.3	0	-	-
6	4	24	12	50.0	4	33.3	16.7
7	1	7	3	42.9	1	33.3	14.0
8	0	-	-	-	-	-	-
9	1	9	4	44.4	1	25.0	11.1
Total	11	62	29	46.8	6	21.0	10.0

nests include four second clutches laid after the loss of the first clutch and one second clutch produced after the successful rearing of a first clutch. Four other clutches were attempted during these periods, but these were lost before they were known to be complete and they have been discounted. The 11 early clutches of 1974 were all commenced before 23 April while the late clutches were started after 14 May. As in 1973 the early clutches were all first clutches while the late clutches include five second clutches (laid after the loss of the first clutch). The incomplete clutches started in 1974 have also been omitted from these calculations.

The difference between breeding success for early and late nests in 1973 and 1974 (Tables 21 to 24) were tested using values of number of eggs laid and number of young fledged. There was no significant difference ($\chi^2 = 1.67$, $P > 0.05$) between numbers of young fledged in early nests (Tables 21 and 22). There was also no significant difference ($\chi^2 = 3.02$, $P > 0.05$) between 1973 and 1974 in the percentage breeding success for late nests (Tables 23 and 24).

Table 21 and 23 show that in 1973 breeding success for early and late nests; 21.0% and 20.7% respectively, is practically the same. There was, however, a significant difference in success between early and late nests in 1974 ($\chi^2 = 6.67$, $P > 0.01$) as shown in Tables 22 and 24.

The data suggest that with the coot at Attenborough there may be an advantage some years in breeding early. The factors causing this advantage have not been identified. The variable results for 1973 and 1974, with respect to the percentage of

young fledged from those hatched, might be connected with the recent habitat change over the study area (see page 15 to 21).

e. Comparison of Attenborough breeding data with other studies.

The Attenborough data when compared with the findings of Alley and Boyd (1947) and Sage (1969) shows that whereas the hatching and fledging rates differed, the overall breeding success rate were similar (Table 25).

The only other study to report overall breeding rates was that of Askaner (1959). His figures, along with other published data, are shown in Table 25, for two different areas were very variable. Askaner (1959) claimed this variability was due to the fact that, at the site where the percentage breeding success rate was 69.0%. the coot were artificially fed in a situation where a good food supply was already in existence while at the other site no artificial feeding occurred and the habitat was very poor in available food.

Lelek's (1958) percentage rate for eggs which hatched are in accordance with the three sets of British data. All the other studies record much higher hatching rates, with Kornowski (1957) recording a very high fledging rate. Havlin's (1970) hatching rate was based on the number of sterile eggs, or the remains of such eggs found in the nest after the incubation period and on the egg losses found during incubation.

Askaner's (1959) high success rate seems, in some degree, to parallel the Attenborough findings for site E28/E1 in 1973/74 respectively. Here artificial feeding on a poor habitat helped the coot to achieve better than average results (see page 68). The continuous successful breeding of the moorhen

Table 25. COMPARISON OF COOT BREEDING DATA
from different areas of Europe

Locality	Authority	Eggs Laid	No. of Eggs Hatched	% of Eggs Hatched	No. of Young Fledged	% of Young Fledged	% Breeding Success
Nottingham	Present Study	753	371	49.3	152	41.0	20.2
Hertfordshire	Sage (1969)	343	116	33.8	71	61.2	20.6
Somerset	Alley & Boyd (1947)	121	42	34.7	28	66.7	23.1
Czech	Lelek (1958)	352	154	43.8	NO DATA		
ØCzech	Havlin (1970)	1868	1618	86.6	NO DATA		
Sweden	Askaner (1959)	86	34	39.5	6	17.7	7.0
*Sweden	Askaner (1959)	29	22	75.9	20	90.9	69.0
Germany	Bezzel (1959)	240	189	79.0	NO DATA		
Germany	Kornowski (1957)	550	NO DATA		244		44.4

Ø Havlin states hatching losses definitely not more than 20%

* Askaner. Data collected from site where Coot artificially fed.

(Siegfried and Frost 1975) seems to be a similar situation and all three reports point to the availability of food being the critical factor in the ability to fledge young.

The method used by Havlin (1970) to calculate the number of eggs hatching would, if it had been used at Attenborough, have produced a much higher hatching rate than that recorded (See Discussion). Very few coot nests at Attenborough were found to contain eggs once both parents were seen on the water together with their young.

It is possible that the adult coot either removed the unhatched eggs or ate them, or they were taken by crows as they were abandoned. Immediate predation by the crow is considered unlikely as eggs disappeared immediately after incubation in areas which experienced little crow activity. The coot, however, has been known to eat the eggs of great crested grebe (McCarton and Simmons 1956) and presumably could remove its own eggs easily. Plater (1969) records that a moorhen was seen to remove one of its own eggs from its nest, carry it to an island, and feed it to one of its chicks.

RELATION WITH OTHER WATER BIRDS

Almost all the literature which refers to the coot comments on its relations with other waterfowl, especially wildfowl.

Cramp (1947), Kornowski (1957), Lelek (1958) and Blums (1973) all state that the amount of damage caused by breeding coot, to other water birds, is almost negligible. Kornowski (1957) stated that ducks which entered the territory were seen off, but not hounded out of the area and ducks with young were seldom attacked. Lelek (1958) reported that the coot's relationship with "the duck can be characterised as neutral", but that it is intolerant of the moorhen. Blums (1973) has registered nineteen bird species in the nesting territory of the coot during the period April to August. The moorhen he listed as being the most violently attacked. He stated "the aggressive behaviour ..... is distinctive at the beginning of the reproduction period, yet it is manifested irregularly and proves to be of little effect". He concluded "that the coot does not interfere with the reproduction of the ducks and other waterfowl in Latvia".

