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Authors: Bell, Michael C., Delany, Simon N., Millett, Matthew C., and Pollitt, Mark S.

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ORIGINAL ARTICLES

Wintering waterfowl community structure and the characteristics of gravel pit lakes

Michael C. Bell, Simon N. Delany, Matthew C. Millett & Mark S. Pollitt

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Wintering waterfowl community structure and their association with lake characteristics were studied in the Cotswold Water Park, a complex of more than 120 gravel pit lakes in southern England. The major distinction in community types was between assemblages dominated by diving waterfowl and those dominated by dabbling waterfowl. The trophic status of lakes was found to be a major determinant of community structure: young lakes in the early stages of a natural process of eutrophication tended to support the most diverse assemblages of diving waterfowl. The abundance of individual species was strongly related to lake size and assemblage type. Some effects of food supply and the recreational use of lakes were also apparent. The relevance of the findings for the sustainable value of the lakes for wintering waterfowl is discussed.

Key words: communities, Cotswold Water Park, gravel pits, lake characteristics, wintering waterfowl

Michael C. Bell, Simon N. Delany**, Matthew C. Millett & Mark S. Pollitt, The Wildfowl & Wetlands Trust, Slimbridge, Gloucester, GL2 7BT, UK*

Present addresses:
**The Centre for Environment, Fisheries and Aquaculture Science, Lowestoft Laboratory, Pakefield Road, Lowestoft, Suffolk, NR33 0HT, UK*
***Irish Wildbird Conservancy, Ruttledge House, 8 Longford Place, Monkstown, Co. Dublin, Ireland*

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British wetlands are of outstanding importance for wintering waterfowl (Owen, Atkinson-Willes & Salmon 1986, Davidson, Laffoley, Doody, Way, Gordon, Key, Pienkowski, Mitchell & Duff 1991). The most recent population estimates by Kirby (1995) indicate that Britain currently supports in excess of 3.8 million waterfowl (excluding gulls), which is more than a third of the estimated total northwest European population (Rose & Taylor 1993). The protection of waterfowl habitat in Britain is thus of vital concern, as recognised under national and international legislation (Ramsar Convention Bureau 1990, Stroud, Mudge & Pienkowski 1990).

Dramatic losses and degradation of natural water-

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fowl habitat in Britain have occurred during this century, owing to drainage and pollution of wetlands (Owen et al. 1986). However, these losses have been partially offset by the creation of new wetland habitat. The potential benefits to wildlife of both functional wetlands, such as water storage reservoirs and water treatment systems, and wetlands created purposely for wildlife are increasingly recognised by both industry and conservationists (Merritt 1994). In recent years, some of the most significant gains have been from flooded mineral extraction pits, particularly gravel pits (Andrews & Kinsman 1991). Amongst other wildlife, waterfowl have benefited conspicuously from this habitat creation, both in winter and in the breeding season (Owen 1983); wintering waterfowl numbers on gravel pits have increased proportionately with total area of water (Owen et al. 1986).

In order to protect the sustained value of these created wetlands for waterfowl, it is vital that we understand the nature of dependence of waterfowl on habi-

Table 1. Lake habitat variables used in the analyses presented in this paper. See text for explanation of analyses.

			Analysis Options		
Variable	Scale	Transformation	ANOVA	Regression	Simplified regression
Area	ha	$\log_e$	•		
Perimeter length	m	$\log_e$	•		
Mean depth	m	$\log_e$	•	•	•
Indentedness	circle equivalents[1]		•	•	•
Exposure	0=sheltered, 1=exposed		•	•	
Tree cover	% of perimeter		•	•	
Islands	number in lake	$\log_e$	•	•	•
Age	years (in 1992)	$\log_e$	•	•	
Nitrate	mg/l^{-1} total oxidisable N		•	•	•
Phosphate	$\mu g/l^{-1}$ soluble reactive phosphate		•	•	•
pH			•	•	•
Conductivity	$\mu S/cm^{-1}$		•	•	•
Alkalinity	mg/l^{-1} $CaCO_3$		•	•	•
DOM	absorbance units at 275 nm		•	•	
Light Penetration Index	Secchi disk depth/depth		•	•	
Bed hardness	0=soft, 1=hard		•	•	
Coarse gravel (mineral ≥20 mm)	DAFOR[2]		•	•	
Medium gravel (mineral 4-20 mm)	DAFOR		•	•	
Fine gravel (mineral 2-4 mm)	DAFOR		•	•	
Coarse sand (mineral 1-2 mm)	DAFOR		•	•	
Medium sand (mineral <1 mm)	DAFOR		•	•	
Clay pieces	DAFOR		•	•	
Coarse detritus (organic ≥1 mm)	DAFOR		•	•	
Detritus (organic <1 mm)	DAFOR		•	•	
Clay	0=present, 1=absent		•	•	
Invertebrate taxa	number of taxa identified	$\log_e$	•	•	•
Invertebrate abundance	total over all taxa	$\log_e$	•	•	•
Open water plant taxa	number of taxa identified	$\log_e$	•	•	
Marginal plant taxa	number of taxa identified	$\log_e$	•	•	
Plant abundance	DAFOR		•	•	•
Open water TRS[3]	Average over taxa		•	•	•
Marginal TRS	Average over taxa		•	•	
Overall TRS	Average over taxa		•		
Reserve status	0=absent, 1=present		•	•	
Game fishing	0=absent, 1=present		•	•	
Coarse fishing	0=absent, 1=present		•	•	
Wind-surfing	0=absent, 1=present		•	•	
Water-skiing	0=absent, 1=present		•	•	
Sailing	0=absent, 1=present		•	•	
Recreation	Number of recorded activities				•

