A QUANTITATIVE MODEL OF THE DISTRIBUTION OF MUTE SWANS WINTERING IN DANISH WATERS

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The winter distribution of Mute Swans (Cygnus olor) in Danish waters was analysed in terms of habitat characteristics. Mute Swan densities obtained from four countrywide aerial surveys were investigated: the habitat variables considered were water depth, ratio of coastline to counting unit area, sediment types and concentrations of nutrients. Using a linear regression procedure, a model resulted that explained c. 44% of the density variation. As a next step, systematic variation in density depending on geographical position was added. This resulted in an increase in explanatory power to c. 66 % of the variation. The resulting model of the spatial distribution of Mute Swans wintering in Denmark conforms well with reality, and demonstrates that there is a strong relationship between habitat variables and densities. Furthermore, the model predicts that unexploited habitat is available for the species in northwestern Denmark. Distributions and densities for two years with a total of c. 45,000 wintering swans were compared with another two years when numbers increased to c. 73,000. This increase did not result in an increased exploitation of the northwestern areas, identified as being partly unutilised by the model, neither did it result in a spread over larger areas. It is therefore suggested that either the carrying capacity for wintering swans in Denmark was not reached in any of the four census periods, not even in the southeastern areas with the highest densities or that a behavioural or energetic barrier prevents the utilisation of the northwestern part of Denmark by Mute Swans.

Key Words: Mute Swan, distribution model, winter habitat, Denmark.

Descriptions of habitat preferences of the Mute Swan have commonly emphasised breeding habitat, Bauer & Glutz (1968), Cramp & Simmons (1977), Scott & Birkhead (1983), Birkhead & Perrins (1986), while fewer studies have investigated wintering habitats, Sears (1989), Kirby *et al.* (1994), Rees *et al.* (1997). Moreover, few attempts have been made to quantify the characteristics of wintering habitats.

With its many sheltered and shallow waters, narrow tidal range, long coastline, and productive inlets and lakes, the Danish territory provides excellent wintering grounds for the Mute Swan. It is by far the most important wintering area for this species in North Western Europe (Wieloch 1991). The majority of Mute Swans in Denmark winter in marine habitats and, in contrast to Britain and Ireland (Rees *et al.* 1997), only a minute part (approximately 4-5%) winter in lakes and other fresh-water habitats.

The majority of Mute Swans wintering in Denmark breed in Denmark, Sweden and Germany, but swans from Norway, Finland, Poland, Estonia, Latvia, Lithuania and the Netherlands also winter here (Andersen-Harild 1994). Thus the main autumn migration routes go north and northwest (*ibid*).

Large-scale data have been collected on the abundance and distribution of Mute Swans, together with many other species of waterfowl, through countrywide aerial surveys in the periods 1968-1973, (Joensen 1974) and 1987-1992 (Laursen *et al.* 1997); (Pihl *et al.* 1992). These data form an excellent basis for analyses of the relationships between habitat characteristics and the abundance and distribution of the Mute Swans. The winters 1984/85, 1985/86 and 1986/87 were all ice-winters, and in January 1988 only c. 41,300 individuals were recorded. This number is below average and was probably caused both by starvation deaths in the preceding winters, and by a low average number of offspring in summer 1987, resulting from poor condition of the swans after a series of hard winters. Possibly some of the swans also wintered elsewhere in the following years.

A measure of how cold a winter is, is the sum of temperatures for days with frost, and in the winters 1984/85-1986/87 this frost sum was between 193-273 (reversed sign), compared to an average in the order of 100 (Søfartsstyrelsen 1992). During the period of mild winters between 1988-1992, the number of Mute Swans wintering in Denmark rose to c. 73,000 (frost sum for these winters were between 8-38, Søfartsstyrelsen 1992). The numbers of Mute Swans recorded in 1968-1973 were at the approximately same level as the numbers recorded in 1987-1992. The mean in the first observation period 1968-1973 was 53,200, with a maximum of 69,200 (January 1970). In the second observation period (1987-1992) the mean was 58,900, and the maximum 73,500 (January 1991).The wintering population in Denmark thus seems to have been fluctuating around the same relatively constant mean in the period, with a modest rise of c. 11% from 1968-1973 to 1987-1992. Likewise the maxima seems to have been approximately the same. The fluctuations are largely influenced by weather conditions in Denmark, as some Danish Mute Swans migrate out of Denmark in severe winters, and as the swans generally have a lower survival rate in those winters (Bacon & Andersen-Harild 1989). It is known from the aerial surveys that the distribution pattern of the Mute Swan in Denmark is relatively constant from year to year. Such a