Cramp (1947) in discussing coot territories on St. James's Park, London, implied that coot, far from being an ecological competitor with wildfowl by restricting their breeding habitat, are themselves restricted largely to unsuitable habitats by the breeding duck. Cramp stated "and as the outside banks were subject to human interference and Duck Island was the favourite nesting site for ducks, they (meaning coot) were in practice, restricted to the two small islets".

Ryder (1959) reported how ducks with young, including the small

cinnamon teal (Anas cyanoptera) can successfully defend their broods against the very pugnacious American Coot.

Nylund (1945), Kornowski (1957) and Blüms (1973) all recorded great crested grebe building nests as close as one m. to the nests of incubating coot without any aggression from the coot.

Aggressive Behaviour

At Attenborough interspecific aggression was recorded on very few occasions apart from that towards the moorhen, even the moorhen was not always attacked, however. The great crested grebe was rarely attacked even though on several occasions it was found nesting as close as one m. to the coot. Plates 60f and 61 (the grebe eggs have been uncovered for photographic purposes) show two of these occurrences. On each occasion the grebe commenced nesting after the coot was on eggs and the coot must therefore accept the building grebe without any molestation, or the grebe ignores the coot aggression which is insufficient to drive it away. When the great crested grebe follows the coot into a nesting site, the coot must be hatching its young - the period which researchers (Kornowski 1957: Wagner 1962: Blüms 1973) have stated is the time of maximum aggression - while the grebe is incubating within a metre or so of it.

Coot aggression was recorded during the breeding season directed at moorhen, mallard, tufted duck, canada goose, mute swan, little grebe, great crested grebe, brown rat and water vole. On many occasions, however, all of these species, apart from the brown rat, were tolerated within the immediate environment of nests containing eggs and/or small young.

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Plate 60f Two examples of Great Crested Grebe nests being built very close to the nest of a Coot

Plate 61 Note in Plate 61 that the Coot eggs are just hatching while the Grebe's nest has two eggs only

The intensity of the aggression is dependent on the species. Plate 62 illustrates the type of coot aggression shown towards the larger waterfowl. One coot incubates while the other, on the nest ramp, stands with head and neck in a straight line 'phut-phutting' at the canada goose. The goose completely ignored the coot which did not leave the ramp.

Similar aggression was shown towards a mute swan and six cygnets which stopped to feed about 1.5 m. from an incubating coot. The coot sat up and went into the 'head and neck straight posture' and started to produce a metallic 'chuck' call, repeated every second or so. The swan ignored the coot as did the coot's mate which was preening on a nearby island. As the swans moved away the sitting coot relaxed and continued to incubate.

Coot were seen to attack duck without young and on three occasions coot were seen attacking a female mallard when they had small young. One female mallard retreated taking her four young with her: the coot only attacked the adult mallard and not the young. The coot at site E18 in 1974 was however repulsed by a female mallard. The coot was incubating three eggs on 11 June when a female mallard and four small young went close to the nest. The sitting coot came off the nest and attacked. The female mallard 'stood' on the water and attacked with bill and wings. It drove off the attacking coot and then as the mate of the sitting coot arrived the mallard drove them both back about two m. while her young retreated. As the mallards left the area the coot resumed sitting.

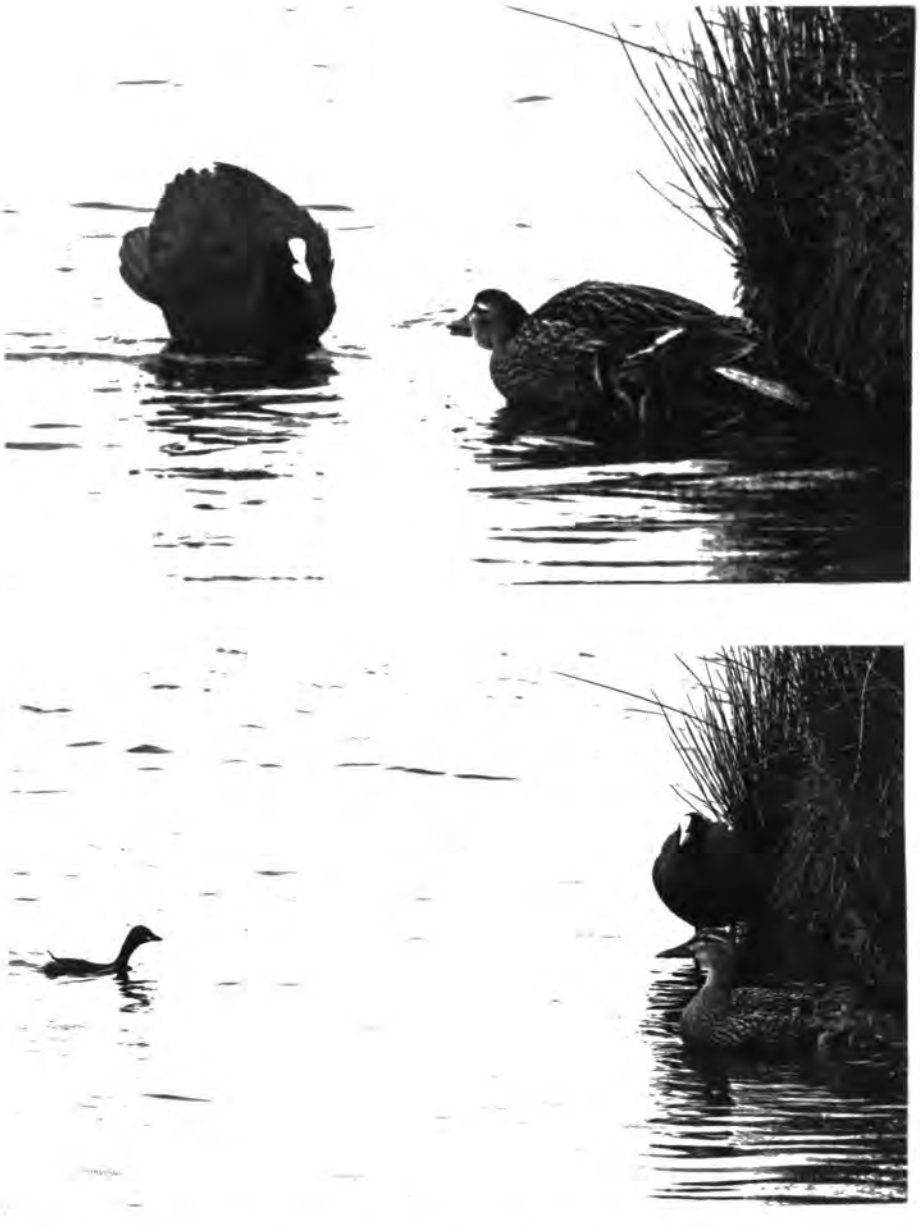
On many occasions the coot is a recipient of aggression from species such as little grebe, mallard, and great crested grebe. On

