SIZE AND QUALITY OF THE COOT *Fulica atra* TERRITORY IN RELATION TO AGE OF ITS TENANTS AND NEIGHBOURS

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ABSTRACT The size and composition of the breeding territory of the Coot *Fulica atra* has been studied in relation to the age of the breeding birds, the age of their neighbours, and the date of arrival in the territory. Old pairs arrive earlier than young pairs. Old pairs have larger territories, measured as its water area. Vegetation elements along the shore are important constituents of the territory, measured as length of unprotected shore. It appeared that the composition of the territory, measured in this way, depends on the age of the male, not on that of the female. Old males have more than young ones. Likely the size and composition are separate resources with a different role of the female in its defence. Important predictors of the length of the unprotected shore which the male territory holder is able to defend are two ratios: his age to the mean age of the neighbours and his age to the sum of the ages of his neighbours.

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INTRODUCTION

In many species of birds breeding characteristics such as laying date, clutch size and number of young fledged are related to age. Such is true e.g. for: the Great Tit (Kluyver 1951, Harvey *et al.* 1979, Perrins & McCleery 1985), the Song Sparrow (Nol & Smith 1987), the Lesser Snow Goose (Finney & Cooke 1978, Haman & Cooke 1987), the Kittiwake (Coulson & White 1960, 1961, Coulson 1966), the California Gull (Pugesek 1981, 1983, Pugesek & Diem 1983), the Glaucous-winged Gull (Reid 1988) and the American Coot (Crawford 1980). Nest location and territory size are related to age in colonial birds such as the Glaucous-winged Gull (Reid 1988). The time spent by the American Coot in territory defence increases with age (Ryan & Dinsmore 1980).

Recently, as a result of life-history-theory predictions, there is a great deal of discussion as to whether such age-related phenomena reflect individual changes (maturation, increase in experience, increase in parental effort) or selective mortality (Curio 1983, Nur 1984, Pugesek 1984, Nol & Smith 1987, Hamann & Cook 1987, Reid 1988). Although the main field of discussion deals with subjects similar to those as mentioned above, age dependent differences in reproductive output and territorial behaviour are also of interest for the dynamics of bird populations.

Since 1964 we have studied the annual numbers of breeding birds in a population of the Coot *Fulica atra* at the Westeinderplassen near Aalsmeer. These numbers show an undulating pattern, that can be explained as being the combined effects of winter severity on survival and a delayed density-dependent factor (Cavé & Visser 1985). As Coots are highly territorial during the breeding season, territorial strife could reasonably be responsible for the density dependence of breeding-bird numbers. If age groups have different capacities in territorial contest, so that old birds obtain more of the critical resources than young ones, this may then lead to delayed effects in density dependence. There is some support in the literature for the assumption that capacity, in territorial contest or effort, increases with age in

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the Coot. Ryan & Dinsmore (1980) report for the American Coot an increase of time spent in territorial defence and a decrease in feeding time of the young combined with a higher reproductive output, presumably related to territory quality. Alisauskas (1987) found that morphometric characteristics related to fighting ability correlate with age in this species. In the European Coot the white frontal shield (a display structure used in competitor assessment) is larger in old birds than in young ones (Visser 1988).

The aim of the present paper is to study the relationship of territorial characteristics with age of the breeding bird. Age is thought to represent a competitive ability in territorial behaviour. Asymmetry in competitive ability in territorial behaviour between age-groups will then be reflected in the characteristics of the territory of the bird. However, if both members of a pair are involved in territorial defence, as is the case in the Coot, then the ability of the partner is also important. Male and female do not necessarily compete for the same resources, so one may expect that some aspects of the territory are more dependent on the age of the male and others more on the age of the female. Further, asymmetry between breeding pairs in territory-holding potential may depend on the time of arrival in the area or time of occupation. There are also opposing neighbours involved in territorial contest. Their number and capacities possibly affect the characteristics of the territory a pair is able to hold. In the present paper we want to analyse the size and composition of Coot territory in relation to age of the breeding birds, age of their neighbours, and date of arrival in the territory.

MATERIAL AND METHODS

The study area of some 155 ha is located near the village of Aalsmeer, 17 km southwest of Amsterdam. It consists of numerous small artificial islands, mainly in use for horticulture and recreation. A more detailed description is given in Cavé & Visser (1985).