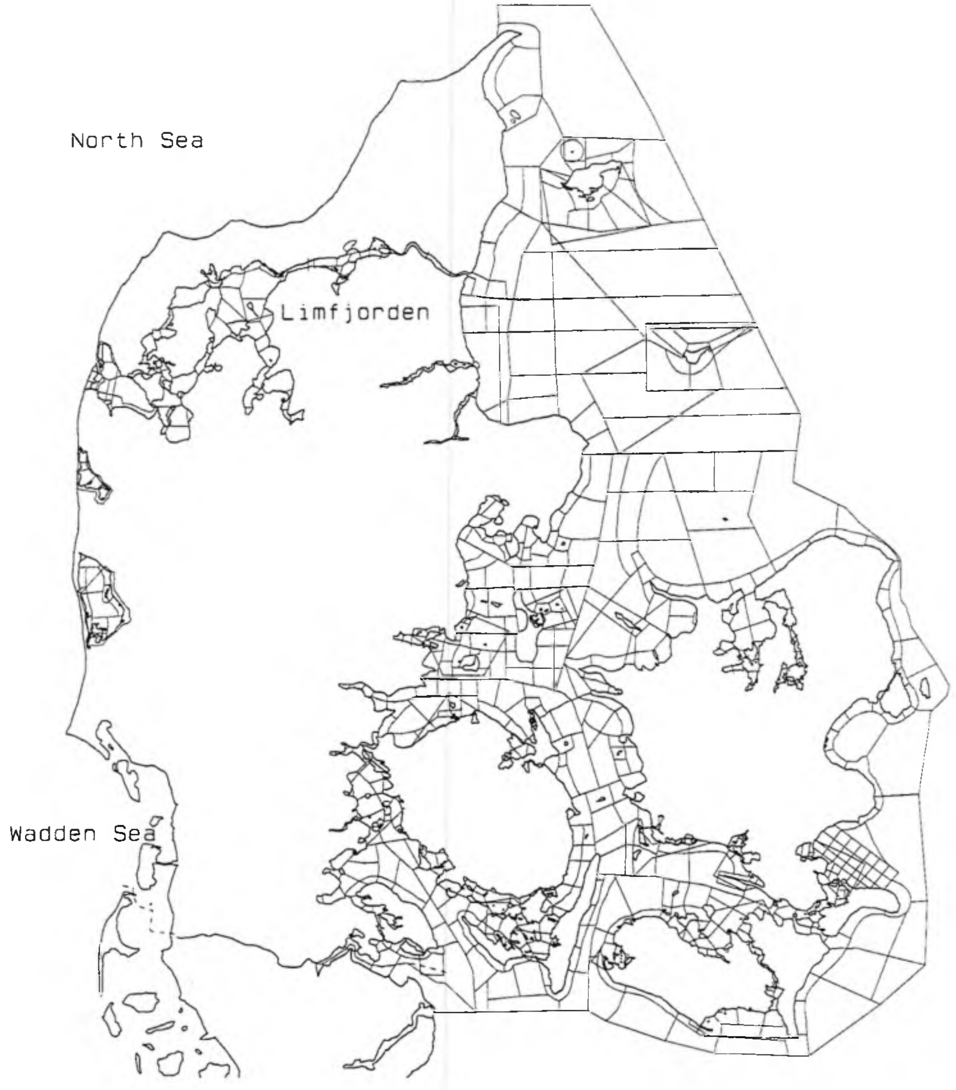

Figure 1. Study area showing division into counting units in Danish waters.

constancy could be due to the differing profitability of the sites caused by habitat features, presuming that the macrophytic communities which provide food resources are relatively stable. It could also be caused by site-faithfulness (philopatry), known to be important in many species of migratory waterfowl (Prokosch 1984; Robertson & Cooke 1999). A discussion of the benefits and possible evolutionary basis of winter philopatry is given in Robertson & Cooke (1999). The reason for birds not occupying apparently suitable habitats may be due to density dependent effects not yet offsetting advantages of flocking at 'traditional' sites, or a lack of information concerning suitable sites. The available information will depend strongly on how exploratory a given species is.

In the light of the above two hypotheses were tested in this work:

Hypothesis 1: The density of Mute Swans on a given location is determined mainly by quantifiable environmental characteristics.

If this is correct, it suggests that the philopatry and habitat use are not merely caused by 'tradition' and therefore the following hypothesis becomes relevant.

Hypothesis 2: With an increasing wintering population in Denmark, density dependent habitat selection will force the Mute Swans to disperse over larger areas.

Methods

Study Area

For the purpose of the aerial waterfowl survey, Denmark and its surrounding waters are divided into c. 1600 survey units (Joensen 1974; Laursen *et al.* 1997). Many of these units constitute habitats not dealt with in this study (such as lakes, meadows and marshes) as only marine units are considered here.

The division of the area into units covered in this analysis is shown in **Figure 1**. The North Sea and the Wadden See are excluded, although they were covered by the aerial surveys. The Wadden See is biologically distinct from the inner Danish waters, because of its tidal flooding, and supports a very limited number of Mute Swans. The Danish North Sea coast is also distinct due to pronounced wave exposure. Because of this exposure there is virtually no submerged vegetation in the shallow parts, and hence no food resources for the Mute Swan.

The 803 counting units analysed here cover a total of 27,400 km^2, which constitutes the main part of the inner Danish waters. The part of this area with a depth less than 10m has an observational coverage of 100%.

The division into counting units were not originally planned for this kind of quantitative analysis, and the units therefore have varying sizes and shapes.

Species Data

Midwinter aerial counts of waterfowl were undertaken by the National Environmental Research Institute (NERI) in the following periods: 1988: 5 January to 22 February; 1989: 11 January to 28 February; 1991: 13 January to 3 February; 1992: 10 January to 11 March. These winters were mild, Søfartsstyrelsen (1992), with practically no ice cover of units surveyed during the study period. Counts from 1987 are not included in the present analysis, because in an ice-winter swans concentrate in ice-free areas, causing an aberrant distribution pattern.