four occasions mallard with young were seen to attack territorial coot; each time the coot gave way, on one occasion even fleeing from its own territory.

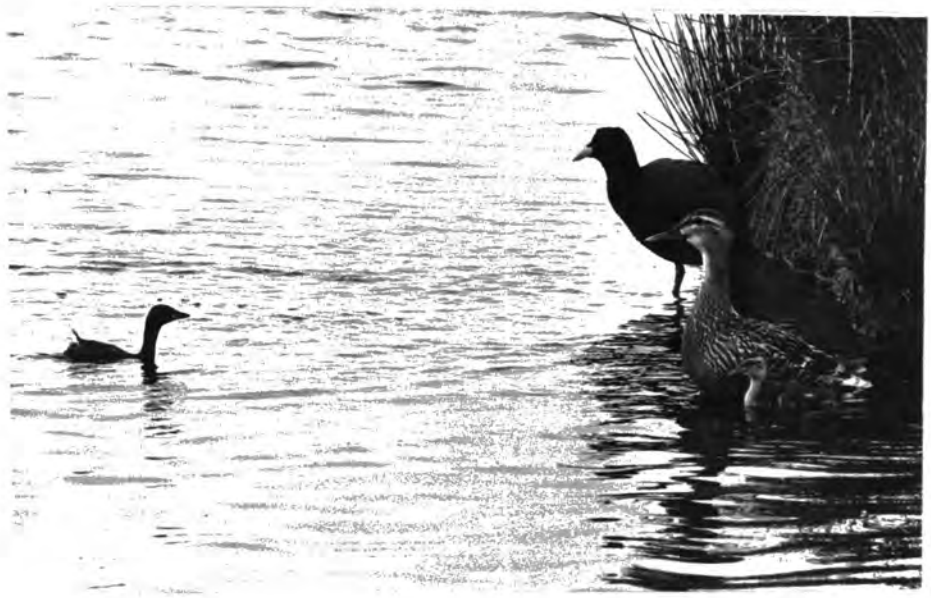
Plates 63 to 67 illustrate clearly that if a species intrudes into the close proximity of another nest it may be attacked. The coot in Plate 63 had hatched five young eight days previous and they were all feeding about 30 m. from their nest site when the female mallard and two young swam past the coot family at about a m. distance; no aggression was noted at this time. The mallard proceeded to the island holding the coots' nest and was apparently going to leave the water by the side of the nest. Immediately one of the adult coot charged across the water positioning itself between the mallard and the nest site. Plate 63 shows the coot about to start swanning. The mallard immediately placed herself between her young and the coot. An adult little grebe which had that morning hatched two young just five m. from the coot nest, then arrived. Plates 64 and 65 show successive stages of the encounter; the coot relaxes and the mallard apparently gives all her attention to the little grebe (as does the coot) keeping one duckling on each side of her, i.e. one immediately next to the coot. Plates 66 and 67 illustrate the 'panic' of the mallard as the little grebe dives to attack and the coot (Plate 67) also attacks. The mallard safely took her young away as neither the little grebe nor the coot pressed the aggression any further. At this site the coot and the little grebe ignored one another.

Most of the coots interspecific aggression is directed at the moorhen. Twice coot chased moorhen across a narrow island

Plate 62 Typical aggressive posture of the Coot towards larger water birds



Plates 63, 64, 65, 66 and 67 Successive photographs in a three species aggressive encounter. Please see text (page 120/121) for full details



Plates 65, 66 and 67

without breaking off the pursuit. Even so, a moorhen managed successfully to lay an egg in the nest of an incubating coot (see Plate 54) and on at least three occasions moorhens successfully hatched eggs and reared young in the middle of coot territories.

At all times, however, the interspecific aggression of the coot is never as violent as the intraspecific aggression. An example from my field notes of 20 May 1973 illustrates the differing reaction of territorial coot towards its own, and that of other, species.

"Site E11/E16

Time 09.30

(Neither E11 nor E16 had eggs or young at this time)

An adult coot from E11 was seen charging and then splattering at a moorhen. The moorhen fled into the territory of E16 drawing the pursuing coot with it. The two coot from E16 immediately started to splatter towards the pursuing coot from E11. The three coots (two from E16, one from E11) went into paired display. This lasted for fully two minutes before the E11 coot returned to its own territory. The moorhen continued to feed in the territory of E16 without any aggression being directed upon it."

Non-aggressive Behaviour

Blums (1973) stated that the coot's aggression is "manifested irregularly". This was confirmed at Attenborough as the following field notes and photographs show.