[1] Ratio of perimeter length to the circumference of a circle of equivalent area.
[2] Five-point Dominant, Abundant, Frequent, Occasional, Rare scale.
[3] Trophic Ranking Score from Palmer (1989)

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tat factors. This concern is all the more urgent in the light of the increasing demands for the development of wetlands for human uses which compete with the wildlife interest, notably water-based recreation (Liddle & Scorgie 1980, Tuite, Hanson & Owen 1984). There has been much research into the selection of breeding habitat by waterfowl and the factors affecting breeding success (e.g. Sillén & Solbreck 1977, Pöysä 1984, Fox & Bell 1994, Pöysä & Virtanen 1994) but relatively few studies have sought to identify important habitat features for waterfowl outside the breeding season (e.g. Tuite et al. 1984, Fox, Jones, Singleton & Agnew 1994, Suter 1994). In the present paper we adopt a community-level approach to examining the relationship between wintering waterfowl and their habitat in a complex of gravel pit lakes in southern England. Two aspects of the ecological relationships and dependencies among the wintering waterfowl are addressed: 1) patterns of community composition; and 2) lake characteristics associated with these patterns. These facets of waterfowl ecology are relatively poorly understood except in purely qualitative terms, yet they are very important in any consideration of the sustainable value of wetlands for birds.

Study area

There has been sand and gravel extraction in the upper Thames catchment since the early 1920s. At present, there are more than 120 active and worked-out pits in two main areas, straddling the border between Gloucestershire and Wiltshire. The Cotswold Water Park was established in 1967 to serve the needs of the various recreational and wildlife interests at these pits under an integrated framework. The Water Park covers some 5,700 ha, of which almost 20% is open water (Bell 1992). Individual lakes range in size from 0.1 to 38.6 ha, averaging 6.6 ha.

The gravel itself is a calcareous fluvio-glacial deposit, derived from Jurassic oolitic limestone. The gravel aquifer maintains a water-table 1-3 m below ground level. The gravel pit lakes are relatively shallow, since the gravel deposits are mostly 3-5 m thick (Barker & Rushton 1983).

The nature conservation value of the Cotswold Water Park has been recognised for many years. The Water Park was listed as a grade 1 site (i.e. equivalent to National Nature Reserve status) in a review of sites of national importance to nature conservation in Britain (Ratcliffe 1977), by virtue of being the most extensive marl lake system in Britain. Gravel pit lakes in the Cotswold Water Park often support dense stands of submerged plants, including the stoneworts (Characeae) so typical of marl lakes (Stewart & Church 1992), with a rich associated invertebrate fauna (Millett 1993, Bell 1996). The combination of shallow water and abundant potential food resources makes the Water Park extremely attractive to waterfowl, both in the breeding season (Hilton, Bell & Menendez 1994) and in winter (Delany 1993, Pollitt 1995). Presently, the wintering waterfowl of the Cotswold Water Park include five species of National Importance (>1% of the British winter population, Waters & Cranswick 1993): great crested grebe *Podiceps cristatus*, gadwall *Anas strepera*, pochard *Aythya ferina*, tufted duck *A. fuligula* and coot *Fulica atra* (Delany 1993).