The surveys were carried out from small aircrafts at a height of 60-90 metres with a speed of 130-160 kmh^{-1} (Laursen *et al.* 1997; Pihl & Frikke 1993). As the Mute Swan is easily detected, virtually all individuals in marine habitats were counted in the aerial surveys.

Environmental Data

The environmental data are divided into geographical data (e.g. the coastline/area ratio), sediment classification data (e.g. the proportion of a unit which has a sandy bottom), physical data (e.g. the proportion of unit which lies within a given depth interval), chemical data (e.g.

concentrations of phosphorus and nitrogen) and biological data (concerning phytoplankton, e.g. the rate of primary production by micro-algae). There are no data on macro-algae, which the Mute Swan utilises.

In **Table 1** the environmental variables used in this analysis are listed along with their abbreviations.

The chemical and biological data were collected in 1991 by the Danish counties and NERI (Ærtebjerg *et al.* 1992). The sample points for chemical and biological data did not in all cases coincide with the location of the counting areas. Whenever they do not coincide, the nearest adjacent sampling point is used. The sediment classification data were obtained from a fine scale map displaying sediment types in the Danish waters, National Forest and Nature Agency (1992), which was digitised by means of a colour scanner. Furthermore, a map of the counting areas was digitised using AutoCad, along with sea maps displaying depth contours and coastline. These different kinds of information were gathered in a single database, organised according to GIS-principles in 100x100m squares and in vector representation respectively, and processed by means of programs written in PASCAL, to obtain data outlined in **Table 1**.

Analysis

Initially the year-to-year Mute Swan density correlations of the counting units considered here are computed for the years 1988, 1989, 1991 and 1992.

Multiple linear regressions using the statistical package SAS (SAS Institute Inc. 1990) were used to determine the effect of habitat variables on Mute Swan densities. Despite its limitations (see the Discussion), this method is comparatively simple and robust.

One of the potential dangers of applying multiple regression is 'overfitting' the data. In this study this was addressed by two approaches. First, a backward elimination method to exclude variables with a non-significant contribution to the regression ($P>0.05$), and to determine the most parsimonious model. Second, data were divided on a random basis into a calibration set (80% of data points), and a test set (20% of data points). Before the final regression on the total data set is performed, the predictive value of the regression is evaluated by making a regression on the calibration set, and evaluating it on the test set.

The modelling was performed in two steps:

(1) A model was made on the basis of environmental variables, excluding geographical position.

This exclusion was made in order to evaluate the significance of the geographical position separately. In an initial attempt, the geographical position was included in a straight-forward regression. The position variables tended to outweigh the other variables at the northwest and southeast 'corners', so that no individuals would ever be predicted in the first case and there would be individuals regardless of habitat features in the last case.

Independent of these technical obstacles, it makes sense from a biological point of view first to make a model based on habitat features, and then secondly consider the geographical position, as this at least partly separates habitat potential and ease of migration or other behavioural limits. An initial attempt to reverse the inclusion order resulted in a first model solely based on position, which had very low explanatory power, because there

Table 1. Abbreviation, description, unit, number of observations and source of the environmental data from inner Danish waters. Chemical and biological data were measured in 1991.

Abbreviation	Description	Unit	N	Source
Georgraphic Data				
EAST	Easting of unit	UTM (Zone 32)	803	**
NORTH	Northing of unit	UTM (Zone 32)	803	**
COAST/AR	Length of a unit's adjacent coastline divided by the unit's area	km^{-1}	803	Computed
Sediment classification***	All sediment classifications are fractions (scale 0-1)			
MUD (interval)	Frequency of mud in the depth range given by (interval)	-	803	National Forest and Nature Agency (1992)
SANDMUD (interval)	Frequency of sandy mud in the depth range given by (interval)	-	803	National Forest and Nature Agency (1992)
SAND (interval)	Frequency of sand in the depth range given by (interval). Locally gravel and coarser materials	-	803	National Forest and Nature Agency (1992)
RESSED (interval)	Frequency of residual sediments in the depth range given by (interval). Till, locally with a thin cover of sand, gravel or stones <1m. On a few locations quarternary clay and peat.	-	803	National Forest and Nature Agency (1992)
Physical				
DEPTH (interval)	Fraction of the area that is within the depth limits of (interval). Scale 0-1	-	803	National Forest and Nature Agency (1992)
SECCHI	Secchi depth	m	709*	Ærtebjerg *et al.* (1992)
Chemical				
NWIN	Total (organic and inorganic) concentration of nitrogen in winter	$\mu g l^{-1}$	764*	Ærtebjerg *et al.* (1992)
NSUM	Total concentration of nitrogen in summer	$\mu g l^{-1}$	794*	Ærtebjerg *et al.* (1992)
PSUM	Total concentration of phosphate in summer	$\mu g l^{-1}$	793*	Ærtebjerg *et al.* (1992)
OPWIN	Concentration of ortho-phosphate in winter	$\mu g l^{-1}$	782*	Ærtebjerg *et al.* (1992)
OGNWIN	Concentration of organic nitrogen in winter	$\mu g l^{-1}$	764*	Ærtebjerg *et al.* (1992)
OGPWIN	Concentration of organic phosphate in winter	$\mu g l^{-1}$	781*	Ærtebjerg *et al.* (1992)
OGNWIN	Concentration of unorganic nitrogen in winter	$\mu g l^{-1}$	786*	Ærtebjerg *et al.* (1992)
Biological				
CHLA	Concentration of chlorophyll a	$\mu g l^{-1}$	788*	Ærtebjerg *et al.* (1992)
PRIM	Primary production by phytoplancton	$mgm^{-2}d^{-1}$	657*	Ærtebjerg *et al.* (1992)