"Site E8

Date 24 June 1973

(This was the double brooded site - on 24 June the first young of the second breed was seen for the first time on the ramp). In the nest area at 12.00 hours were two female mallard with seven and two small young respectively and a moorhen with five young. One adult coot was on the nest, one adult feeding the small young on the bottom of the ramp and two large young coot from the previous clutch. Observations continued for twenty minutes but no aggression was seen.

Date 1 August 1973

Adult coot drives young moorhen from immediate area of the nest.

Date 9 August 1973

Both adult coot ignore young moorhen which enters nest area to feed.

Site C14

Date 4 June 1973

(Young hatched at this nest on 22 May).

Female mallard with four small young swam right past nest at distance of ten m. Both adult coot ignored it. At this site on 20 May (just two days before the young hatched) one adult coot was on the nest with its mate preening on a small island about five m. away when another coot came within about six or eight m. of the nest while diving for food. Although observations continued for twenty minutes no aggression was seen.

Site E16

Date 15 June 1974

(Young hatched at this nest on 18 June)

One coot was incubating when within a few minutes two broods of mallard (one with very small young, the others half-grown) passed by very close to the nest. The incubating coot totally ignored both broods."

Plates 68 and 69 illustrate non-aggressive behaviour between a pair of coot with small young and a family of almost fully grown mallard. In Plate 69 an up-ending mallard is between a coot feeding a small chick and the other adult coot. Plates 70 and 71 show families of coot and mallard, both well grown, feeding together. These were observed at least fifteen minutes without any aggression being seen. Plate 72 shows a coot with a young chick within 0.5 m. of an adult great crested grebe - again no aggression was seen.

The coot's relationship with the great crested grebe is difficult to understand. On two coot nest which were abandoned after eggs were laid - reasons unknown - great crested grebe subsequently built their nests and successfully incubated eggs. At another site, E18 in 1974, coot commenced nest building on 20 April, the first and second eggs were laid on 18 and 19 May. On 22 May the nest was flattened and empty; two adult coot were still in the nest area. A new nest was started on 28 May, it was empty on 1 June but held three incubated coot eggs on 4, 18 and 21 June. On 22 June, although it was a very cold day, the area was apparently not occupied by the coot. On 26 June, a moorhen was observed sitting on the nest which was now slightly lower in

Plates 68, 69, 70 and 71 Examples of aspects of the mutual tolerance normally found between the Coot and Mallard

Plate 72 Coot and Grebe often raise families within metres of each other

height. On 30 June the moorhen was checked incubating five moorhen eggs: there being no sign of any coot eggs. On 3 July the nest was very much flattened and it contained one very fresh egg of a great crested grebe. On 7 July it contained four eggs of this species. The grebe was observed incubating on eight occasions before two grebe chicks were first seen on 5 August. Two adult coot previously seen on 21 June reappeared on 29 July but were not seen again before observations ceased on 24 August 1974. On 24 August two adult and two immature grebe were still in the area.

It is unlikely that my observations led to the abandonment of any of the eggs which disappeared. After each nest visit observations were continued until the sitting bird was seen to resume its place on the eggs. This almost certainly rules out the loss of the coot eggs to the crow. However, no observational evidence was obtained which suggests how these changes, involving three species laying and incubating in one nest, came about.

My observations confirm those of Cramp (1947), Kornowski (1957), Lelek (1958) and Blüms (1973) that the coot does not affect the reproduction of ducks and other waterfowl with which it shares a habitat. Ducks appear to be able to withstand coot aggression at all stages of the breeding cycle. The number of occasions that coot nests, containing incubated eggs, were lost to other species, particularly great crested grebe, seem to indicate that this was not a random occurrence. It appears as if the grebe does gain an advantage, by nesting in close proximity to the coot, which has something to do with the siting of the nest itself.

DEVELOPMENT AND CARE OF THE YOUNG.

When the young coot are first hatched they are, unlike most nidifugous young, completely dependent on their parents for food. They also, like all nidifugous young, require their parents to provide them with protection and warmth during their early life.

Boyd and Alley (1948), Alley and Boyd(1950), Hinde, Thorpe and Vince (1956), Kornowski (1957), Wagner (1962), Kear (1965) and Blums (1973) all give excellent descriptions of various stages in the development and care of young. Some of these papers are based on experimental evidence with captive coot and moorhen, while others such as the ones by Alley and Boyd (1950) and Wagner (1962) use experimental data on captive coot in conjunction with detailed field study. In view of the amount of available material only aspects of the development and care of the young which can be photographically illustrated have been covered.

Coot are 'good' parents in that they are prepared to defend their young against all manner of species, even Man if necessary. Plate 73 shows an adult coot, nest E28 in 1973, sitting on the side of the nest which still contained four small young. As the boat approached the adult attempted to call off the young but only one chick ventured into the rough water. The adult therefore came back on to the nest and remained there until I left.

Plate 74 shows two young not more than a few hours old; at this stage they are indifferent to Man. (According to Alley and Boyd (1950) this indifference lasts for at least eight hours). Their bill was red with a prominent white tip and small crimson feathers were found all round the base of the bill. The crown and nape were dull red and thin purple bands ran from above the bill

Plate 73 Coot will defend their young even in the face of aggression from humans

Plate 74 The young remain unafraid of man for just a few hours

Plate 75 Within a few hours of being dry the young can swim

Plate 76 Young Coot have huge feet which enable them to run, swim and dive very easily

into the crown. Just above the eye was a small purple patch. Running from the base of the nape towards the eye was a thin band of golden yellow feathers. Even at this stage they have the ability to swim (Plate 75) and dive if necessary. Plate 76 illustrates the large feet and very small wings of the two day old chick. Plates 77 and 78 illustrate typical aspects of the young coot's life at this age. The young follow the adults everywhere, each adult looking after a proportion of the chicks, for at least three to five weeks and they are fed by food being passed from bill to bill. However, many instances were observed of independent feeding including picking insects off the water, upending and diving for weed from the age of approximately 22 days.

