Territorial Regulation of the Progress of Breeding in a Population of Coots *Fulica atra*

By
JON FJELDSÅ

(Med et dansk resumé: Territorialadfærens betydning for yngleforløbet hos en bestand af Blishøne Fulica atra)

INTRODUCTION

The establishment of the hypothesis of territorial behaviour as a factor limiting breeding numbers is so far based mainly on behavioural evidence and is still week or inconsistent on the population level. However, the reluctance against this hypothesis by some authors is hardly better supported, as it is based largely on argumentation rather than critical field study. According to the function of individual selection to maximize the genetic survival of individuals, animal species are expected to reproduce as rapid as they can, and correspondingly behaviour should evolve to support the maximal production of progeny rather than to control it (e.g. LACK 1947-48, 1954 b, 1968, WILLIAMS 1966). According to this view the development of the »self-sacrifying altruism« of desisting from breeding to prevent undue further increase at high population levels should be an impossibility.

The extreme opposite standpoint is taken by e.g. WYNNE-EDWARDS (1962) and SKUTCH (1967), based upon a much questioned theory of interdemic selection. The main basis for the divergence between schools pontificating to the edifice of population regulation is thus to be sought in unsolved evolutionary questions. Rather than to ask about the »significance« of a social organization, say territoriality, it may, therefore, be more to the point to state directly the mechanism of selection by which it might act at the gene pool.

Independent of what is the ultimate significance of territorial behaviour, it may, when once in existence, form the basis for a »modificatory steering« of natural selection. If an exodus of part of the population into inferior habitats, or a direct influence on the breeding in individual pairs may be generally attributed as consequences of this behaviour, the operation of individual selection becomes distorted: As fitness differences between population members would thus be accentuated, there should be a selection against production of offsprings which would have reduced prospects of attaining a certain social standing (FRETWELL 1969). As an »unfit« surplus may, in longlived species, accumulate in case of even a slight overproduction, the reproductive patterns may thus become adjusted to the rate of survival, say the reproductive necessities (BROWN 1969), instead of survival being, in an environment of limited resources, a consequence of the reproductive rate (LACK 1954 a, HÜTTENMOSER 1962). Population levels at which a floating surplus exists may, for these reasons, give raise to reproductive traits which else seem inconsistent with the hypothesis of the evolutionary maximizing of genetic survival (e.g. polygyny, delayed maturation, low reproductive rates).

It follows that, to understand fully the relative roles of reproductive – and mortality factors in population regulation, it is exceedingly important to state, broadly, to what extent the social organization regulates fitness dif-

Dansk orn. Foren. Tidsskr. (1973) 67: 115-127.

ferences between individuals, and particularly whether it leads to the formation of a floating surplus of potential breeders. This is important, not only because the production of offsprings may be economized, but also because the surplus would act as an evolutionary factor.

The existence of a floating surplus is accepted in several ecological textbooks, but the evidence is still very vaguely documented. Some of the removal experiments upon which it is founded do in fact show nothing but the existence of a male surplus. Cases of a surplus including potentially breeding females on a larger scale are scarcely proved. Most evidence in the literature is, apart from some polygamic species, still inconclusive or anecdotal. An exception is the experiments of WATSON & JENKINS (1968). In a few other cases it seems perfectly clear that territorial behaviour delays breeding (e.g. HARRIS 1970), or even reduces the reproductive efficiency in many pairs directly (e.g. FJELDSÅ 1973).

This paper reports some results from one season of population studies on Coots, *Fulica atra,* in the marsh Utterslev Mose in Copenhagen. The study is prefatory for planning a longterm program on the proximate and evolutionary function of territorial behaviour in this species. The results are, nothwithstanding the provisional status, prepared for press due to their clear-cut demonstration, in the author's opinion, of the direct influence of early-established pairs upon the reproduction in the rest of the population. This may give a fortunate basis for studying, in the future, the ultimate problems outlined above.

THE STUDY AREA

Utterslev Mose (map Fig. 1) is situated between Utterslev and Gladsaxe in Copenhagen. It consisted primarily in about 140 ha of reed marshes with only 2-3 ha of open water. In 1939, after the decision to establish the area as a nature sanctuary within Copenhagen, the reedbeds were cleared up and dredged to a depth of 1.75 m over 52 ha area. Later, further 7 ha of 0.2-0.5 m deep water appeared as some reedbeds for unknown reasons died off some 20 years ago, giving a total of 59 ha open water. The marsh consists today in three portions, separated by bridges with highways. Here, they are conveniently named West-, Middle-, and East Marsh. The near-by pond Kirkemosen, 3.3 ha, is also included in the study.

The surroundings are parks and built-up areas. Locally the park lawns reach all down to the water edge, but mostly the closest surroundings are wet fields of lush herb vegetation and almost impenetrable swamps of reeds, *Phragmithes communis.* Public traffic to these areas is hindered by canals. The marsh belongs to the Metropolitan Water Board, and only very few persons have access to the area. Notwithstanding the situation in a crowded suburban area, the direct human influence is slight.

Offshore there are several reedy islets. These are the main breeding sites of Greylag geese, *Anser anser,* Mute swans, *Cygnus olor,* Mallards, *Anas platyrhynchos,* Pochards, *Aythya ferina,* and Tufted ducks, *Aythya fuligula,* and some 15 – 25 000 pairs of Blackheaded gulls, *Larus ridibundus.*

Along certain sections, mainly in the Middle- and East marshes, the water is bordered by dense barriers of reeds, with undergrowth of e.g. *Urtica dioica, Epilobium hirsutum, Solanum dulcamara,*

Fig. 1. The distribution of Coots in Utterslev Mose in 1972, -A showing nests where egg-laying took place before May 10, -B nests with later egg-laying. Filled symbols show initial clutches; open symbols show repeat clutches; open symbols marked II show second clutches; figures show number of flocked Coots.