The chemical data represent mean values for summer and winter respectively.
* In some cases the nearest adjacent sampling point was used. In some cases there were no samples taken in the vacinity, therefore N is below 803.
** Estimated centre of bird observations in unit.
*** 2.1% of the bottom is not classified, see National Forest and Nature Agency (1992), but this unclassified fraction is as well as the four bottomtype included in the parameter DEPTH (interval). The sum of the fractions of all bottomtypes in all depth intervals is 1 per unit.

were no distinctions between suited and unsuited habitats.

The density of individuals in a given unit is computed as the average of the observed densities from the four observation periods, and a linear regression was performed as follows:

$$A_i' = a_o + a_1e_{i1} + a_2e_{i2} \ldots a_ne_{in} \quad \text{(Equation 1)}$$

where A_i' is predicted density in unit i (individuals km^{-2}, a_o is intercept (individuals km^{-2}), a_j is regression coefficient number j (individuals km^{-2} u_j^{-1}), e_{ij} is value for environmental variable number j at sample number i (unit: u_j), and n is number of environmental variables.

To prevent intercorrelated variables, (here defined as $R^2 > 0.1$), being retained, the intercorrelated ones with the smallest contribution to variance explication were discarded, and the backward procedure repeated.

2) A second model was made by adding the geographical position (Equations. 2 and 3). Equations 2 and 3 were rearranged to fit a linear regression model (Equation 4).

$$A_i'' = A_i' f(e_i, n_i) \quad \text{(Equation 2)}$$

$$f(e_i, n_i) = \beta_1 + \beta_2 e_i + \beta_3 n_i \quad \text{(Equation 3)}$$

$$A_i'' = \beta_1 A_i' + \beta_2 A_i' e_i + \beta_3 A_i' n_i \quad \text{(Equation 4)}$$

where A_i' is predicted density in unit i, 1. model (individuals km^{-2}), A_i'' is predicted density in unit i, 2. model (individuals km^{-2}), β_1 is regression coefficient (dimensionless), $\beta_2..\beta_3$ are regression coefficients (UTM^{-1}), $f(e_i,n_i)$ is location dependent function (dimensionless), e_i is easting of unit i (UTM), and n_i is northing of unit i (UTM).

Due to the multiplication of all terms by A_i' in Equation 4, the variables for the regression are inevitably intercorrelated, with an associated danger of overfitting. Hence intercorrelated variables cannot be discarded as in the first model. The procedure of using a calibration set and a test set reveals whether the second model can be considered valid.

As an alternative method to test a possible influence of intercorrelated variables, a Principal Component Analysis (PCA) was performed on all variables prior to a new regression (Mardia *et al.* 1979). Using principal component scores instead of the untransformed data ensured that regression variables were uncorrelated, but this method usually complicates the interpretation. This regression was also performed with backward elimination of non-significant variables (here PCA-axes). The explanatory value of this regression was then compared with the explanatory value for the regression where the

Table 2. Year-to-year Mute Swan density correlations (R) in inner Danish waters.

Year	1989	1991	1992
1988	0.663	0.629	0.646
1989		0.635	0.707
1991			0.671

Table 3. Variables retained by first regression (R^2=0.438; n=782; P<0.0001).

Variable	Parameter Estimate
a_o (intercept)	-5.20
COAST/AR	6.62
MUD 0-2	-17.36
SAND 0-2	60.05
RESSED 0-2	23.03
OPWIN	0.079

Table 4. Intercorrelations between the variables retained by first regression (R^2).

Variable	MUD 0-2	SAND 0-2	OPWIN	RESSED 0-2
COAST/AR	0.042	0.067	0.040	0.024
MUD 0-2		0.004	0.024	0.001
SAND 0-2			0.0049	0.008
OPWIN				0.046

untransformed variables are used.

Finally, the population sizes for the different years, the gravity point of observations for each year and the dispersion over the proportion of units that have a depth of less than 2 m were computed in order to evaluate hypothesis (2). Greater depths generally do not provide foraging possibilities for the Mute Swan (Madsen 1998), which even by 'up-ending' cannot reach further down than approximately 105 cm (Clausen *et al.* 1995). The gravity point G_N (northing), G_E (easting) was defined as the sum for all units of respectively northing and easting multiplied by the fraction of all the individuals they contain. G_N is calculated as

$$G_N = \sum n_i A_i / S \qquad \text{(Eq. 5)}$$

Where n_i is northing of unit i (UTM), A_i is the number of individuals in unit i, and S is the total number of individuals. G_E is calculated accordingly.

Table 5. Variables retained by second regression (R^2=0.657; n=782; P<0.0001).