Methods

Winter waterfowl counts

In winter, one coordinated mid-week survey of the waterfowl using each lake has been undertaken in the middle of the months October to March, since 1989/90. On each occasion, individual members of a 9-12 person survey team visited each lake in the study area, recording the numbers and species of waterfowl present. The analyses described in this paper were based on average counts for each lake over all surveys for the six winters 1989/90 to 1994/95. There were 36 possible count occasions for each lake, and the majority of lakes were surveyed on every occasion. Arithmetic mean counts were used in preference to medians to reflect differences between lakes in the overall usage by each species; seasonal patterns and differences between years were not analysed.

Lake characteristics

Extensive, if rather incomplete, information exists on the physical, environmental, recreational and biotic characteristics of lakes in the Cotswold Water Park (Millett 1992, 1993, Bell 1996). Variables used in the analyses presented in this paper are summarised in Table 1.

As an indicator of the trophic status of each lake, average Trophic Ranking Scores (TRS values) for emergent and open water plants in each lake were calculated according to Palmer (1989). This author

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listed TRS values for aquatic plants based on their range of tolerance of trophic status, ranging from 2.5, for species characteristic of dystrophic and oligotrophic waters, to 10, for species characteristic of eutrophic waters. Aquatic plant species occurring in the study area are listed by Bell (1996). The commonest open water species are *Elodea nuttallii* (TRS value 10), *Myriophyllum spicatum* (TRS value 9) and *Potamogeton pectinatus* (TRS value 10). The commonest emergent species are *Typha latifolia* (TRS value 8.5), *Eleocharis palustris* (TRS value 5.8), *Mentha aquatica* (TRS value 7.3) and *Schoenoplectus lacustris* (TRS value 7.7).

Wintering waterfowl community types

Analysis of community composition was based on the 12 most abundant and widespread species in the study area (see Table 2), to avoid domination of the results by the patterns of occurrence of relatively rare species. The data were transformed by $\log_e(x+0.1)$ to down-weight the importance of high values, and centred about both species- and lake-means (Digby & Kempton 1987) so that differences between lakes were measured in terms of species-composition rather than absolute abundance.

The transformed and centred data matrix was analysed in two ways. Firstly, the lakes were classified into groups with similar waterfowl community types using an hierarchical clustering procedure. The CLUSTER procedure of the SAS statistical package (SAS Institute Inc. 1988) was used to perform clustering of euclidean distances by the Lance & Williams (1966) flexible strategy, with b set to -0.25 (see Webster & Oliver 1990). Secondly, canonical variates analysis (CVA) of the data matrix was used to ordinate the lake communities along gradients of species-composition in a way which emphasised the differences between the cluster groups (Digby & Kempton 1987). The results of the CVA were used to aid interpretation of the cluster analysis. The analysis was performed using the CANDISC procedure of the SAS statistical package (SAS Institute Inc. 1988).

One-way analysis of variance (ANOVA) was used to compare lake characteristics and the abundance (absolute numbers and densities) and diversity (number of species) of wintering waterfowl between cluster groups, using transformed data where appropriate (see Table 1). The Shannon diversity index H' (e.g. Begon, Harper & Townsend 1986) was used to measure wintering waterfowl diversity in each cluster group.

Relationship between waterfowl and lake characteristics

Lake area and perimeter length are crude measures of the amount of lake habitat available to wintering waterfowl. For each of the 12 most abundant and widespread species in the study area, the lake size parameter which appeared best to measure the amount of available habitat was selected by tests of linearity in regression analysis. The selected measure of lake size was used in all further analyses for each species, e.g. in calculating waterfowl densities.

Analysis of covariance (ANCOVA) was used to compare waterfowl numbers between assemblage types, with lake size (area or perimeter length, as appropriate) as a covariate; both waterfowl numbers and lake size were log-transformed (see above). The analysis proceeded in two stages. First, the interaction between assemblage type and lake size was examined, testing the hypothesis that the slope of relationship between log-transformed waterfowl numbers and lake size differed between assemblage types. If this interaction term was not significant ($P > 0.05$), the analysis proceeded to the second stage, which was to examine the independent effects of lake size and assemblage type in a reduced ANCOVA model without an interaction term. A significant effect of assemblage type indicated that the value of a given unit of habitat for a species differed according to assemblage type.

Regression analysis, with selection of variables using Mallow's C_p criterion (Burnham & Anderson 1992), was used to explore the relationship of waterfowl densities with lake characteristics. The REG procedure of the SAS statistical package (SAS Institute Inc. 1988) was used to select models and estimate regression parameters. Waterfowl densities were transformed by $\log_e(x+0.01)$, and 36 lake characteristic variables were considered for inclusion in models (see Table 1); there were complete data for only 45 lakes. Owing to this small sample size, it was not possible to consider models within groups of lakes defined by assemblage types. Instead, assemblage type was included as a fixed term in the models, parameterised as a group factor by a set of dummy variables. For comparison, models without assemblage type and with assemblage type only were also estimated.