Since 1966 chicks and full-grown young in this area have been captured and ringed with metal leg rings, coloured leg rings were also used to identify individuals in the field. From 1981 onwards full-grown birds were marked by coded neck collars, enabling easy recognition of individual birds. The majority of the Coots breeding in this area overwinter in open water in the vicinity of the study area and return in late winter or early spring to their breeding site. In 1985 to 1987 the arrival in the breeding area and the formation of breeding territories were closely followed in part of the study area (about 25 ha). In this subarea it is possible to survey a number of territories simultaneously. The subarea was visited at least weekly after it was sufficiently ice-free to allow access by boat (starting dates: 7/3/85; 21/3/86; 19/3/87). The observations terminated at the end of the incubation period, thus they were concentrated on the early phases of the breeding season. All sightings and observations of aggressive encounters with neighbours and other waterfowl were mapped.

The date of first sighting of Coots of known age was used as an estimate of the date of arrival in the area. The date at which a bird is seen for the first time in its territory is used as an estimate of arrival date in its territory (occupation date).Territory boundaries were assessed by a combination of observations of sightings and aggressive encounters with neighbours. After having established the area constituting a territory, the structure and vegetation of the territory were mapped. As it was practically impossible to measure territory boundaries on land, only water area and shore characteristics were measured. For the analysis the following features were considered:

1. Total water area, as a measure of territory size
2. Total shore length, including edges of floating reedbeds and stands of emerging waterplants
3. Length of shore faced by planking (called protected shore), being the barest part of the shore

4. Length of unprotected shore (total shore length minus length of protected shore), representing the part of the shore with more vegetation, probably indicating territory quality.

Only data from pairs that could be identified by neck-collar marks or coloured leg rings were included in the analysis. Age indication of breeding birds is in year of life (so first year means 2nd calendar year). In some cases only the minimum age was known. Such birds are included without distinguishing them from birds whose exact ages were known, except where otherwise stated. The data of one male observed in all three years were excluded from analysis. This male, 7, 8, and 9 years of age in the three observation years respectively, deviated greatly, not only in his territory characteristics, but also in his extremely poor breeding results. The data set from the intensively studied subarea is called data set 1. This data set is the most complete data set and is used in analysis, except where stated otherwise.

Time budget observations were made with the help of students in May 1984, 1985 and 1986. These observations were carried out during a full day with the same pair. For these observations pairs were chosen having young of 5 to 20 days of age and of which the age of the male could be established. At the end of the observation day the territory of the pair was mapped on the basis of the observations of that day. No special part of the study area was chosen for the observations. This data set is called data set 2.

In the Coot both members of the pair are involved in territorial defence and it might be that both members contribute to territory size and/or composition. Therefore, in the regression analyses the age of both male and female were included as independent variables. Often we could trace only a significant regression coefficient for the male, none for the female. As this does not mean that male and female differ in their predictive value for the territory characteristic considered, it was tested whether the two regression coefficients differed significantly (for test used see Overall & Klett, 1972 p.424; Draper & Smith, 1966 p.74). When this was not the case the sum of the ages of male and female was used as a measure of the age of the pair.

RESULTS

Arrival in the territory

Some breeding birds were already present immediately after the area became ice-free. Some of them had already occupied their territory.

The age of both members of 34 breeding pairs observed during the prelaying stage in their territory were known, as well as further details of their breeding history. From these 34 pairs 26 were paired when they were observed for the first time in their territory. In the 8 remaining cases the partner was seen at the latest 12 days later. The dates of arrival in the territory of the partners are closely correlated (Fig. 1). In 3 cases the male was seen first, in 5 the female. As it is always possible that a bird is present but not observed, we think that in most cases pair formation takes place before settlement in the territory. Therefore, for further analysis the first observation of one of the members of the pair in the territory, irrespective of its sex, is taken as an estimate of the date (March days) of arrival of the

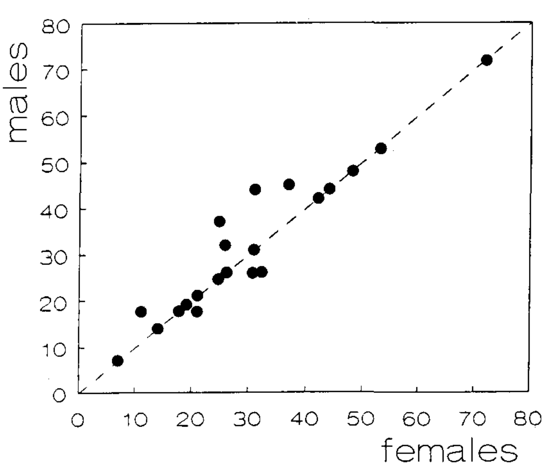

Fig. 1. The relationship between the date of arrival (March days) in the territory of male and female.