Variable	Parameter Estimate
β_1	15.62
β_2	$5.04 \cdot 10^{-4}$
β_3	$-2.88 \cdot 10^{-4}$

Results

The year-to-year correlations for Mute Swans 1988-1992 are shown in **Table 2** (R ranges between 0.629-0.707).

A regression was performed on the calibration set (R^2=0.440; n=626; P<0.0001) and the coefficients from this regression subsequently were applied to the testset (R^2=0.463; n=156; P<0.0001). On the basis of the insignificant difference of the values of R^2, it was concluded that there is no appreciable overfitting.

The variables retained by the regression on the complete dataset using backward elimination are seen in **Table 3** (R^2=0.438; n=782; P<0.0001), and the inter-correlations of these variables are shown in **Table 4**.

The regression on variables transformed by PCA yielded an R^2 of 0.454, and this very similar explanatory value also suggests that the regression is valid. The results from the regression performed directly on the environmental variables were preferred (**Table 3**), because a regression based on a previous PCA are complicated to interpret.

The results from the former regression were transformed by a second step, adding northing (NORTH - UTM coordinates) and easting (EAST - UTM coordinates)

Table 6. Number of observed Mute Swans in Denmark. The majority of the individuals not included in the analysis occupy freshwater habitats. The dispersion over units is calculated as the area of counting units that have a depth less than 2m, and the percentiles of total swan number they contain. For example, the 25% percentile is the area that holds 25% of the Mute Swans wintering in marine habitats in Denmark. The gravity points of individuals is calculated as the sum for all counting units of respectively northing and easting multiplied by the fraction of total individual number they contain (Equation. 5).

Year	1988	1989	1991	1992
Individuals, total	41,273	48,004	73,495	72,663
Individuals, in analysis	39,079	46,016	70,248	68,677
25% percentile (km^2)	64.8	72.3	65.5	74.3
50% percentile (km^2)	193.2	210.1	194.8	206.0
75% percentile (km^2)	403.1	423.5	393.4	397.3
Gravity point (East - UTM Zone 32)	6,133.9	6,131.2	6,135.2	6,129.7
Gravity point (North - UTM Zone 32)	638.4	649.1	647.4	650.1

(**Equation 4**). A regression was performed on the calibrationset (R^2=0.669; n=626; P<0.0001) and the coefficients from this regression subsequently were applied to the testset (R^2=0.609; n=161; P<0.0001). The difference of the values of R^2 tentatively suggests some degree of overfitting, due to the implicit intercorrelation of the variables. However, based on the substantial rise in R^2 of the testset relative to the first regression the model is considered valid. In the regression all three terms (**Equation 4**) were retained by the backward elimination procedure (**Table 5**, R^2=0.657; n=782; P<0.0001).

The coefficient for EAST·A' (β_2) is positive, and the coefficient for NORTH·A' (β_3) is negative. This means that the density of swans on otherwise similar habitats will decline in a roughly NW direction.

The regression on variables from a PCA yielded an R^2 of 0.633, which is a similar explanatory value compared to the R^2 in **Table 5**, suggesting that the inter-correlation of variables does not obscure the regression substantially.

The mean numbers of swans in the different counting units are shown in **Figure 2**. The predictions from the first model excluding geographical position are shown in **Figure 3**, and the predictions from the second model including geographical position are shown in **Figure 4.** The dispersions over units in **Table 6** are calculated as the dispersion over areas with a depth less than 2 m. As it can be seen, the area-sums in the different percentiles are not systematically related to the total number of swans, so the totally utilised area seems to be rather constant. Neither does the gravity point of the observations move northwards and westwards as a result of increased population. As only four years of distribution are considered, a formal test for hypothesis rejection would have