Forekomsten af Blishøns i Utterslev Mose i 1972. A viser fordelingen af reder, hvor æglægning fandt sted før 10. maj, -B reder med senere æglægning. Udfyldte symboler angiver første kuld, åbne symboler omlagte kuld, åbne symboler mærket II andet kuld; tal angiver flokke af ikke-ynglende Blishøns.


A
+15
+2
+28
+6
+ca.5
+4
?
+10
+ca.5
B
II
II?
II
II
II
II
II
?
II?
II?
?
?
Initial clutch nest
repeat ,, ,,
II second ,, ,,
+28 28 flocked coots
Water with emergent vegetation
Reed marsh
Nuphar leaves
1 km

and *Bidens tripartita.* At other sections the vegetation is more open, consisting mainly in *Typha* spp. and *Phragmithes,* in many places also *Sparganium ramosum, Glycera fluitans, Scirpus* spp., *Carex pseudocyperus, Rumex* spp., and *Cicuta virosa.* These areas, indicated by black on the maps, constitute the nesting sites of the Coots, together with Great-crested-, *Podiceps cristatus,* Black-necked-, *Podiceps nigricollis,* and Little grebes, *Tachybaptes ruficollis,* and Moorhens, *Gallinula chloropus.*

Apart from Kirkemosen, the area has, during the 1950-ies and 1960-ies, become increasingly polluted by more or less septic water from the inefficient purifying plant of Gladsaxe. The fish died off, and in late summer the water surface was, over large areas, covered by thick mats of algae (mainly *Hydrotictyon reticulatum).* The bird fauna was much impoverished, and outbreaks of botulism among swans, ducks, and coots were recorded in 1967, 1968, and 1969 (Harild 1970, Preuss 1971). Fortunately, the sevage water was since 1970 drained elsewhere, and strenuous efforts were made to precipitate phosphates. In 1972 the algal growth had been very much reduced, and there was a marked increase in several limnic organisms and also among several bird species. The fish stock increased, partly (or mainly?) by introduction. Most of the Middle- and East Marshes are by now β-mesosaprobic, while the West Marsh and eastern part of the East Marsh is α-mesosaprobic.

The macroscopic offshore vegetation, which should constitute a main food of the Coots, is still mainly algae (*Cladophora, Enteromorpha*). Stands of *Nuphar luteum* cover larger areas only in Kirkemosen, and duck-weeds, *Lemna minor,* abound only in channels and very secluded parts. Submerse thalophyts are very scarce in the α-mesosaprobic portions, but in other parts there has been a rapid recent increase mainly of *Ceratophyllum demersum.* The water is turbid, green to olive brown, sight depth in summer 0.2-0.8 m, while approximately 2-3 m in Kirkemosen.

The most prominent feature of animal life is the enormous amount of *Daphnia pulex.* The fauna of the soft gyttja bottom is monotonous, completely dominated by *Chironomus* larvae, while oligochaets (*Tubifex tubifex, Limnodrilus hoffmeisteri*) are scarce. In the shore vegetation there are living mainly *Asellus aquaticus* and *Corixidae* and some snails and leeches.

The examination of the habitat is still in an initial stage, especially regarding quantitative aspects.

The appearance of the marsh prior to the pollution is vividly described by Kaulberg (1947). Recent descriptions are given by Harild (1970), Teibel (1970), and Preuss (1971).

INVESTIGATIONS ON THE COOT POPULATION

Observations on Coots up to 1971 (Harild 1970) are not systematic. According to Kaulberg (1947) there were, shortly after the dredging of the marsh in 1939, more than 1000 breeding pairs, although this may be a slight – if not even great – overestimate. About 1960 there might have been some 50-100 pairs, declining to about 25 pairs in 1969, to increase again after the abduction of sevage. Primo August 1971 I found fully 400 individuals. The 1972-results were about 100-105 breeding pairs, giving an August figure of some 480-490 specimens. The area was visited regularly by boat by the present author and N.O. Preuss. Investigations by boat were made on the 20, 28, and 30 of April, the 2, 7, 12, 16, 24, and 30 of May, the 2, 10, and 14 of June, the 14 and 20 of July, the 10, 15, 21, 22, 23, 24, 25, 26, and 27 of August, the 4 of September, and the 1 of October. During the investigations of April 28, May 16, June 2 and 10, July 14, August 10, September 4, and October 1, larger portions of the reed fringings were systematically searched. The other visits were mainly in order to check known nests in parts of the marsh. Observations from the shore were made on some additional days.

Altogether 128 true nests and 120 pl forms were found, and probably at mos two or three true nests were overlooked. However, some few nests were not found until after hatching so that details on time of egg-laying and clutch are wanting. For 73 nests (57%) clutch size, egg measurements, and egg losses are on exact record. Time of egg-laying of 118 clutches is recorded directly from nest checks made during the laying period, or estimated from freshwater test, or from known time of hatching. Egg losses were calculated from time spanned by observation. Survival of young was calculated from the size of family groups conducted by two adult birds when the youngs were about six weeks old (onset of postjuvenal moult). This calculation presupposes that no pair lost all their young. From those cases where a family remained near a nest, the percentual survival may be calculated from the number of eggs known to have hatched. The main age of mortality is judged from the size of 28 dead-recorded young.