Table 1. Regressions of date of arrival of the pair on the territory (*Y*) on age of the female (*F*), age of the male (*M*), age of the pair (*F+M*), and starting date (*S*). Test for inequality of *F* and *M* is given under (*F=M*). The sign of the regression coefficients is given; *p*-values between brackets. *I* is the number of cases included. Reg. is the regression number referred to in the text.

Reg.	*I*	*F*	*M*	*F=M*	*F+M*	*S*	R^2
1	34	+(0.75)	-(0.01)	(0.14)		+(0.01)	0.33 (0.01)
2	34				-(0.01)	+(0.01)	0.28 (0.01)

pair in the territory. Regression analysis of arrival date on age of female, age of male and starting date of observations (used as a measure of the date at which the area becomes suitable in spring) is given in Table 1. Regression 1 shows a negative relationship of arrival date with age of the male, and a positive one with starting date. The age of the female made no significant contribution to regression.

This suggests that arrival date depends on the age of the male, not on the age of the female. However, the regression coefficients of the age of male and female do not differ significantly. This leads to the conclusion that male and female do not differ in this respect and that the date of arrival in the territory of the pair depends on age of the pair and on starting date (regression 2). Summarising, old pairs arrive earlier than young ones after the area becomes suitable in spring. Age of male and female have no significant different effect on arrival date, although the data suggest that the balance is in favour of the male.

Size and composition of the territory

Firstly we consider the relationships of the ages of male and female to territory size, estimated by the area of water in the territory (Table 2). Regression 1 shows that water area is significantly explained by age of the members of the pair, although the regression coefficients of the independent variables are not significant. The regression coefficients of the age of male and female do not differ significantly and the ages of the members of the pair can be added to the single

Table 2. Regressions of water area of the territory (*Y*) on age of the female (*F*), age of the male (*M*), age of the pair (*F+M*), length of unprotected (*UP*) and protected shore (*P*), arrival date of the pair in the territory (*AP*) and lateness of winter (starting date of observations *S*). Test for inequality of regression coefficients of *UP* and *P* is given under *UP=P*. For further explanation see Table 1.

Reg.	*I*	*F*	*M*	*F=M*	*F+M*	*UP*	*P*	*UP=P*	*AP*	*S*	R^2
1	41	+(0.19)	+(0.07)	(0.89)							0.22 (0.01)
2	41				+(0.00)						0.22 (0.00)
3	41					+(0.00)	+(0.05)	(0.02)			0.23 (0.01)
4	41	+(0.11)	+(0.68)	(0.48)		+(0.07)	+(0.09)				0.32 (0.01)
5	41				+(0.05)	+(0.09)	+(0.11)				0.31 (0.00)
6	31								-(0.06)	+(0.26)	0.13 (0.13)
7	31	-(0.70)	+(0.07)						-(0.60)	+(0.85)	0.25 (0.09)
8	31	-(0.66)	+(0.03)	(0.16)					-(0.62)		0.25 (0.05)
9	31				+(0.07)				-(0.38)		0.19 (0.05)

independent variable age of the pair. Regression 2 shows that old pairs have larger territories than younger ones.

Coots spend most of their time along the shore. Regression 3 shows, as expected, that water area is related to the length of unprotected and protected shore. Large territories have longer shores than small ones. The regression coefficients differ and are therefore not given combined as total shore length. Now the question arises whether water area and age of the pair are related independently of length of protected and unprotected shore. In regression 4 it can be seen that, as in regression 1, the regression coefficients of age of female and male are not significant. However, regression 5 shows that the relationship between water area and age of the pair remains significant after correction for length of protected and unprotected shore. So water area and age of the pair are related independently of shore length.

In the previous section it was found that old pairs arrive sooner than young ones in their territory. One may suspect that early pairs have larger territories, irrespective of age. There are 31 pairs in data set 1 of which we have sufficient data concerning arrival dates and territory characteristics for analysis. Regression 6 gives a nearly significant relationship between arrival date of the pair and water area, when corrected for the lateness of the winter. Early pairs seem to have larger territories then late ones. Including age of female and male gives only a nearly significant relationship for the age of the male with water area (regression 7). Deletion of starting date increases the significance of the age of the male (regression 8). Old males have larger territories than young ones, independent of arrival date. As age of female and male have no significantly different regression coefficients, a similar conclusion may be reached for age of the pair, although not significantly (regression 9). The regression coefficient of arrival date is no longer significant when age of male and female or age of the pair are included. So early pairs do not have larger territories, independent of age.