The young go through several colour changes during their first few weeks. Observations indicate that it is with the growth of the chick that the plumage changes and not with the age. For example, the young of C14 in 1973 all hatched within a few hours. On 11 June when they were 20 days old, one of the young was much larger than the other two. The large chick had no red on the head, it had a white chin, yellow bill and whitish feathers around the back of the head. The two small young had red heads, white bill tips, yellowish feathers around the neck. They had no white on the chin or around the head. Plate 79 illustrates two chicks at about 3.5 to 4 weeks old.

Plate 80 illustrates the way the older young have to approach their parent if it is not to be taken as an aggressor i.e. the head is turned away so that the shield which is just starting to develop is hidden from the parent bird. The shield starts to develop (according to the growth rate of the bird) at about five or six weeks. It commences as a small pale triangular shape, which later

Plates 77 and 78 Adult Coots feed their young for 3 to 5 weeks

Plate 79 Young Coot at about 4 weeks old

Plate 80 Even when it starts to develop a shield the young will still be fed

rounds off at the top. Also at this time, Plates 81, 82 and 83, the chick develops a mainly white neck at the front and white feathers on the breast - the bill being a very muddy grey in colour.

Plate 84 shows an adult coot with three well grown young, all with small white shields and dark bills. The neck is very pale while the general body plumage is dark grey. Plates 85 and 86 show immature coot aged about ten to fourteen weeks. The shields are quite prominent and the bill is starting to turn white. At this stage (Plate 55) they also have the white stripe down the leading edge of the wing and white tips on their secondary feathers and they normally gradually move off their parents' territory. When an immature of C3 pair was 86 days old the following was noted. The immature which had a shield about half size, and a dark bill with just a trace of white at the base of both mandibles, came towards one of its parents. The adult went into an aggressive posture. As the immature came close to its parent it put its head completely under the water. The adult grasped it around the neck for a brief moment and then released it. Both then swam peacefully away.

Plate 87 shows an adult coot which is moulting its secondary feathers. This photograph was taken on 28 July while the adult was feeding young some 25 days old. On 1 August, an adult coot was seen with its primary feathers just out of pin. The four young of this bird were hatched on 16 July 1974, so it was probably in wing moult while it was still incubating eggs.

Many details of plumage were taken from the dead young of A2 pair in 1974. At its time of death it was 78 or 79 days old. Some of the more relevant observations are listed below:-

Plates 81, 82 and 83 The young Coot develops a very indefinite plumage, with lots of off-white feathers around the head, neck and underparts

Plate 84 Adult Coot with well grown young. At this stage the young are seldom fed by their parents

Plates 85 and 86 Immature Coot at about 10 and 14 weeks old respectively

Plate 87 Coot in moult at the end of July

a) Each wing carried a carpal joint claw, they were deeply hidden in the feathers and both were very sharp. Each measured 5 mm.

b) Each wing carried ten Primary and nine Secondary feathers. Each secondary feather was tipped with about 3.5 mm. of white.

c) Along the leading edge of the wing, from the body to the tip of the 10th Primary was a very narrow band of small white feathers.

d) The shield measured 16.8 mm. in length and was 8.2 mm. wide at its widest point. Its colour was yellowish off white.

e) The bill was brownish merging with purplish white.

f) Below each eye was a patch of white feathers. This patch measured 9 mm. in length running along the bottom of the eye and 3.2 mm. in depth.

g) The general body colour was dark grey. It was flecked lightly with white on the ear coverts, chin, throat, down the side of the neck, with slightly heavier flecking occuring from the base of the neck, over the flanks and belly all the way to the vent.

Alley and Boyd (1948) and Kornowski (1957) observed that the brilliant head coloration of the young stimulated the adult to feed. They also reported that very young coot when warned by their parents alarm call, attempt to hide their heads in the vegetation surrounding the nest. This was noted at Attenborough at nest E2 on 27 May 1973, which was constructed in a large isolated Juncus spp. clump. Four young, two of which had only just hatched, were in the nest with two eggs. One of the young which immediately

jumped into the water was caught and replaced in the nest. It then buried its head and neck in the Juncus leaving its rear end sticking out. Another chick climbed out of the nest cup and disappeared by climbing down into the Juncus. The other two young sat in the nest and are the ones featured in Plate 74.

FOOD

Collinge (1936) in his study of 157 stomach contents of the coot found, out of a total animal matter content of 15.9%, some 2.3% was fish. Collinge (1936) who was looking at coot feeding habits because they were, and still are, thought of as a species which habitually harms other waterfowl, concluded that "so far as its food habits are concerned, the coot is an in-offensive and harmless bird".

Blums (1970) who examined the stomachs of 113 coot in Latvia could find no indication that it ate fish. He confirmed that animal food in small quantities (mainly insects) was usually present and that very young coot, i.e. less than 10 days old, are fed on large quantities of insects.

Hürter (1972) who studied coot feeding habits in Switzerland considered it held an intermediate position between the mallard and the pochard (Aythya ferina).

The coot at Attenborough fed on a wide variety of different foods. This variety is illustrated by extracts listed, in chronological order, from my field notes.

1) "9.4.73 Many coot watched feeding on grass. Two birds observed at close range eating moss from the bank of the pond.

5) 22.2.74 Twelve coot feeding on bread thrown from a gravel barge.

6) 16.3.74 Adult reaching up from the water to pick and eat Salix catkins. (Later a coot was seen clambering about in a Salix spp. to reach catkins).