Censusing is based mainly on the nest records. Cautions made to tell apart lately settled pairs and pairs with repeat- and second clutches are given on p. 000. Flocked Coots kept mainly offshore and could be counted directly. From egg-laying until the young were at least one month old direct counts of the breeding pairs were, however, impossible as they lived very hidden among the reeds. In June an observer would scarcely see Coots at all at certain times of the day. Only during shorter periods up to fifty specimens might be seen feeding offshore. At the sight of a boat they skittered, like panic-stricken, into the reeds. Pairs with downy chicks fed in the main within the vegetation. Not until August could a direct count of the whole population be made and correlated with the number estimated from data on egg-laying, clutch size, egg losses, and survival of young. Countings in August were best made at sunset when there was a peak in offshore feeding birds.

THE PROGRESS OF BREEDING

This paragraph will describe, mainly in chronological order, the changes in population numbers and the progress of breeding in Utterslev Mose in 1972.

The situation of nests is shown in Fig. 1. (A) shows nests with egg-laying up to May 10, (B) nests with egg-laying later in the season. The seasonal progress of reproduction is illustrated by Fig. 2, showing (A) temperature curve, (B) clutch size regression, (C) the number of clutches initiated per five days periods, and (D) the seasonal changes in numbers of flocked- and territorial adults, eggs, downy chicks, white-throated juveniles, and fullgrown (dark plumage) immature birds. This diagram is made by a combination of direct count figures and extra- and intrapolation based upon estimated initial dates and values obtained for egg losses and young survivorship.

Unfortunately, the events in early spring were not followed up with the necessary accuracy. Coots arrived to Utterslev Mose through late March. Whether all birds arrived that early is not known. Neither was the early establishment of territories followed up.

By ultimo April almost all coastal sections suited for nesting (black colour on maps) were divided into territories. There was a total of 62 established pairs. Territories were defended about 40 m out on open water, thus not including the central portions. In the West Marsh which, due to the structure of the vegetation and the shallow feeding areas, is probably most attractive to Coots, there were 37 established pairs, each holding x 60 x 18 m (but modulus 50 m) of reedy coast. This density corresponds well to that given by KORNOWSKI (1957) for eutrophic lakes and by ASKANER (1959) for urban ponds. In the other marshes most pairs were much wider spaced.

Few pairs nested less than 40 m apart, and these were in most cases separated by a projection of a reedbed. Two nests were placed only 12 m apart, but these were very well hidden in Typha-vegetation, and the pairs may have had little mutual contact.

The first eggs were laid on some excellent sites on islets from the turn of March-April, and the rate of egg-laying increased up to medio April, correlated with a gradual increase in temperature. Egg-laying remained high throughout April, to cease in early May when all 62 early-established pairs had laid eggs. The earliest clutches were large, up to 10-12 eggs, – one clutch of 14 eggs was probably laid by two females, each laying seven eggs. Clutch size regression declined to about six primo May (Fig. 2 B).

During this period there was, in addition to the established stock, a pronounced surplus which I at first believed to be immature firstyear birds. By the end of April there were at least 70 such specimens, mainly moving about in small parties and apparently not mated. The position of these birds on Fig. 1 A is mainly referring to a counting on May 7, at about 11.00 a.m. Whether all these birds had arrived during March cannot be stated for certain. Their main residence was in the shallow parts of the West Marsh, and loafing was on shores of lawns which were not defended as territories. The birds were immediately attacked when they approached the reedy portions of the shore.