Next we considered the relationship of shore length and age of the breeding birds as Coots spend most of their time along the shore. It was found that total shore length is not related to age of the breeding birds, neither taken separately or combined, whether or not corrected for water surface.

However, it may be that special elements of the shore are of importance. The parts of the shore with more vegetation have more nesting possibilities, cover and perhaps more food. We therefore considered the relationships of age of the breeding birds and length of unprotected shore in the territory, as an estimate of the part of the shore with more vegetation (Table 3). Regression 1 shows that length of unprotected shore is positively related to the age of the male, but not to the age of the female. As the regression coefficients for age of male and female differ significantly, we must conclude that old males have more un-

Table 3. Regression of unprotected shore (*Y*) on age of the female (*F*), age of the male (*M*), age of the pair (*F+M*), water area (*W*), protected shore (*P*), arrival date of the male (*AM*), and lateness of winter (*S*). For further explanation see Table 1.

Reg.	*I*	*F*	*M*	*F=M*	*F+M*	*W*	*P*	*AM*	*S*	R^2
1	41	-(0.63)	+(0.00)	(0.03)						0.32 (0.00)
2	41					+(0.00)	-(0.02)	0.26	(0.00)	
3	41	-(0.28)	+(0.00)	(0.01)		+(0.07)	-(0.01)			0.47 (0.00)
4	31							-(0.01)	+(0.03)	0.25 (0.01)
5	31	-(0.25)	+(0.00)	(0.01)			+(0.39)	+(0.95)	0.47	(0.00)

protected shore at their disposal than young ones, independently of the age of their partner. Length of unprotected shore in the territory is positively related to water area and negatively to length of protected shore (regression 2). Regression 3 shows that old males have more unprotected shore, not only independently of the age of their partner, but also corrected for protected shore and water area.

In the previous section it was shown that old males arrive earlier than young. So one may ask whether early males have more unprotected shore at their disposal. A significant correlation is found between length of unprotected shore and arrival date of the male in the territory, taking into account the lateness of winter (starting date) in the 31 pairs of which there is sufficient data available about territorial features and arrival dates. The arrival date of the male, not of the pair, is used here as the choice of unprotected shore depends on the male. Early males have more unprotected shore at their disposal (regression 4). Inclusion of the age of male and female in the model shows a significant relationship between age of the male and length of unprotected shore, independent of arrival and starting date (regression 5). The regression coefficients of male and female again differ. So the relation between age of the male and length of unprotected shore seems to be independent of date of arrival in the territory. Early males do not have territories richer in vegetation independent of age.

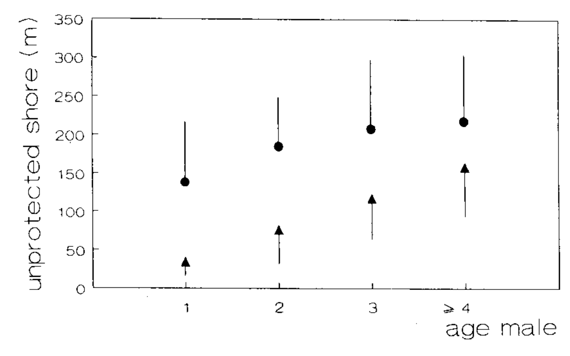

Fig. 2. The relationship between age (years) of the male and length of unprotected shore for both data set 1 and 2. Data set 1, closed triangles; data set 2, dots. Vertical bars, 95 % confidential interval.

Further data on territory size and quality were obtained with data set 2. The relationship between length of unprotected shore and age of the male is shown both for data set 1 and 2 in Fig 2. It is quite obvious that there is a positive relationship between the length of unprotected shore and the age of the male. The regression between these variables (taking replicates into account) is significant for both data sets (data set 1: $p < 0.001$; data set 2: $p = 0.04$). Further it can be seen in Fig. 2, that the unprotected shores of data set 2 are remarkably longer than those of data set 1. One reason for this difference might be that the data of set 2 were obtained later in the season, when there were young, while those of set 1 were collected during the pre-laying and incubation period. It is possible that later in the season the pairs that reach the stage of rearing young are able to improve their territories at the expense of those that leave. However, changes in the size of the territory during the season could not be studied with our limited observations. Whatever the reason for this difference between the level of the two data sets might be, it does not invalidate the general result that old males have more unprotected shore at their disposal than young ones.