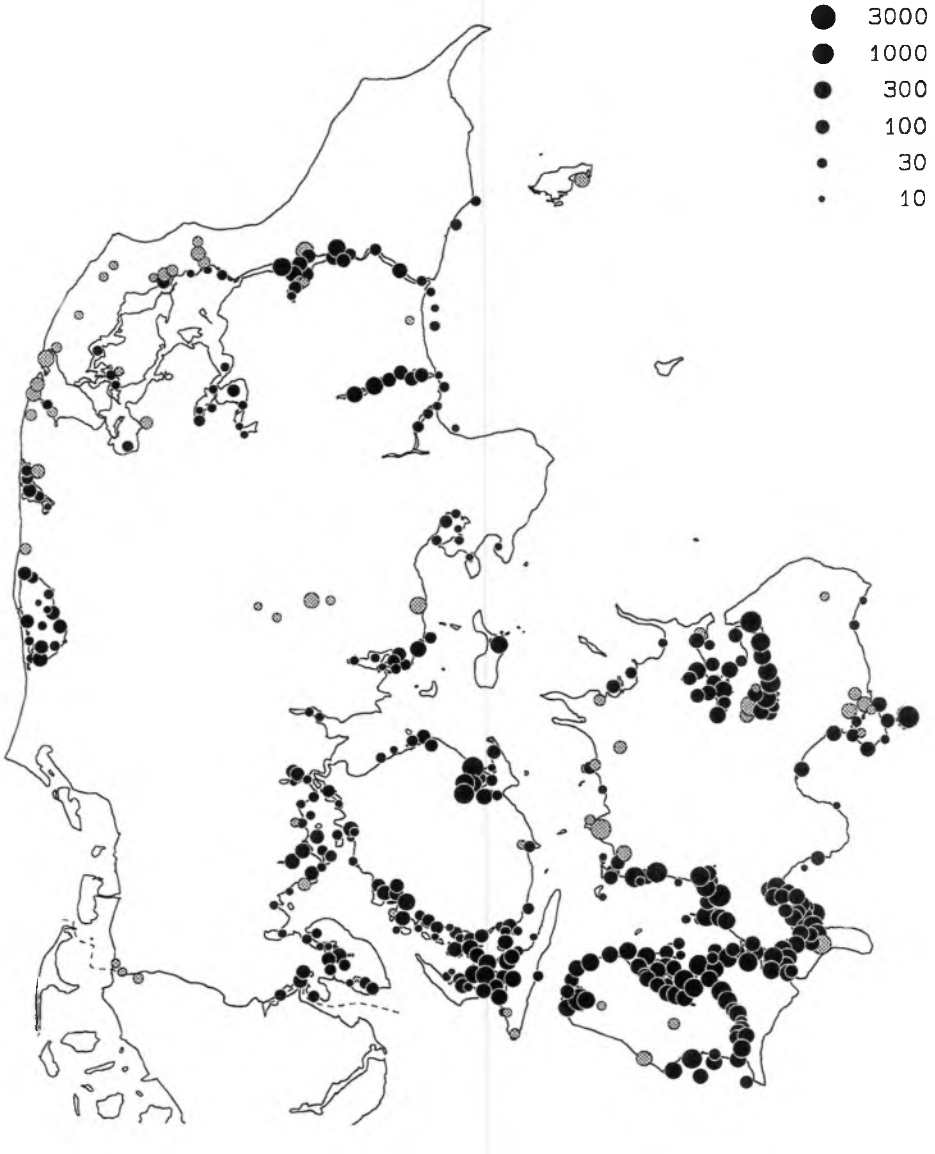

Figure 2. Mean numbers of Mute Swans in Denmark 1988, 1989, 1991 and 1992. Grey dots mark the occurrence of units not included in analysis, either because of missing variable(s) or because the units are a freshwater habitat.

insufficient statistical power. But the data from this study do not give any support for hypothesis 2.

Discussion

The Mute Swan has a relatively high constancy in distribution from year to year. A combination of habitat variables and geographic location explains 66% of the distribution pattern of wintering Mute Swan density in Denmark. The density of swans can thus to a large extent be explained by environmental factors, and so hypothesis 1 is confirmed.

The model also makes sense in biological terms. Considering the first regression, the density of swans is expected to rise when the coastline/area ratio (COAST/AR) is high. The higher this value is, the more sheltered the area in question is. These sheltered areas have more restricted wave and current action, and large waves and strong currents will hinder the foraging of Mute Swans.

Areas with sandy sediments between 0-2m depth seem to provide the best foraging possibilities for the swans, presumably due to occurrence of prevailing food plants including *Zostera*, *Ruppia* and *Potamogeton*. Unfortunately there are no large-scale studies that can provide quantitative relations between depth and sediment, versus the 'real' food abundance. Probably sediment type offers a proximate prediction of the plant communities, but how strong food availability is coupled to sediment types is presently unresolved.

The positive regression coefficient of ortho phosphate concentration in winter (which is strongly correlated with the other nutrient mineral concentrations) in the model might partly be due to a 'fertilising' effect on the water plants. Normally *Zostera* has a depth limit far beyond the reach of Mute Swans. The often reported setback of *Zostera* due to eutrophication is associated with the depth limit (Ærtebjerg *et al.* 1992), and eutrophication does not necessarily affect growth in more shallow areas negatively. The density of swans in habitats considered suitable by the model decreases along a roughly northwest axis, as seen when comparing **Figure 3 and 4.** This decrease is in concordance with the main flyways of swans wintering in Denmark, (Andersen-Harild 1994), assuming that the areas with the shortest flying distances will be preferred.

According to hypothesis 2 the swans should redistribute over larger areas, as the density of the preferred habitats increase. The swans, however, showed no tendency to spread over larger areas with increasing population, neither did they displace to the northwest (**Table 6**). This finding is not in concordance with the predictions associated with hypothesis 2, so this hypothesis is not supported by these data.

From the 1970s to the mid-1980s, the wintering swan populations of the Scandinavian-Baltic group (this group does not include the Netherlands) have experienced an increase from c. 103,000 to c. 127,000 (23%) (Atkinson-Willes 1981; Rüger *et al.* 1986; Monval & Poirot 1989; Wieloch 1991). Approximately half of the Scandinavian-Baltic swan group winter in Denmark, and an estimated rise of 11% in the number of swans wintering in Denmark tentatively indicates that the relative proportion wintering here has not risen or even slightly decreased over this period. In the same period the Western and Central European population of Mute Swans (of which the Scandinavian-Baltic