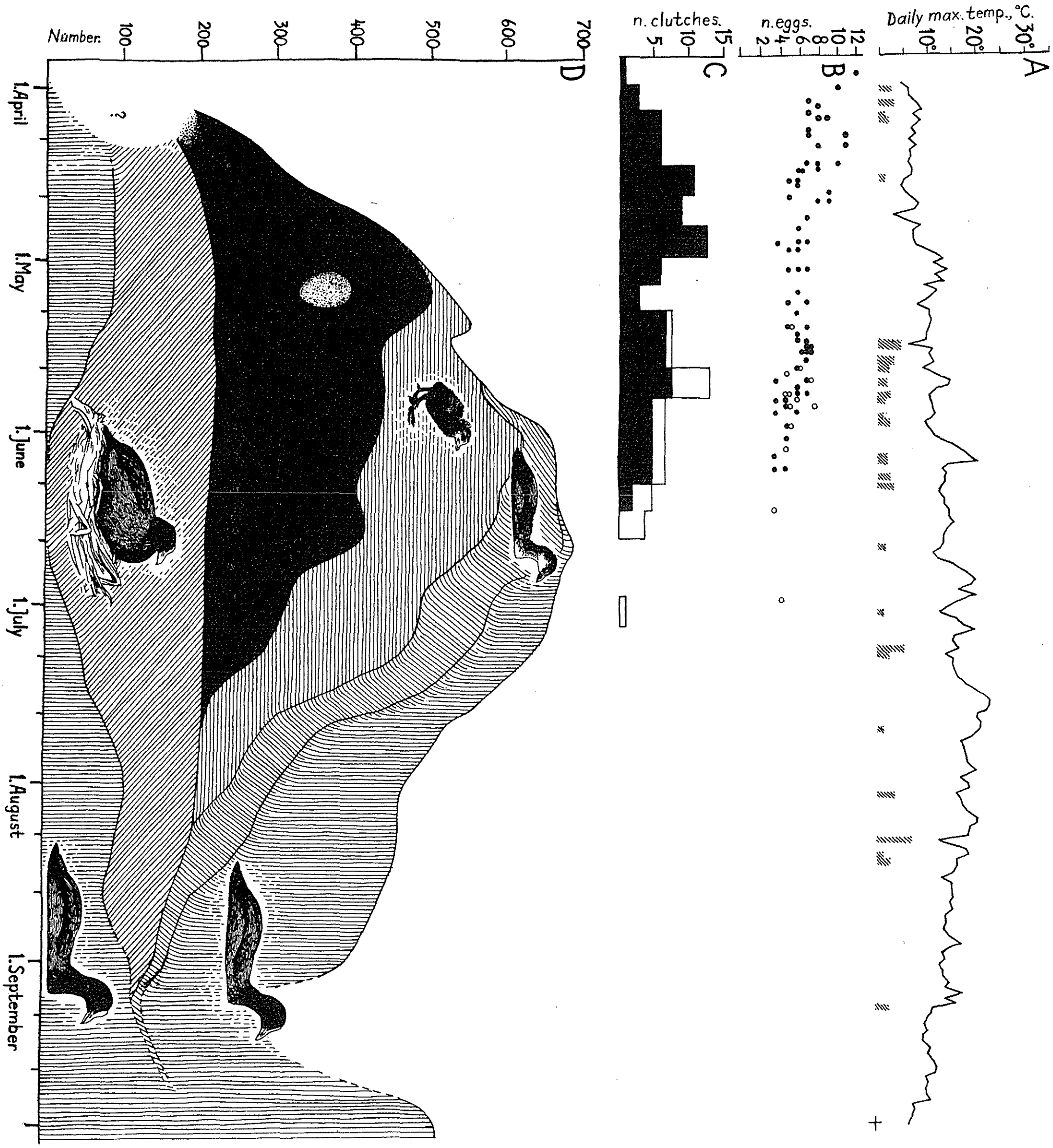
By May 10 hatching had started in 12 nests, 11 of which in the West Marsh; by May 15 in 20 nests. The families might be seen close to the nest for a couple of days, but one week after the onset of hatching they were only heard from within the reeds, and some nests had already been taken over by Blackheaded Gulls. Occasionally parties of downy chicks were found among the herb vegetation in the gulleries. In contrast to many other Coot localities, families with downy chicks were scarcely seen out on open water. Not until the young had adopted juvenal plumage did the families appear regularly at the vegetation fringe.

Within a couple of days after hatching of the earliest clutches new nests appeared near-by, and eggs were laid immediately. In some places territorial combats were seen. Also in other, less suited parts of the Marsh new nests appeared. By ultimo May the rate of egg-laying thus approached that of ultimo April, notwithstanding cool and rainy weather (Fig. 2 C). There was a corresponding, rapid decline in the offshore flocks. On June 10 I saw only three specimens which had probably not yet established a territory, but among the new-established pairs three probably laid no eggs. Clutch size averaged about six, declining further from the end of May when the birds started their body moult.

On the islets of the West Marsh, which throughout the season appeared to be preferred by the Coots, the egg-laying occurred in two clearly separate peaks, approximately on April 10 ± 5 and on May 16 ± 6 (repeat- and second clutches omitted, see below). In the rest of the West Marsh egg-laying took place approximately on April 20 ± 9 and on May 24 ± 7. In other parts of the study area where the nests were more widely spaced, the subdivision into two nesting peaks was not clear-cut, although still definite. Egg-laying averaged later, as few clutches were initiated before April 20. It seems, therefore, that after the subdivision of the attractive West Marsh into territories early in the season, there was a gradual dispersal to the less attractive sites in the other marshes. Nevertheless many non-established birds remained flocked in the West Marsh until hatching in early nests was completed. As soon as the early families disappeared into the drier parts of the reed swamps with their chicks, their territories were apparently taken over by new pairs. Even though the peaks of egg-laying differed between the separate parts of the study area, the total amount of egg-laying thus gave a bimodal distribution cirve (Fig. 2 C).

Fig. 2. Population changes and reproduction of Coots in Utterslev Mose during the breeding season of 1972. A shows curve of daily maximum temperature and days with >5 mm of precipitation (hatched); B seasonal variation in clutch size, -open dots showing repeat- and second clutches; C number of clutches initiated per five days periods, -open columns showing repeat- and second clutches; D seasonal changes in number of flocked Coots (▥), territorial Coots (▧), eggs (■), downy chicks, 0-3 weeks old (▤), juveniles, 3-7 weeks old (▨), and young Coots in postjuvenal plumage (▥).

Ændringer i bestandsstørrelse og forplantning hos Blishøns i ynglesæsonen 1972 i Utterslev Mose. A viser den daglige maksimumstemperatur samt fordeling af dage med > 5 mm nedbør (skraveret), B viser sæsonmæssige ændringer i kuldstørrelse (åbne symboler angiver andet eller omlagte kuld), C viser antallet af ægkuld påbegyndt pr fem-dages periode (åbne søjler angiver andet- eller omlagte kuld), D viser sæsonmæssige ændringer i antallet af Blishøns i flokke (▥), antallet af territoriehævdende Blishøns (▧), æg (■), dununger, 0-3 uger gamle (▤), ungfugle, 3-7 uger gamle (▨) og ungfugle, der har fuldført postjuvenil fældning (▥).