Given the small sample size and large number of variables, the likelihood of spurious results is large, arising particularly from cross-correlations between the variables. Detailed interpretation of models for

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individual species would not be justified. Instead, generalisations were sought, by examining the direction and magnitude of effects across species: t-values of the partial regression coefficient for each selected variable (Sokal & Rohlf 1981) were averaged across models, considering positive and negative effects separately. These averages were calculated for groups of species defined by dabbling, diving, grazing and fish-eating waterfowl guilds.

In order to identify models which were more easily interpreted for individual species, a reduced set of variables was defined which summarised what were considered to be the most important habitat factors and which avoided the major cross-correlations (see Table 1). This approach was adopted after it was found that preliminary analyses, in which environmental variables were summarised and reduced in number by finding principal components (Webster & Oliver 1990), improved neither the amount of variation explained by models nor their ease of interpretation.

Results

Wintering waterfowl communities

Five main types of wintering waterfowl assemblage were distinguished by cluster analysis of data for the 12 most abundant species (Fig. 1, Table 2).

Lakes in group 1 were important for dabbling waterfowl, with high densities, absolute counts and proportions of mallard *Anas platyrhynchos*, teal *A. crecca* and gadwall. Other species were unimportant in this assemblage compared with their occurrence in other groups - this applied particularly to pochard and coot - although there were relatively high densities of mute swan *Cygnus olor*, great crested grebe and tufted duck.

There were relatively low numbers of most species except goldeneye *Bucephala clangula* and Canada goose *Branta canadensis* in group 2 lakes. Mute swan and cormorant *Phalacrocorax carbo* were also prominent members of this assemblage.

Large numbers of many species occurred in lakes of group 3, but the assemblage was chiefly characterised by the diving waterfowl, particularly coot and pochard. Wigeon *Anas penelope* and Canada goose, both grazing species, were also important in this assemblage.

Group 4 lakes were important for all diving waterfowl, particularly pochard, although at lower densities than in assemblage 3. Dabbling and grazing waterfowl were unimportant in this assemblage.