Competition with neighbours

Up to this point the age of the pair has been considered without taking into account the age of the surrounding pairs. One may expect that age and number of neighbours affect the size and composition of the territory. In the previous section it was found that the area of water of the territory, used as a measure of territory size, depends on the age of both the male and the female. The effect of the age and the number of neighbouring pairs on this measure of territory size could not be studied because of lack of sufficient data.

It was further found that length of unprotected shore in the territory is related to age of the male only. For 19 territories of data set 1 the age of the male owner and that of all the surrounding

Table 4. Regressions of length of unprotected shore (Y) on N, $M/\Sigma O$, $N{*}M/\Sigma O$, and protected shore (P). M = age of male; N = number of neighbouring males; ΣO = sum of the ages of the neighbouring males. For further explanation see Table 1.

Reg.	I	N	$M/\Sigma O$	$N{*}M/\Sigma O$	P	R^2
1	19	+(0.05)	+(0.00)			0.62 (0.00)
2	19	-(0.99)	+(0.10)	+(0.25)		0.69 (0.00)
3	19		+(0.04)	+(0.01)		0.69 (0.00)
4	19		+(0.05)	+(0.01)	-(0.17)	0.73 (0.00)

males were known. Using these 19 males we were able to study the effects of their age, and the age and the number of neighbouring males on the length of unprotected shore in its territory (Table 4). Assuming the age of the male (M) to be a measure of its competitive power, and the sum of the ages of his neighbouring opponents (ΣO) as a measure of the total competitive power of the neighbours, then $M/\Sigma O$ seems to be a reasonable index of its competitive power relative to those of its neighbours. However, also the number of opponents (N) are likely to be involved. Regression 1 gives a significant positive regression coefficient for both N and $M/\Sigma O$. The positive regression coefficient of N is unexpected at first sight. However, an increase in N independent of $M/\Sigma O$ means a lower mean age of the neighbours. It might be, therefore, that the relationship between unprotected shore and $M/\Sigma O$ is different for different N's. To test this we use the interaction term between N and $M/\Sigma O$ given by $N{*}M/\Sigma O$. This interaction term represents the competitive power (age) of the male relative to that of the mean neighbouring male. Regression 2 shows that the contribution to regression of the number of opponents (N) vanishes when $N{*}M/\Sigma O$ is included. Excluding N (regression 3) delivers significant regression coefficients for both $M/\Sigma O$ and $N{*}M/\Sigma O$. Regression 3 has a higher R^2 than regression 1 and has therefore been chosen for further analysis. Regression 4 shows that protected shore is not significantly involved.

Summarizing, the amount of unprotected shore a male holds depends both on his age relative to the sum of the ages of his opponents and on his age relative to the opponent's mean age. Visualizing, if a male has neighbours of a certain mean age, the amount of unprotected shore at his disposal decreases with the number of neighbours, as in that case he has to resist more opponents of a given competitive force (ΣO increases). On the other hand, when the sum of the ages of the neighbours (ΣO) is given, the defended amount of unprotected shore increases with the number of opponents, since their mean age decreases. This latter finding means that it is easier for a male to defend his territory against a certain opposing force (represented by the sum of the opponents' ages) composed of young birds than if this force is made up of older birds.

DISCUSSION

The aim of this paper was to study the effects of the age of the members of the pair and those of the neighbouring pair on the size and composition of their territory.

Age is considered as some measure of competitive ability of the birds in territorial strife. It was found that the size of the territory, measured as water area of the territory, depends on the mean age of the pair, while the composition of the territory, measured as length of unprotected shore, depends only on the age of the male.The first question to be answered is, whether water surface and unprotected shore represent different resources, both subjected to competitive strife. The above finding suggests indeed that such is the case.

If water area and length of unprotected shore are different resources, it may be that the contribution of the members of the pair in competitive strife for the resource in question is different in the two cases. Field observations show clearly that both members are involved in territorial defence, although the time budget data of Salathé & Boy (1987) for the European, and of Ryan & Dinsmore (1979) for the American Coot suggest that the male spends more time on it than the female. So the above mentioned difference in contribution of the members of the pair in obtaining water area or unprotected shore, possibly reflects a different behaviour of the two sexes, i.e. a relatively larger share taken by the female in defending the water area. In the case of unprotected shore, it is clear that the male is the principal defender. However, in the case of the water area the role of the female is uncertain. So, although the data suggest a different role for the female in these two cases, our results remain ambiguous.