A
Daily max. temp., °C.
10°
20°
30°
B
n. eggs.
2
4
6
8
10
12
C
n. clutches.
5
10
15
D
Number.
100
200
300
400
500
600
700
?
1. April
1. May
1. June
1. July
1. August
1. September

The case is further substantiated by Fig. 3 which shows time divergency of egg-laying between closest nests, compared with the distance between them. It appears that two pairs could not settle to breed simultaneously unless about 30 m apart (one exceptional case, indicated by arrow, has already been mentioned (p. 119). In nests found 5-30 m apart, the time divergency of egg-laying was >32 days, which corresponds to the time of laying, incubating and hatching of an average-sized clutch. Territorial behaviour is thus exclusive both in space and time (see stippled lines on diagram).

Such an exclusion in time is scarcely mentioned in the literature. Only in few population studies surplus birds were accidentally found to settle successfully in optimal ranges late in the season. ORING (1969) found, in captive Gadwalls, *Anas strepera,* that nests were tolerated as close together as 2½ m, provided they were initiated 10-15 days apart. FJELDSÅ (1973, Fig. 14) found a similar time divergency in case of local crowding in Horned grebes, *Podiceps auritus,* but only in localities with poor food supply.

Some late Coot nests certainly were repeat clutches as 24% of the early clutches were unsuccessful. Nests on places accessible from land were most vulnerable and may have been disturbed by foxes and possibly also by boys. In seven cases a new clutch appeared in the same nest, and in other cases a new nest appeared in the close vicinity. Supposed cases of renesting were initiated on May 22 ± 8. In eight territories a new clutch appeared medio June, 29 ± 4 days after hatching of the initial clutch; – two of these cases were in the initial nest. These are probably true second clutches, although this could not be proved by individual recognition. Cases of second clutches in Coots are well known in the literature, although probably not very frequent.

In order to exclude, as far as possible, cases of repeat- and second clutches in the late peak of egg-laying, much effort was made to obtain simultaneous records of as many neighbour birds as possible in each separate reedy section. Due to the cryptic habits of the birds, especially those with chicks, this was, however, not easy. The checking was mainly based on alarm calls and piping from the young. As male and female have very different voices separate counting of both sexes could be made. In 40 (60%) of the places where a new nest appeared after May 10 a new female was noted in late May-early June, in addition to the initial one. To be certain of not overrating the number of late settlers I rank all late nests in places where the appearance of a new female could not be stated as repeat- and second clutches. These are specially indicated in Fig. 1 B and Fig. 2 B, C, and omitted in Fig. 3.

The supposed addition of 40 breeding pairs corresponds very well to the 70-80 flocked birds seen primo May. Although individual birds could not be followed it is reasonable to think that these birds were identical.

This interpretation of the events is further supported by the result of the detailed census of August 10. 308 flocked specimens, mainly in the West Marsh, comprising adults in remiges moult and juvenile birds which had completed the postjuvenal moult. Examination by 15-50 x 60 telescope of 56 such birds on firm ground gave a ratio of 1.8 dark-heeled (juvenile) for each yellow-heeled (old) specimen, i.e. a total of approximately 200 young and 110 old specimens. 45 family groups traced along the reed fringes, mainly near their nest sites, comprised 88 old birds and probably 87 juveniles or large chicks. This gives a total of 480 specimens, 200 of which were adults. The latter figure corresponds well with the supposed total of 62 pairs plus 70-80 flocked specimens at the turn of April-May and the supposed maximum of 100-105 pairs primo June.

Investigations after August 10 revealed little of interest. At the end of the month the post-breeding flock in the West Marsh was much disturbed by unsuccessful attempts on mass capture for ringing by night, and as the birds gained flying powers they emigrated to an apparently favourable feeding locality in the Middle Marsh, and still later to the East Marsh. At the turn of August-September some emigration took place, but later in the autumn there must have been an influx of new birds; -on October 1 there were at least 515 Coots in the marsh.

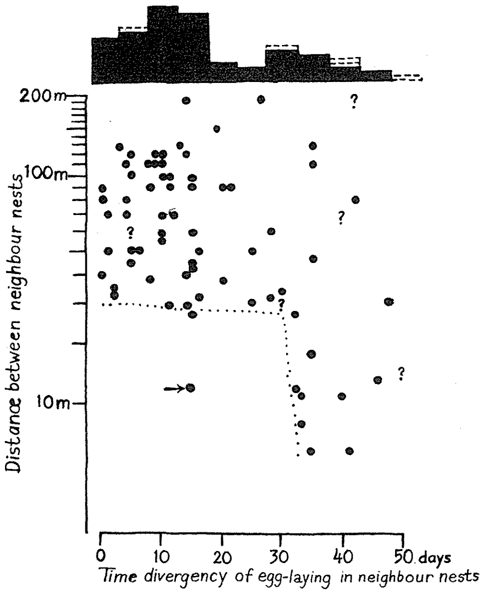


Fig. 3. Time divergency of onset of egg-laying in neighbour nests, compared with the distance between them. The histogram on the top shows frequency distribution of time divergency. ? means that one clutch might have been a second- or repeat clutch. The dot indicated by an arrow is commented in the text (p. 119).

Tidsafvigelse mellem æglægningens begyndelse i naboreder, sammenlignet med afstanden mellem dem. Histogrammet øverst angiver tidsafvigelsernes hyppighedsfordeling. ? angiver, at én rede muligvis repræsenterede andet- eller omlagt kuld. Punktet angivet med en pil kommenteres i teksten (s. 119).