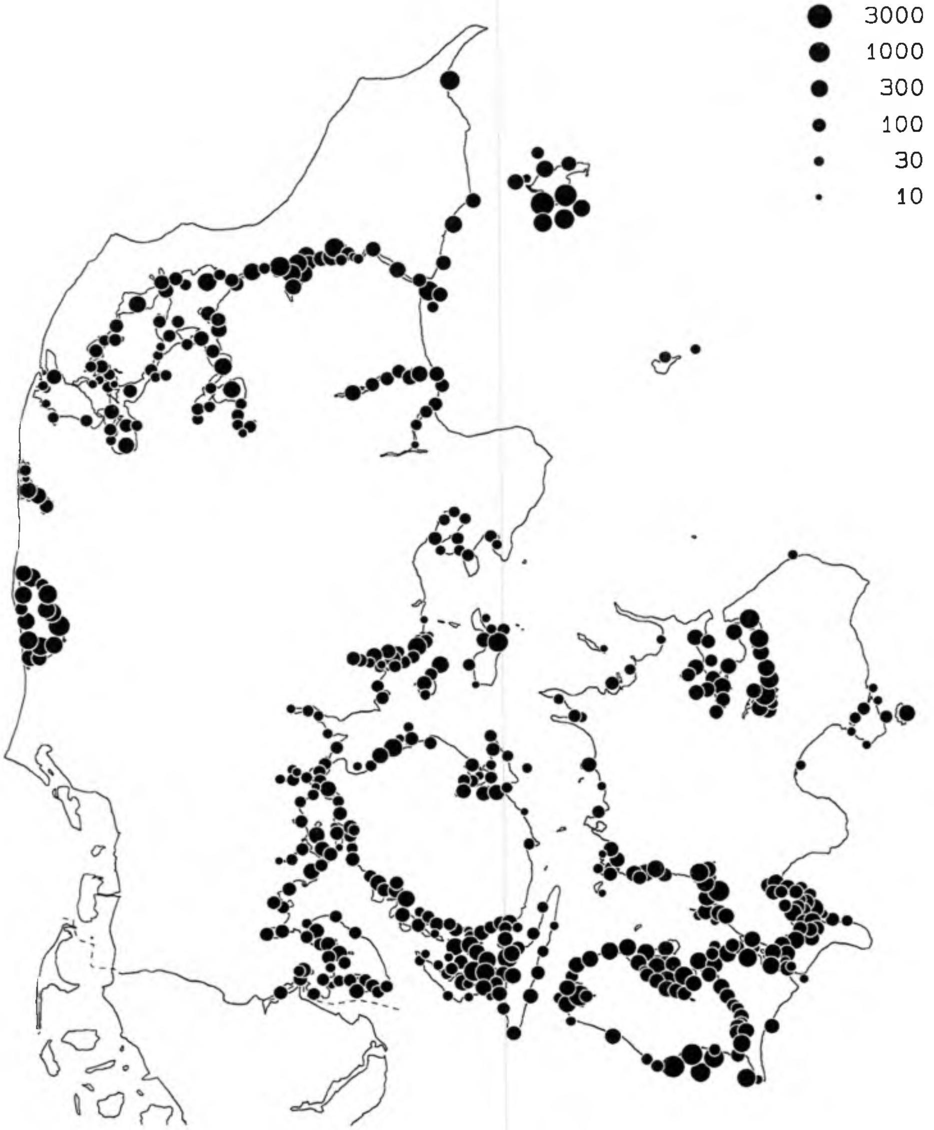

Figure 3. Numbers of Mute Swans predicted by the regression model without geographical position. The densities are transformed to number of individuals by multiplication with unit area.

Group is a part) have expanded to the east and south (Wieloch 1991).

This could, again tentatively, suggest that the carrying capacity of the Danish waters has been reached by the wintering swans, provided that the models offer an adequate measure of habitat suitability. Consequently the results from this study are ambiguous with respect to the question of density effects. On the one hand, it is clearly demonstrated that the occurrence of swans is strongly correlated with the occurrence of proper habitats. On the other hand, if the carrying capacity had been reached, the swans would be expected to spread over a larger amount of suitable habitats with rising numbers, which was not the case.

The areas identified by the two models as 'vacant' (comparing **Figures 3 and 4**) do provide suitable feeding grounds. In the Limfjorden (see **Figure 1**), the main area in question, there are large beds of *Zostera* in shallow water (Limfjordskomiteen 1987, 1989, 1990). Strong competition from other waterfowl does not appear likely as the main cause for the rejection of hypothesis 2, as the Mute Swans due to their long necks can utilise a proportionally large part of the submerged vegetation compared with other herbivorous species. Competition from Whooper Swans *Cygnus cygnus* , which also have long necks, could potentially play a role in northwestern Denmark, where notable concentrations were recorded at some occasions (Joensen 1974; Laursen *et al.* 1997). However, in Denmark this species extensively utilises arable crops (Laubek 1998).

Theoretically there could be a seasonal shift in distribution, so that the swans moved southward as the winter progresses, as reported for Whooper Swans in the U.K. by Rees *et al.* (1997). However, besides the midwinter counts, there have been countrywide counts outside the breeding season on several occasions in August, October and November (Joensen 1974; Laursen *et al.* 1997). On none of these occasions, the presumed 'vacant' areas were utilised notably more than in mid-winter.

On the premise that the models *do* capture the major aspects of habitat suitability, the following two possibilities seem likely, where the one does not exclude the other:

1) The wintering grounds generally are not close to carrying capacity, and most of the density dependent regulation of the population consequently occurs at the breeding grounds.