7) 24.7.74 Black-headed gulls observed trying to eat a dead fish, 100 to 150 mm. long, in the water. Adult coot with young (E2 area) attracted to the fish; adult ripped it open very easily and its young immediately started to feed on the fish with the black-headed gulls.

11) 23.10.74 Adult feeding on G. maxima. It was seen to eat a strand at least 300 mm. long by merely 'sucking' it down.

12) 25.10.74 Both adults of E2 feeding vigorously on reed sweet grass.

13) 25.10.74 Coot, possibly an immature, feeding like a shoveler (Spatula clypeata) on the top of the water. Unable to identify food being taken.

10) 7.10.74 Three adult coot feeding very actively on small water animal - possibly pond skaters (Gerris spp.).

9) 4.10.74 Adult feeding on Carex acutiformis.

4) 9.9.73 Adult from C2 seen pulling and eating leaves off a Salix bush.

2) 12.5.73 Adult from E8 seen picking small animals off R. hydrolapathum leaves by the nest - feeding them to small young.

3) 1.7.73 Three young coot (66 days old) feeding themselves on Juncus spp. Ripping it off very easily.

8) 23.8.74 Six large immatures with small shields feeding in the old river by the church. Eating large quantities of horned pondweed (Zannichellia palustrus) and duckweed (Lemna spp.)"

A food regularly consumed by certain coot at Attenborough was a species of freshwater mussel (Unio spp.). This was seen taken on numerous occasions, but with only one pair (E2) was it apparently one of the main foods taken in the winter months. One of this pair was frequently seen diving for the mussels. Plates 88 and 89 show the bird bringing in a clump of mussels; and the same bird trying to break up the clump on the ice fringed bank. One day, within 20 minutes, I retrieved mussels off this coot four times as it returned with them to the bank. Plate 90 shows these clumps to consist of five or six individual mussels of about 2 to 3.5 cm. each in length. After the loss of these four clumps the coot started to shake the mussels to pieces in deep water, diving to retrieve any lost in the process. On two occasions clumps which appeared as large as those illustrated in Plate 90 were swallowed whole. The territory of these birds included a stretch of water kept open, even in very icy weather, by the barges carrying gravel. Most of the mussels were taken from this channel which ran past the main car park. The barge channel in this section was dredged to 7.5 m. The birds were therefore able to dive to this depth, a depth also confirmed by the study of Ingram and Salmon (1935) who recorded a coot diving to 7.3 m. The success of this pair in exploiting mussels as a regular food source was illustrated on 6 December 1973, when 42 coot were feeding on grass on the car park while both birds of this pair were successfully diving for mussels in the barge channel.

Observations recently carried out on a brood of coot at the Wildfowl Trust refuge at Martin Mere, Lancashire, shows that coot can catch small live fish and that these may at times

Plate 88 Carrying in a clump of mussels collected from approximately 7.5 metres depth

Plate 89 Using the bank as a type of wedge, the Coot breaks up the clump

Plate 90 Four clumps of mussels 'taken off' the Coot

be important as a food source. On a recently constructed mere the adult coot were feeding six, four days old, young on Three-spined sticklebacks (Gasterosteus aculeatus). The adults manipulated the fish for several seconds with their bills before offering them to the young (Plate 91). If, as was usual, the young experienced difficulty with the fish, the adult would 'snatch' it back, move it around in the bill before offering it again. In two hours of observation some fifteen fish were given to various young.

My observations confirm that coot will eat a wide variety of food, both animal and vegetable. However, I never recorded it taking either eggs or young of other birds and can only conclude, from my observations, that it is unlikely to harm other birds with which it shares its habitat.

Plate 91 Adult bringing in a Three-spined Stickleback as food for its young

DISCUSSION

Territory Abandonment

Observations on territorial abandonment (see page 43) and on the age at which fledged young leave the territory of their parents (see page 121) make the statement (see page 46) by Wagner (1962) that flocks of coot which began to congregate in early June contained other than adult birds in both 1957 and 1958 very difficult to reconcile, with some of his other data. For example, his records indicate that egg laying started between the 15 and 20 April. Given that continental coot incubate their first clutches from the 2nd, 3rd or 4th egg (Lelek 1958: Kornowski 1957: Blums 1973), then the earliest hatchings would be around the 10 to 15 May. Therefore, by the 13 June, the first young of the year (allowing 24 days for incubation) would be about 34 days old.

If Wagner's young were birds of the year it seems likely that their parents had abandoned territory and taken their young with them. Data suggesting such early territorial abandonment by the coot during a successful breeding cycle have not been reported. Nor can the young birds Wagner referred to, be immatures of the previous year as I found it virutally impossible to distinguish immature from adult coot in the field once birds have reached the age of about 140 days. While they remain in their parents' territory, the small shield of the immatures is a good identification feature. However, when the autumn migrating coot arrive they have, or quickly acquire, small shields which make them virtually indistinguishable from the

immatures already on territory. At Attenborough an enlarged shield was always found on territory holders regardless of the time of the year. Witherby (1941) commented on the seasonal variation in the shield size of coot and how the enlarged shield is associated with territory maintenance and breeding activity. Gullion (1951) found that American Coot which were permanently paired and defending territory retained the enlarged shield regardless of the time of the year.

The speed with which coot will abandon territories in harsh climatic conditions (see page 41) indicates that if conditions remain unsuitable then long term territorial abandonment will occur as happens in Eastern Europe (Kornowski (1957): Wagner (1962): Blums (1973)). Whether all the coot which subsequently reoccupy the territories when climatic conditions improve are the original territorial birds as is suggested (see page 42) will only be discovered by a method of permanent marking, such as colour ringing or wing tagging, which allows individual birds to be identified in the field.