Lakes in group 5 supported relatively low numbers

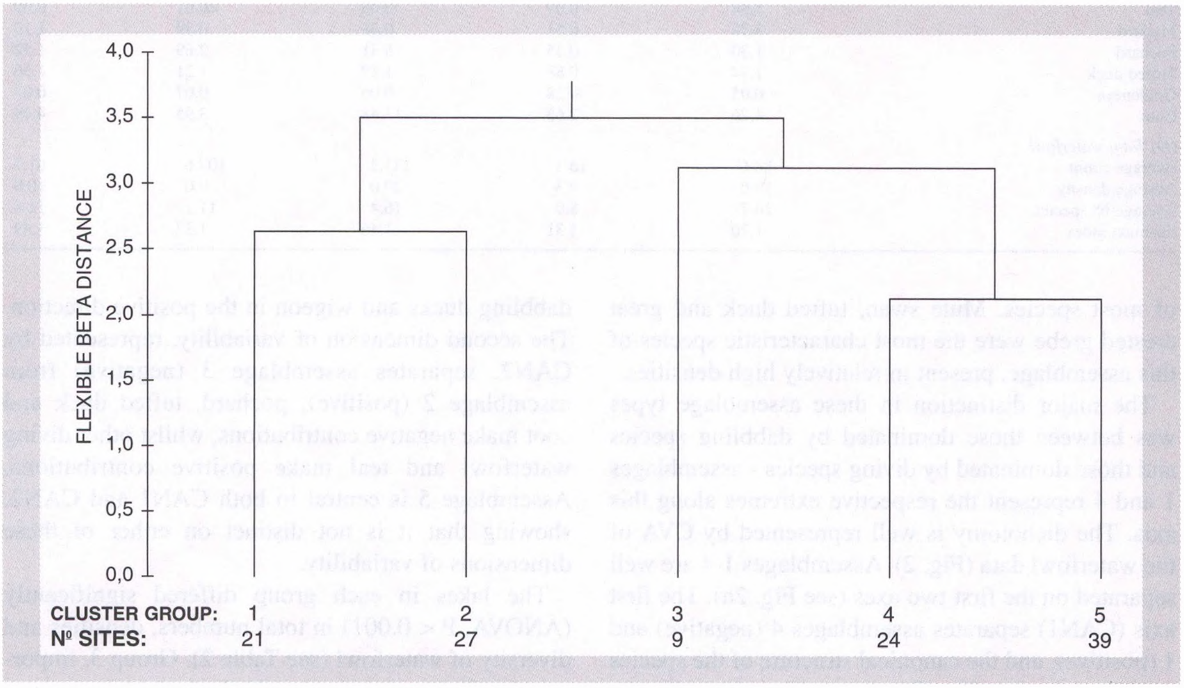

Figure 1. The hierarchy of relationship between wintering waterfowl assemblage types in the Cotswold Water Park identified by cluster analysis.

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Table 2. Summary of wintering waterfowl counts in groups of lakes defined by assemblage types (1-5): (A) average counts; (B) average proportions (%) and (C) average densities (birds/ha⁻¹) of the 12 most abundant species; (D) average counts, density and diversity of total wintering waterfowl.

	Assemblage Type				
Species	1	2	3	4	5
(A) Average counts					
Great crested grebe	1.6	0.5	2.8	2.9	1.7
Cormorant	0.7	0.1	0.2	1.3	0.2
Mute swan	1.2	0.3	2.5	0.9	1.7
Canada goose	4.1	3.2	13.6	2.4	2.3
Wigeon	7.4	0.2	27.4	0.1	0.9
Gadwall	3.2	0.3	3.6	0.5	0.5
Teal	12.5	0.9	0.5	<0.1	0.7
Mallard	15.9	1.8	4.1	3.5	5.3
Pochard	6.5	2.7	43.1	29.9	7.9
Tufted duck	7.0	1.5	15.2	10.5	8.1
Goldeneye	0.5	0.7	0.4	1.2	0.2
Coot	25.9	3.6	116.8	53.2	31.6
(B) Average proportions (%)					
Great crested grebe	1.6	3.1	1.3	4.9	4.0
Cormorant	0.4	1.3	0.1	1.0	0.4
Mute swan	2.9	5.8	1.6	0.9	5.1
Canada goose	2.7	16.0	8.5	1.1	4.3
Wigeon	6.0	0.4	10.8	<0.1	0.8
Gadwall	5.9	2.3	4.0	0.4	0.9
Teal	15.3	6.6	0.3	<0.1	0.5
Mallard	23.8	9.2	2.1	5.2	12.2
Pochard	6.5	9.4	16.9	24.2	12.5
Tufted duck	10.6	6.6	7.3	18.3	18.7
Goldeneye	0.5	4.7	0.2	1.1	0.4
Coot	23.8	27.2	47.0	43.0	40.2
(C) Average densities (birds/ha⁻¹)					
Great crested grebe	0.29	0.09	0.33	0.31	0.26
Cormorant	0.06	0.01	0.03	0.10	0.03
Mute swan	0.37	0.12	0.32	0.08	0.31
Canada goose	0.40	3.04	1.78	0.14	0.28
Wigeon	0.48	0.03	3.33	0.01	0.10
Gadwall	1.01	0.09	0.64	0.03	0.07
Teal	2.84	0.09	0.06	<0.01	0.08
Mallard	3.78	0.51	0.48	0.39	1.10
Pochard	1.30	0.45	6.31	2.69	1.52
Tufted duck	1.74	0.88	1.89	1.21	1.56
Goldeneye	0.05	0.28	0.06	0.07	0.03
Coot	4.26	2.63	13.48	3.95	4.49
(D) Total waterfowl					
Average count	88.6	16.3	233.2	107.6	61.7
Average density	17.0	8.3	29.0	9.0	10.0
Average Nº species	14.7	8.9	16.4	11.1	11.4
Shannon index	1.70	1.31	1.46	1.32	1.49

of most species. Mute swan, tufted duck and great crested grebe were the most characteristic species of this assemblage, present in relatively high densities.

The major distinction in these assemblage types was between those dominated by dabbling species and those dominated by diving species - assemblages 1 and 4 represent the respective extremes along this axis. The dichotomy is well represented by CVA of the waterfowl data (Fig. 2). Assemblages 1-4 are well separated on the first two axes (see Fig. 2a). The first axis (CAN1) separates assemblages 4 (negative) and 1 (positive), and the canonical structure of the species contributions (see Fig. 2b) shows this to be a distinction of diving species in the negative direction and dabbling ducks and wigeon in the positive direction. The second dimension of variability, represented by CAN2, separates assemblage 3 (negative) from assemblage 2 (positive); pochard, tufted duck and coot make negative contributions, whilst other diving waterfowl and teal make positive contributions. Assemblage 5 is central to both CAN1 and CAN2, showing that it is not distinct on either of these dimensions of variability.