Old pairs arrive earlier in the territory than young, and it might be that earliness, not age, determines the size and quality of the territory. This possibility is not supported by our data, since no effects of arrival dates, independent of age, on the territory characteristics considered could be found. Petrie (1984) also found in the Moorhen that time of establishment of the territory and its subsequent size were not related. So it is not the earlier date of arrival of old birds that give them better chances in territorial strife, but some other feature related to age. It seems, on the other hand, that laying date is more directly related to the date of arrival in the territory and age of the breeding birds than to territory characteristics, as can be demonstrated with data obtained from data set 1. Laying date shows a significant correlation ($r = 0.37$; $p = 0.04$) with water area, and a nearly significant one ($r = 0.34$; $p = 0.06$) with length of unprotected shore. However, regression of laying date on starting date (a measure of the lateness of the winter), arrival date, age of the pair, water area and length of unprotected shore shows a positive relationship with arrival date ($p < 0.01$), and a negative one with age of the pair ($p < 0.01$), but not with water area ($p = 0.75$) and length of unprotected shore ($p = 0.47$). It could be shown further that when the birds arrive late in their territory the time between arrival and laying is shorter ($p < 0.01$), while, independently of arrival date, this time interval is shorter for old birds ($p = 0.01$). The time of laying in relation to age of the pair will be discussed in detail in a later paper. These findings do not support the idea that there is a direct effect of territory characteristics on laying date. However, it may be that laying date is related to other characteristics, not specified in this paper, like the availability of cover, and nesting possibilities early in the season as has been stated repeatedly (Salathé 1986; for the American Coot Sugden 1979, Gorensel et al 1981,1982, Kartrud 1985).

It was shown that the length of unprotected shore a male is able to hold depends on his age relative to those of his neighbours. Petrie (1984) found for the Moorhen that territory size depends on the weight of the male relative to that of its neighbours. Body weight was thought to represent competitive power (called resource holding potential RHP), as we also consider the case is for age. It is therefore interesting to compare the findings of the two studies. The situations are different in two main aspects. Firstly, each male has always two neighbours in the case of the Moorhen; in our case this number varies. Secondly, the Moorhen territories are very simple in form, being parts of ditches. The territories of our Coots were often in branched ditches and pools, with patches of unprotected shore.

The interesting point we were able to show, and which is an addition to Petrie's findings, is that total opposing force (represented by the sum of the ages of neighbouring males) and the forces of the individual opponents (represented by mean age of the neighbouring males) are involved. This finding simply means that it is easier to resist a number of relatively weak opponents individually, rather than the same force concentrated in a single strong opponent.

Since the parts of the shore richer in vegetation, represented by unprotected shore, are the subject of territorial strife, the question arises what makes them so important. The most obvious reason for this preference is food supply. The localities where Coots search for food for their young are restricted to special places for each kind of food. For instance diving for mussels *Dreissena polymorpha* often occurs under overhanging trees or shrubs, while diving for caddis-fly larvae is especially done near vegetation emerging from the water surface. This suggests that food is concentrated at special places within the territory. However, we have no direct measurements of food distribution.

A second reason for the preference of more vegetated territories might be protection against predation. Salathé (1986) found a distinct relationship between the visibility of the nest and predation rate. Petrie (1984) showed in the Moorhen that the chance of the nest being robbed is negatively related to the size of the territory. Predation and accidents might also play a role in a preference of foraging along the shore when the chicks are following their parents. Further, the availability of nesting sites may play a role.

We have seen that territorial characteristics change with age of the breeding birds, at least with age of the male. There are morphometric differences related to age such as a larger size (Perdeck 1985), and changes in relative dimensions like those found in the American Coot (Alisauskas 1987). Changes of tarsal colour with age in the European and American Coot (own obs.; Crawford 1978) and frontal shield size (Visser 1988) suggest changes in testosterone levels with age. So there seems to be age-related morphological and endocrinological characteristics which are possibly also involved in fighting ability.

Our findings may have two different interpretations: 1. the birds improve with age; 2. only those birds having the better territories remain in the population. Alisauskas (1987) showed that young birds are more variable in size and secondary morphological traits related to age, suggesting that selective mortality against small size (and poor fighting ability) plays some role. Only the study of territory characteristics of individual birds over a number of years could show whether individuals improve during life or not. We have insufficient data to study this point, but in other aspects of breeding, i.e. laying time, individual birds improve during life.