Breeding Coot and Emergent Vegetation.

The almost total dependence of coot on emergent vegetation for breeding purposes, claimed by Kornowski (1957), Wagner (1962) and Sage (1969), was not fully confirmed in this study. The move from emergent vegetation to Salix for nest sites in 1974 (see page 79) apparently did not adversly affect the ability of the coot to hatch its eggs. Hatching rates were 48.0% and 51.0% in 1973 and 1974 respectively. Most Salix sites were on small islands and therefore safe from human pressures. Predation

pressures on incubating coot at Attenborough were practically nil (see pages155/162) and as most Salix sites seemed less susceptible to small sudden changes in water levels, especially early in the season, than the emergent vegetation, the coot were probably not disadvantaged in the early stages of their breeding cycle by the shift from emergent vegetation to Salix.

After hatching, however, it is almost certain that the young were in greater danger from predators, particularly the pike, when they were in territories with reduced emergent vegetation. When feeding in territories with emergent vegetation young coot usually remained on the fringe of such vegetation, ready instantly to move into it, if danger threatened, where they remained motionless and 'disappeared'. At most Salix nest sites the young had to continually cross open water if they wished to feed in the emergent vegetation which still fringed the larger islands and the mainland. As the young were usually brooded in the nest itself for several weeks they also had to cross the open water again as dusk approached.

The coot hatching rate in 1974 was 3% higher than in 1973, however the fledging rate for 1974 was 13% less than in 1973. It is suggested that some of the additional loss in 1974 was caused by more successful predation by the pike (see page 161) when the young coot were in the relatively open water between nest site and feeding areas. Plates 60c and 60d illustrate clearly the more open situation of many nest sites in 1974.

Double Broods

The coot will lay replacement clutches several times (see page 101) but there is little doubt that in Europe the bird

is normally single brooded (see page 105). The only researcher who questions whether the coot is generally single brooded is Havlin (1970). He believed that in good climatic breeding seasons that as many as 10% of Czechoslovakian coot could be double brooded. He based this figure on the number of late nests found in seasons when the climate was favourable for breeding coot. The data for Attenborough, however, clearly indicates that to use late nests as a criterion for estimating double brooding could lead to serious over-estimating of numbers. At Attenborough both double brooded coots had started their second clutches by the 4 June (actual dates 29 May and 4 June). In 1973 six other clutches were started after the 29 May; four of these were first clutches, the other two were replacement clutches. In 1974 only two clutches were started after 29 May, one a first clutch, the other a replacement clutch. In both 1973 and 1974 the last clutch laid was a first clutch, respective dates being 15 and 19 June. The pairs laying these clutches had been on territory since early April.

If the criterion of calling the last 20% of all nests as late nests is justified then in the 1973 breeding season two or 14% of the late nests were attempts at double brooding. The total number of complete clutches in 1973 was 69 (Table 14); of these 3% were attempts at double brooding. Thus in good climatic years it might be expected that 10 to 20% of all late nests could be attempts at double brooding while approximately 3% of all complete clutches might be attempts at double brooding. Over the study period at Attenborough 124 clutches were completed, of these two or 1.6% were attempts at double brooding. If the

two breeding seasons at Attenborough are typical then Havlin's (1970) claim of 10% of coot being double brooded is not justified.

Behaviour Adaptation and Predation by the Carrion Crow

The normal behaviour pattern of the crow at Attenborough while seeking food consisted of a systematic flying patrol from one 'look-out' post to another. The modification of its behaviour pattern (see page 157) enabled the crow to be more successful at predating coot eggs and certainly some eggs were lost to crow because of disturbance to incubating coot by the method of research. It is impossible to evaluate the losses of eggs suffered by the coot before the crows modification of behaviour was noted and appropriate steps taken (see page 157) to eliminate any further egg losses. However because of the ability of the coot to withstand, under normal circumstances (see page 157), predation pressure from crow it is believed that such losses did not seriously affect the overall breeding data as presented in this thesis. This study did not confirm the finding of Lack (1958b) that the coot is very vulnerable to predation by crow.

In view of the possible importance of a behaviour modification of this type, by a predator, on past and future studies at Attenborough and elsewhere it is disucssed in reference to this study and the study of Hornby (1971).

Hornby (1971) studied the reed bunting population at Attenborough over three years and his main conclusion was that the Attenborough population of this species was not self-perpetuating because of the extremely high nest predation; with

the carrion crow as the chief predator. He stated that the reed bunting population was only maintained by immigration of birds from more successful breeding areas.

If, however, the crow on territory at the time of Hornby's (1971) field work had adapted to his presence as they adapted to mine then there seems little doubt that the majority of the reed bunting nests be found would have been subsequently predated by the crow - as in fact he reported. Besides being a species with little, if any, defence against the crow once its nest site is disclosed the reed bunting normally nests at Attenborough in open vegetation (Hornby 1971 and pers. obser.) where the adults when feeding young are easily seen. Hornby (1971) visited most nests on at least two occasions; once when he found and recorded nest data and the second time to ring the nestlings, when they were between six and eight days old. In discussing the high predation rate by the crow Hornby (1971) states that "it does not seem unreasonable to assume that.... avian predators are guided to the nest by watching the parents as they take food to the young". He also mentioned that he took great care not to leave tracks as it could help predators to find the nest.

On the basis of research experience for this thesis it would seem that the leaving of tracks was not the critical factor: if the crows were observing Hornby as they observed me then the nest site would have been disclosed by his research activities and subsequently predated.

The ability of the crow to modify its behaviour patterns to take advantage of new situations, as happened in this study

would suggest that for any habitat where crow are numerous, as they were at Attenborough, extreme care is needed in monitoring behaviour of the crow as the research work continues.