DISCUSSION

The results outlined above should clearly demonstrate that the reproductive development in a large portion of the Coot population was regulated directly by the behaviour of other pairs. As long as the 62 early pairs held territories 70-80 additional birds remained flocked offshore. The fact that they bred after the early pairs went into the reed swamps with their chicks proves that they were not immature. The curve of egg-laying shows a bimodality which was not correlated with weather or other obvious environmental factors. Furthermore, egg-laying in two nests on nearly the same place was, except for one case, more than 32 days apart. This makes it likely that the protraction of breeding was not simply due to a slow reproductive development in part of the population members, but was directly determined by the time at which suited nest sites became available after completed nesting among early pairs. Accordingly, territorial behaviour seemed capable of preventing a large portion of the population from breeding.

In other habitats, viz. with conditions favouring a rearing of young along the margins of the reedbeds, which is the case in many lakes, a complete suppression of breeding might be expected to follow in part of the population. In smaller ponds and tarns territories may be claimed up to autumn departure (Kornowski 1957). The progress of breeding, and the existence of a surplus which does not breed at all, may thus vary locally. While Hasse & Wobus (1971) found only one peak on nesting, which was in some years even very synchronous, in pond areas in Oberlausitz, Bezzel (1962) found a bimodal curve, like the present, in Ismalingen. He did not study the causes, but supposed that it might be due to cases of repeat clutches.

The age of sexual maturity in Coots is not definitely stated in the literature. Bopp (1959) supposes breeding when one year old, but does not state his evidence. Among museum specimens, which may be aged from the relative length of the remiges, I have found undoubtable first-year specimens with brood patches or even with statements on the label that they had nest with eggs. However, Fog (1969) recorded assemblages of 500-1000 adult, apparently non-breeding, moulting Coots in Vejlerne in Jutland in June-July. A surplus of non-breeding birds, mainly straying about by night, is mentioned also by Rosenberg (1960) and Sage (1969), byt not by Askaner (1959), Bopp (1959), and Kornowski (1957). The true status of non-breeding Coot flocks is, of course, not easy to state for certain; -as will be seen from Fig. 2 D, there were flocked Coots in Utterslev Mose during most of the season 1972, although at most very few specimens were non-breeders. As most birds lived very hidden in June, a casual observer might get an erroneous impression of the seasonal changes in adult numbers. It is consequent that great attention and care should be taken to state the existence of a non-breeding surplus, and particularly to analyse cases of assemblage of larger numbers of Coots by midsummer. As, from the present study, most birds seem to be capable of breeding, the assemblage of large flocks in Vejlerne may consist in birds which were excluded from breeding elsewhere.

The age of the late settlers in Utterslev Mose cannot be stated for certain, although some indices may be given. In some bird species egg width gives a reasonable statistical basis for considering age groups. The present case is not clear-cut because the largest clutches primo April had very variable, and generally smaller eggs, suggesting that energy reserves might be critical for the formation of large clutches of full quality eggs (cf. LACK 1967). (Judged from museum clutch series and Mr. S. BRUHN (pers.comn.), eggs from early clutches are generally very small in springs following severe ice-winters). Egg length- and volumes from Utterslev Mose gave slight seasonal trends, but the egg width generally increased through April to about 37.5 ±1.2 mm at the end of that month, and 37.4 ± 1.3 mm for eggs in repeat- and second clutches at the turn of May-June. Initial clutches laid in May and primo June followed a lower moving average, about 35.7 ± 0.9 mm, indicating that these birds had not laid eggs previously. Supra-aquatic nest heigth was about 21 ± 3.5 cm in April, with regression sloping to 17 ± 2.5 cm for repeat- and second clutches. Initial clutches laid in May and primo June followed a lower regression, mainly 12.5 ± 2.0 cm. From these indices it seems possible to charracterize roughly the breeding population of Coots in Utterslev Mose 1972 as consisting in one early nesting population of old birds and one population of first-year birds which were excluded from breeding until the former birds abandoned their territories after hatching.

It is not possible to state whether this interaction influenced the fecundity of individual pairs. Thorough investigations are necessary in order to state whether the seasonal regression of clutch size is adaptive with respect to the prospects for raising young, or whether it is best attributed to proximate factors, such as difficulties in attaining a territory. There are no indices, from the present data, that cluch size in late pairs was correlated with the distance to a neighbour nest, and data on early pairs do not lend themselves to such an analysis, as they were all well spaced.

The two nesting peaks gave clearly different survival of young. Evidently, early breeding was advantageous as these pairs raised average 3.4 fledglings each (including repeat- and second clutches), while late pairs raised average 1.9 fledglings. Percentual survival was 50% for early broods, 34% for late broods. This difference cannot easily be explained away from differences in age of the parents, as average survival of young in the late peak of nesting was the same for initial- as for repeat- and second clutches. Due to the age differences of young from early and late clutches during autumn, they may further have different off-season survival. A poorer condition among youngs from late broods is suggested by the fact that their postjuvenal moult was very incomplete. Furthermore, data from hunting bags in October-November (525 specimens examined) show that the lowest weights, and the relatively shortest remiges, were found in those young which had retained many remnants of their first plumage in their postjuvenal plumage. Differences in off-season condition may further be supposed to influence the prospects of establishing a territory in the following spring. The failure in establishing a territory in early spring may, thus, considerably reduce the contribution of progency to the future generations.