In order to understand the maximalisation of lifetime reproductive output it is very important to know whether age-related differences in breeding behaviour result from individual changes with age in breeding effort or breeding capacity, or whether this is caused by selective mortality. In order to understand the population-dynamic consequences of age-related phenomena it is irrelevant whether or not they result from selective mortality.

Territory size and composition were analysed in relation to age because Cavé & Visser (1985) suggested that increase in territory size with age may be responsible for delayed density dependence in breeding bird numbers. Two aspects of the results of this paper are of importance in this respect. Firstly, that territory size and composition depend on age. Secondly, that the amount of unprotected shore a male can defend depends on its age-related resource holding potential, relative to those of its neighbours. This latter finding shows that there is competition, with old birds having the better chances, at least for special characteristics of the territory. These findings make it likely that exclusion of breeding at high density especially affects the young birds. They further suggest that the density at which such an exclusion occurs depends on the age structure of the population. However, we have a poor knowledge of the floating population, and the data given in this paper only refer to pairs that have settled, not to the process of settlement.

The next step in the analysis is to incorporate our knowledge of territorial behaviour in modelling breeding bird density. Cavé & Visser (1985) assumed in their model of breeding bird density delayed density dependence by age dependent territorial behaviour. The basic idea of their model is that a damped oscillatory system subjected to the effects of some exogenous random factor (i.e. mortality due to winter severity) may lead to stable oscillations (Nisbet & Gurney 1976, Royama 1981). The same principles are applied in modelling cyclic Red Grouse populations (Potts *et al.* 1984, Rothery *et al.* 1984, Watson *et al.* 1984). We have now more reason to assume delayed density dependence by age dependent territorial behaviour in the Coot.

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SAMENVATTING

Dit artikel gaat over de grootte en samenstelling van het broedterritorium van de Meerkoet in relatie tot de leeftijd van de broedvogels en hun buren. In Cavé & Visser (1985) werd het vermoeden uitgesproken dat oude broedvogels grotere en betere territoria hebben dan jonge broedvogels. In dit artikel wordt daar nader op in gegaan.

De waarnemingen (1984 tot en met 1987) zijn in een gedeelte van de Westeinderplassen uitgevoerd. In dit terrein zijn Meerkoeten gedurende een lange reeks van jaren geringd. Tevens zijn er kleurringen, en (van 1981 af) halsbanden aangelegd. Dankzij dit programma zijn er in het proefterrein veel broedvogels van bekende leeftijd en geslacht die individueel zijn te herkennen.

Eerst werd onderzocht of mannetje en vrouwtje op een verschillende datum in het territorium verschenen. Dit bleek in veruit de meeste gevallen niet het geval te zijn (Fig.1). De volgende vraag was of het tijdstip waarop het territorium bezet wordt afhankelijk is van de leeftijd van de broedvogels. Tevens werd nagegaan in hoeverre de datum waarop het terrein ijsvrij wordt hierbij van invloed is. De analyse van de gegevens (Tabel 1) laat zien dat oude mannetjes eerder in hun territorium verschijnen dan jonge. Voor de wijfjes kon (onafhankelijk van de leeftijd van de man) geen invloed van de leeftijd op de aankomstdatum worden aangetoond. Er kon echter niet aangetoond worden dat de leeftijd van man en vrouw een verschillende invloed op de aankomst datum hadden. Hieruit werd de conclusie getrokken dat oude paren vroeger een territorium bezetten dan jonge paren, hoewel de gegevens suggereren dat de leeftijd van de man hierbij prevaleert. De som van de leeftijden van de beide partners werd hierbij als maat voor de leeftijd van het paar genomen.

Vervolgens werd de vraag gesteld of de grootte van het territorium samenhangt met de leeftijd van de broedvogels. Als maat voor de grootte van het territorium werd het wateroppervlak gekozen. Het bleek (Tabel 2) dat oude paren een groter wateroppervlak tot hun beschikking hebben dan jonge paren. Verschillende effecten voor man en vrouw konden niet aangetoond worden. Een territorium met een groot wateroppervlak heeft ook een lange oever. De vraag rijst of het verband tussen leeftijd van het paar niet een uitvloeisel is van een verband tussen leeftijd en oeverlengte. Bij de analyse werd onderscheid gemaakt tussen (met hout) beschoeide en onbeschoeide oever. Onbeschoeide oever is veel meer begroeid dan beschoeide oever en we hebben reden om aan te nemen dat die begroeiing van belang is voor nestplaatsen, voedsel en schuilplaats. Het bleek nu dat onafhankelijk van beschoeide en onbeschoeide oever er een verband is tussen leeftijd van het paar en wateroppervlak. Het verband tussen leeftijd van het paar en het wateroppervlak is dus niet het gevolg van de correlatie tussen oe-