Are some Coot Polygamous?

Frequently the question of dump nesting appears in literature with respect to coot. Almost every researcher (see page 106) who has carried out field work on coot breeding biology reports himself puzzled that a bird which shows such violent interspecific aggression, especially during the breeding season, can allow odd eggs, groups of eggs, or even whole clutches to be deposited in its nest.

At Attenborough dump nesting occurred in at least three nests (see page 107). At one of these nests, C1 in 1974, two separate clutches were laid almost simultaneously: the eggs from the differing clutches were identified by ground colour. At this nest it was very easy to watch the activities of the resident and also the adjoining pairs. At no time were more than two birds seen in the nest area and interspecific aggression between the neighbouring pairs was at the normal intensity. If the parasitic laying bird was forcing itself on an occupied nest then I would have expected the level of aggression to be so high that either nest or eggs would have been damaged. Such damage was never recorded and it is concluded that either the parasitically laying bird:-

a. deposits its eggs when both resident coots are absent from the nest so that its presence goes unnoticed, or

b. deposits its eggs with the consent of the resident pair or with the permission of the coot incubating at the time of the egg laying.

'a' seems improbable: once incubation commences the nest is rarely unguarded even for a moment or two. It is difficult to see how, in the light of coot normal interspecific behaviour, a strange bird would be allowed to deposit a series of eggs in an occupied nest. 'b' appears unlikely but seems more probable than 'a'.

If, however, one or both of a pair of resident coots were to be polygamous then this could explain how these seemingly impossible egg laying feats occur. No observation evidence was collected to suggest that polygamy does take place but it is difficult to account in any other way for the occurrence of two birds laying regularly in the same nest.

SUMMARY

The territoriality and breeding biology of the coot (Fulica atra) at the Attenborough Nature Reserve in Nottinghamshire, during the period August 1972 to August 1974, is described.

Some territories were maintained throughout the year. Both members of a pair defended territorial boundaries. Territorial fidelity was high throughout the year for both successful breeding pairs and non-breeding, territory holding pairs. 19 pairs are believed to have remained on territory throughout the study period. Unsuccessful breeding usually led to abandonment of territory in May or June. The behaviour which assists in maintaining territory boundaries is described. Changes in the type of nest site used are discussed in relation to the change in habitat occurring since the breach in the banks of the River Erewash in November 1972. Territory size was extremely variable, the smallest being 0.09 ha., the largest 1.37 ha. No correlation was found between territory size, clutch size or breeding success. There are indications that the size of a territory was governed by the amount of food it contained. The smallest territories and the highest density of territories being found where the food supply was particularly good.

Nesting occurs mainly from April to mid-June, with peak egg laying in the last week in April and the first week in May. One clutch only is normally laid by successful breeding pairs, but if the first clutch is lost a renest clutch will be attempted. The mean clutch size, calculated from 124 completed clutches, was 6.1 ± 0.14 eggs with a mean egg size of 53.78 x 37.68 mm. The mean length of eggs laid early in the breeding season was significantly longer than that of the remainder.

Both sexes build the nest, incubate the eggs and feed and take care of the young. Incubation lasts for 23/24 days and incubation of first clutches commences with the third or fourth egg. The young fledge at approximately 8 weeks.

The data on clutch and egg size, laying dates, breeding success are compared with those of other British studies, with British Trust for Ornithology Nest Record Card data and with continental European data. The overall mean clutch size for Britain calculated from 490 clutches is 6.0 ± 0.08 eggs. The mean clutch size for continental Europe, calculated from 2561 clutches, is 7.9 ± 0.03 eggs.

Factors affecting breeding success such as predation, eggs being chilled in the nest, observer caused losses, habitat preference, early and late nesting are discussed. The overall percentage breeding success was 20.2%. 152 young were fledged from 135 territorial pairs, an overall fledging rate of 1.1 per territorial pair, that is 1.3 young per breeding pair as 15 pairs on territory never laid eggs. The percentage breeding success rate was similar to that in previous British coot studies.

Intraspecific aggression occurred throughout the year but was most common during the breeding season. Interspecific aggression occurred between the coot and many other water-birds in summer but only with the moorhen in winter. Even during the breeding season when the coot can be aggressive towards other species its aggressive outbursts on other species are irregular and have little, if any, long term effect.

The coot was found to be an adaptable feeder. Observations suggest the coot is unlikely to harm other waterfowl with which it shares a habitat.

ACKNOWLEDGEMENTS

I am grateful to the Faculty of Science, University of Durham for permitting me to register as an external student and to Dr. Kenneth Ashby for acting as my supervisor. Of the many people involved with the Attenborough Nature Reserve I would particularly like to thank Norman Lewis for help with the field work and Keith Corbett for help in the field and for providing access to his Common Bird Census data. My grateful thanks to Simon Harries who helped in many ways with the field work.

I would like to thank Trent Gravels Ltd., and the Nottinghamshire Trust for Nature Conservations Ltd. for access to the pits and the reserve. The British Trust for Ornithology for the loan of the Coot Nest Record Cards; David Rogers and Ronald Harrison for permission to use their unpublished data in this thesis; Michael Smart of the International Waterfowl Research Bureau for the many translations he did for me on important research papers; Dr. William Hale, Head of Biology of the Liverpool Polytechnic who, on my move to Lancashire, willingly undertook to obtain copies of papers for me, and who obtained for me, access permission to the Polytechnic's Science Library; Dr. Roy Morgan of Edge Hill College of Higher Education and Julian Greenwood for their willing help with the mathematical data collected and Mrs Angela Teago who typed the final draft of the thesis.

The last thanks are reserved for my wife and our three young children, without their fullest cooperation and my wife's help and willingness to become a 'Coot widow' this thesis would never have been completed.

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