Certain changes of the vegetation during the summer may, however, indicate other possible interpretations of the breeding events. While in May and June the bottom was covered by filamentous algae, macroscopic algae were wirtually absent from the shallow portions of the West Marsh during the grazing peak in August. This was in striking contrast to August 1971, although probably the abduction of sevage has played a major role. As there was an increase of *Cladophora* and *Enteromorpha* in the West Marsh in September, after most Coots had moved elsewhere, grazing pressure may also have played some role. This might indicate that the population was close to the carrying capacity of the locality and, consequently, that the protraction of breeding was strictly adaptive to secure all pairs prospects to raise young. However, as judged from our knowledge of the feeding ecology of the Coot (e.g.HURTER 1972), it may be doubted that the food situation was critical, even though the filamentous algae might have been overgrazed. Although largely sustained upon algae in late summer, Coots may eat almost any kind of vegetation. By midsummer they eat mainly leaves of reeds. Several kind of invertebrate food may also be taken.

After one season of field study it is, therefore, open to dispute what inference that can be made regarding the ultimate significance of the apparent territorial regulation of breeding, -whether it is limiting the propagation or is only adaptively spacing the population both spatially and chronologically.

It is to be hoped that investigations over the years to come may help to establish these ultimate problems and, furthermore, may illustrate the evolutionary consequences of the exclusive function of territorial behaviour. This must be elucidated by following the population, by marking the young, over several generations. In 1972 only 38 young Coots from known nests have been ringed in Utterslev Mose.

Data presented by HASSE & WOBUS (1972) (although not analysed by them) suggest pronounced, apparently cyclical changes of local Coot populations. Their data on production of young suggest a delayed density-dependent pattern. Such changes may give further prospects for the evaluation of the problems of population regulation.

SUMMARY

1. The reproduction of Coots in the marsh Utterslev Mose in Copenhagen was studied from April to October 1972. Census is based mainly on nest records, while the seasonal changes in number of flocked and territorial adult birds, eggs, downy chicks, and juveniles (fig. 2 D) are stated by a combination of direct counts and axtra- and intrapolation from initial dates of egg-laying, and data on clutch size, egg losses, and juvenile mortality.

2. In April 37 pairs subdivided the most attractive part of the marsh into territories while additional 25 pairs dispersed to settle in other parts. 70-80 flocked specimens remained as a non-breeding surplus, mainly keeping on open water, outside territories, near the most attractive places (fig. 1 A).

3. After hatching in early nests the families vithdrew into the reed swamps. Within a very short time new pairs settled to breed. 40 new breeding pairs were stated, in addition to several cases of repeat- and second Clutches. At the same time the offshore flocks dwindled away (fig. 1 B). Thus there was, in late May and early June, a second peak of egg-laying (fig. 2 C).

4. The time divergency in egg-laying between nests on nearly the same place was 32 days (fig. 3), indicating that the protraction of nesting was directly determined by the time at which early pairs had completed their nesting and abandoned their territories.

5. Seasonal changes in moving averages for egg breadth and nest heigth indicate that the 40 late pairs were mainly first-year birds.

6. Early nesting was clearly advantageous. Those Coots which did not acquire a territory until May probably gave a very poor contribution to the next generation. Evidently, territorial behaviour might, therefore, accentuate indicidual differences in fitness for breeding.

7. Problems on population control are discussed, together with ideas on the mechanism of selection by chich the social organization might act at the gene pool of the population.

ACKNOWLEDGEMENTS

My sincerest thanks are due to cand. mag. NIELS OTTO PREUSS for his co-operation during the field work and for placing his own data on Coot nests at my disposal. I am furthermore indebted to Mrs. JYTTE HØSTMARK for the final typewriting of the manuscript.

DANSK RESUME

Territorialadfærens betydning for yngleforløbet hos en bestand af Blishøne *Fulica atra.*

1. Blishønens ynglebiologi blev udforsket i Utterslev Mose i København fra april til oktober 1972 som en indledning til mere langsigtede undersøgelser. Bestandstakseringer blev hovedsageligt baseret på redefund, medens ændringer i antallet af voksne fugle i flokke, territoriehævdende fugle, æg, dununger og ungfugle (fig. 2 D) blev skønnet ved en kombination af direkte optælling og extra- og intrapolering ud fra tidspunktet for æglægning i de enkelte reder og data over kuldstørrelser og tab af æg og unger.

2. Tidligt i april blev rør- og dunhammervegetationen i den mest tiltrækkende vestlige del af mosen delt ganske ligeligt mellem 37 territoriehævdende par, medens yderligere 25 par spredte sig til mosens øvrige dele. Desuden optrådte 70-80 individer i flokke, hvis væsentligste tilholdssteder var udenfor territorierne (fig. 1 A).

3. Efter ægklækningen i de tidligste reder forsvandt disse familier ind i rørskovene og levede meget skjult i de følgende uger. I løbet af få dage efter klækningen blev redestederne overtaget af nye par, og samtidigt svandt flokkene af ikke-ynglende fugle ind. Bortset fra flere tilfælde af andet kuld og omlagte kuld blev 40 nye ynglepar fastslået. Til trods for temmelig regnfuldt vejr blev der således et nyt æglægningsmaksimum i sidste halvdel af maj og begyndelsen af juni (fig. 1 B, fig. 2 C). På de foretrukne ynglelokaliteter, øerne i den vestlige del af mosen, foregik årets æglægning således i to klart adskilte maxima, nemlig 10.±5 april og 16.±6 maj.