verlengte en wateroppervlak. Oude broedvogels zijn eerder in hun territorium dan jonge. Het kan dus zijn dat oude broedvogels een groter territorium hebben omdat ze eerder aanwezig zijn. Dat is niet het geval. Oude vogels hebben een groter territorium onafhankelijk van de datum waarop ze in hun territorium verschijnen.

We vermoeden dat de vegetatie van onbeschoeide oevers een belangrijk element van het territorium is. Daarom werd nagegaan of de leeftijd van man en vrouw invloed heeft op de lengte van de onbeschoeide oever. Het blijkt nu (Tabel 3) dat oude mannen meer onbeschoeide oever hebben dan jonge en dat dit onafhankelijk is van zowel wateroppervlak, lengte beschoeide oever, datum van aankomst in het territorium en van het moment waarop het terrein ijsvrij is. De leeftijd van het wijfje speelt hierbij geen rol. Fig. 2 laat het verband tussen leeftijd van de man en onbeschoeide oever zien. De gegevens van de twee lijnen zijn op een verschillende manier verkregen (data set 1, data set 2). Een belangrijk verschil tussen data set 1 en 2 is dat de eerste groep waarnemingen uitgevoerd is in de periode tot aan het broeden. De tweede groep waarnemingen heeft betrekking op waarnemingen tijdens het verzorgen van de jongen. Het is mogelijk dat de territoria dan groter zijn omdat later in het seizoen een deel van de vogels hun territorium heeft verlaten.

De lengte van de onbeschoeide oever die een man bezet hangt niet alleen af van zijn eigen leeftijd maar ook van het aantal buren en hun leeftijd. Stel dat de som van de leeftijden van de buren (ΣO) een maat is voor de totale druk die de territorium eigenaar van zijn buren ondervindt en de leeftijd van de territorium eigenaar (*M*) een maat voor de druk die hij op zijn buren uitoefent, dan geeft het quotient $M/\Sigma O$) de krachtsverhouding tussen de territoriumhouder en het totaal van zijn buren weer. Tabel 4 (regressie 3, 4) laat zien dat niet alleen deze verhouding van belang is, maar ook die tussen de leeftijd van de territorium eigenaar en de gemiddelde leeftijd van de *N* buren ($N{*}M/\Sigma O$). Als een man buren heeft van een bepaalde gemiddelde leeftijd dan heeft hij minder onbeschoeide oever al naar gelang hij meer buren heeft. Immers de som van de leeftijden van de buren neemt toe met het aantal buren (*N*) als de gemiddelde leeftijd constant is. Als echter de som van de leeftijden van zijn buren gegeven is, heeft hij meer onbeschoeide oever al naar gelang hij meer buren heeft (de gemiddelde leeftijd neemt af met het aantal buren als de som van de leeftijden constant is). Dit laatste betekent dat een bepaalde druk van buren beter te weerstaan is als deze bestaat uit (een groter aantal) jonge buren.

Cavé & Visser (1985) kwamen tot de conclusie dat het golvend patroon van het aantal broedparen van de Meerkoet op de Westeinderplassen het gevolg is van de combinatie van een uitgesteld dichtheidsafhankelijke factor en variatie in jaarlijkse overleving onder invloed van de strengheid van de winter. Zij vermoedden dat het uitgesteld dichtheidsafhankelijke effect op het aantal broedparen, veroorzaakt wordt door leeftijdsafhankelijk territorium gedrag. De in dit artikel besproken gegevens ondersteunen deze veronderstelling. Ten eerste werd er een verband aangetoond tussen leeftijd van de eigenaar(s) en territorium eigenschappen. Ten tweede blijkt het aantal en de leeftijd van de buren hierbij een rol te spelen. Dit laatste resultaat laat zien dat er concurrentie is om territoria en dat oude vogels bij deze concurrentie in het voordeel zijn. Dit heeft tot gevolg dat jonge vogels bij hoge dichtheid een grotere kans hebben als broedvogel uitgesloten te worden dan oude.