2) Some behavioural and/or energetic barrier prevents the use of the 'vacant' areas, and this could be connected with the migration distance. This presumed barrier might also consist of the long distance with few suitable habitats in a large stretch on the east coast of Jutland.

Further research is needed to clarify the questions raised by this study. This includes investigations of the site fidelity of individuals with return rates of marked individuals, investigations of carrying capacity of selected areas, and investigations of fluctuations in life history parameters with time. The latter investigation should be based on the assumption that different conditions, e.g. in weather, over the years would provide a natural experiment clarifying density dependent mechanisms.

The derived model has a number of imperfections and sources of noise. First, a linear model should be considered as an approximation, as non-linear or even non-monotonic species density responses to an environmental gradient are not unusual (Gauch 1986). Another source of noise is

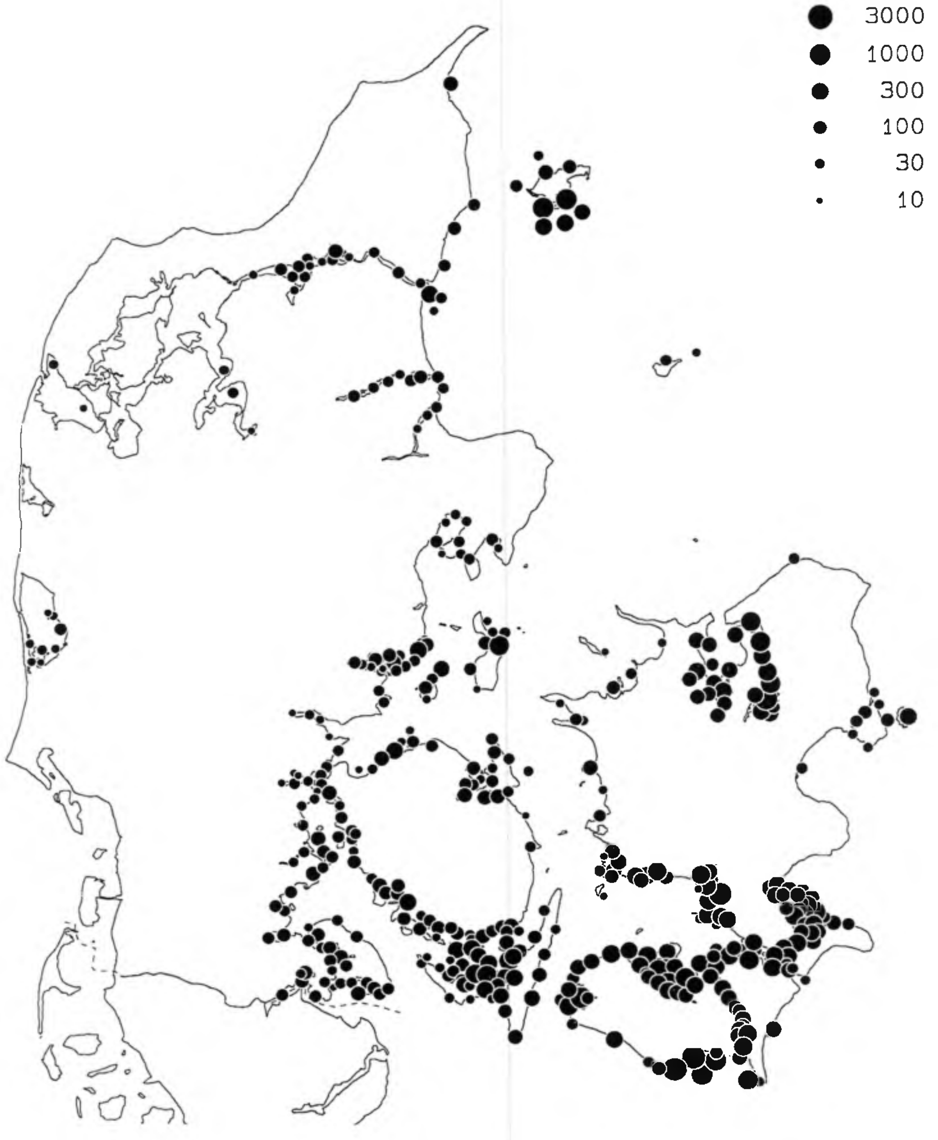

Figure 4: Numbers of Mute Swans predicted by the regression model including geographical position. The densities are transformed to number of individuals by multiplication with unit area.

the different shape of the units, especially with regard to the coastline to area ratio, which depends on the shape of the units. Also, many potential parameters could for practical and economical reasons not be included in this study: a unit's exposure to wind, currents, wave action, tidal waters and human disturbance.

Some of the environmental variables considered are only indirectly causal or proximate with respect to the Mute Swan, mediated especially by abundance and composition of submerged vegetation. The classification into four sediment types could be refined, but even at this crude classification level, the existence of sediment data for an area of this size is unique. Despite these imperfections of the model, it has a considerable explanatory value, indicating a high degree of determinism in the distribution of Mute Swans wintering in Denmark. As the level of year-to-year constancy is below the explanatory value of the model, it seems unlikely that any other modelling approach based on presently available data could provide a substantial improvement.

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