4. Tidsafvigelsen for æglægning mellem reder placeret mindre end 30 m fra hinanden var mere end 32 dage, svarende til summen af æglægnings-inkubations- og klækningstiden for et kuld (fig. 3). Dette skulle vise, at forsinkelsen af æglægningen hos en stor del af bestandens medlemmer direkte var bestemt af de tidlige ynglepars territorieforsvar, som varede ved, indtil deres ægklækning var overstået.

5. Ud fra ændringer i det løbende gennemsnit for ægbredde og redernes højde over vandet for første-, andet- og omlagte kuld skønnes, at de 40 sene ynglepar fortrinsvis var ét-årige fugle.

6. De 62 tidlige par fik gennemsnitligt hver 3.4 unger på vingerne, mod gennemsnitligt 1.8 unger for de 40 sene par. De fugle, som ikke magtede at etablere et territorium tidligt på foråret, synes således at give et meget lille bidrag til den kommende generation. Territorialadfærden synes således at kunne forstærke forskelle i forplantningsdueligheden mellem aldersgrupperne.

7. Problemer vedrørende territorialadfærdens eventuelle bestandsregulerende rolle, og selektionsmekanismer hvorved denne adfærd kan tænkes at påvirke bestandens gen-pulje, drøftes.

REFERENCES

Askaner, T., 1959: Några iakttagelser över häckningsbeteende och häckningsresultat hos sothönan *(Fulica atra).* – Vår Fågelvärld 18: 285-310.

Bezzel, E.I., 1962: Beobachtungen über Legebeginn und Legezeit bei Entenpopulationen. – Anz. Orn. Ges. Bayern 6: 218-233.

Bopp, R., 1959: Das Blesshuhn *(Fulica atra).* – Wittenberg-Lutherstadt.

Brown, J.L., 1969: Territorial behavior and population in birds. – Wills. Bull. 81: 292-329.

Fjeldså, J., 1973: Territory and the regulation of population density and recruitment in the Horned grebe *Podiceps auritus arcticus* Boje, 1822. – Vid. Meddr. Dansk Nat. Hist. Foren., in press.

Fog, J., 1969: Studier over Blishønen *(Fulica atra)* i Vejlerne og danske ynglefugles trækforhold. – Dansk Orn. Foren. Tidsskr. 63: 1-18.

Fretwell, S., 1969: The adjustment of birth rate to mortality in birds. – Ibis 111: 624-627.

Harild, P. Andersen, 1970: Utterslev Mose. – Feltornithologen 1970 (3): 127-130.

Harris, M.P., 1970: Territory limiting the size of breeding populations of the oystercatcher *(Haematopus ostralegus)* – a removal experiment. – J. Anim. Ecol. 39: 707-713.

Hasse, H. & U. Wobus, 1971: Das Blesshuhn *(Fulica atra* L.) in der Oberlausitz. – Abh. u. Ber. Naturk. Mus. Görlitz 46: 1-15.

Hurter, H. -U., 1972: Nahrung und Ernährungsweise des Blässhuhns *Fulica atra* am Sempachersee. – Orn. Beob. 69: 125-149.

Hüttenmoser, S., 1962: Vermehrungsrate, Populationsdruck und Existenzbasen der Vögel. – Orn. Beob. 59: 73-83.

Kaulberg, A.S., 1947: Søborg Mose. – København.

Kornowski, G., 1957: Beiträge zur Ethologie des Blässhuhns *(Fulica atra* L.). – J. Orn. 98: 318-355.

Lack, D., 1947-48: The significance of cluch size. – Ibis 89: 302-352, 90: 25-45.

Lack, D., 1954 a: The natural regulation of animal numbers. – Oxford.

LACK, D., 1954 b: The evolution of reproductive rates. – In HUXLEY, HARDY & FORD eds. Evolution as a process. London, 143-156.

LACK, D., 1967: The significance of cluch size in waterfowl. – Wildfowl 18: 125-128.

LACK, D., 1968: Ecological adaptions in birds. – Bristol.

ORING, L.W., 1969: Summer biology of the gadwall at Delta, Manitoba. – Wills. Bill. 81: 44-54.

PREUSS, N.O., 1971: Fuglelivet og forureningen i Utterslev Mose. – Dansk Natur – Dansk Skole 1971: 25-27.

ROSENBERG, E., 1960: Sothönan, *Fulica atra* Linné. – In K. CURRY-LINDAHL ed. Våra Fåglar i Norden. II. ed. – Stockholm: 681-691.

SAGE, B.L., 1969: Breeding biology of the coot. – Brit. Birds. 62: 134-143.

SKUTCH, A., 1967: Adaptive limitation of the reproductive rate of birds. – Ibis 109: 579-252.

TEIBEL, E., 1970: Fuglelivet i Utterslev Mose. – Dansk Orn. Foren. Tidsskr. 64: 248-252.

WATSON, A. & D. JENKINS, 1968: Experiments on population control by territorial behaviour in red grouse. – J. Anim. Ecol. 37: 595-614.

WILLIAMS, G.C., 1966: Adaption and natural selection. – Princeton N.J.

WYNNE-EDWARDS, V.C., 1962: Animal dispersion in relation to social behaviour. – Edinburgh-London.

MS received 1st February 1973

Author's address:
Zoological Museum,
Universitetsparken 15,
2100 Copenhagen Ø