The lakes in each group differed significantly (ANOVA, $P < 0.001$) in total numbers, densities and diversity of waterfowl (see Table 2). Group 3, important for diving and grazing birds, had highest numbers of species present, total waterfowl numbers and

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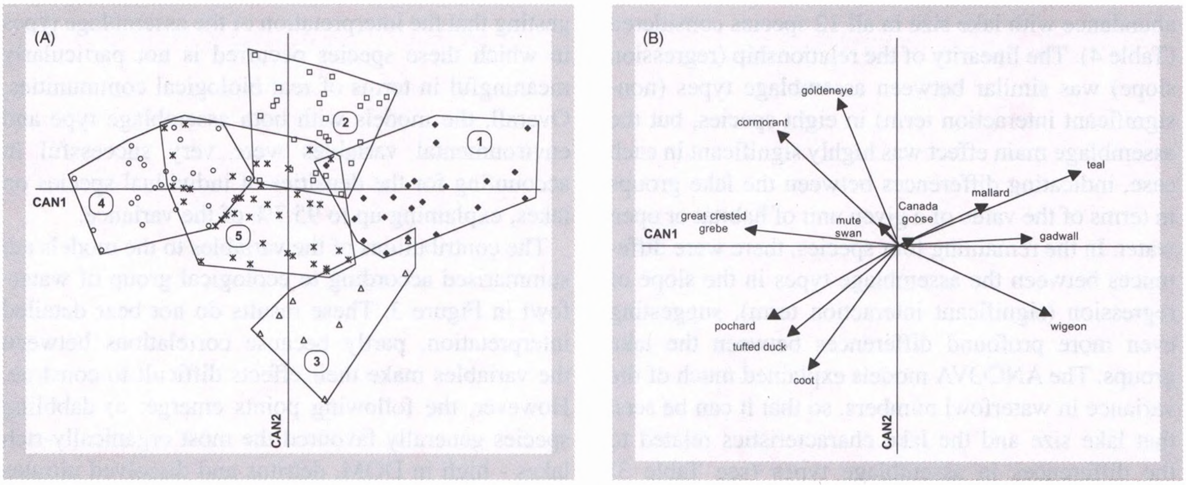

Figure 2. The results of canonical variates analysis of wintering waterfowl count data: (A) scores on the first two axes (CAN 1 and CAN 2), according to species and (B) according to assemplage types.

densities, whereas group 2, important for goldeneye, had the lowest values. The dabbling assemblage of group 1 had the highest Shannon diversity. Group 4 had almost as low a Shannon index as group 2, indicating the dominance of the diving bird assemblage by just a few species.

The lakes were also distinct in terms of lake characteristics (Table 3). Substratum conditions appeared to be important: lakes in groups 1 and 2 generally had a higher occurrence of sand and gravel in the substratum than those in groups 3-5. Water chemistry was also important in defining the divide between the dabbling and diving bird assemblages: both DOM (Dissolved Organic Matter) and dissolved phosphate levels were highest in group 1, the dabbling assemblage, and lower in groups 3-4, more important for diving birds. The assemblage with the highest waterfowl abundance, densities and species richness, group 3, was defined by the lowest dissolved phosphate levels. Lakes in group 4, supporting a wintering assemblage of mainly diving waterfowl, were typically the largest and deepest in the study area; lakes in group 2, supporting the poorest wintering assemblage, were the smallest and most shallow. This poorest group was also at the lower end of the scale in terms of aquatic invertebrate and plant diversity and plant abundance; these measures were highest in group 1, lakes with a diverse dabbling waterfowl assemblage. Average TRS values, calculated using both open water and marginal plant species, were lowest in group 3 lakes and highest in groups 1 and 5. There was no significant overall difference between the groups in lake age, but lakes with the diverse diving assemblage (group 3) tended to be younger (13.0 ± 2.3 years, mean ± S.E.) than other lakes (25.9 ± 1.8 years) ($F_{1,80} = 4.43$, $P = 0.038$).

Wintering waterfowl and habitat

Analysis of covariance shows that there was a significant effect of assemblage type on the relationship of

Table 3. Significant differences between wintering waterfowl assemblage types (1-5) in site characteristics, tested by one-way ANOVA.

Variable	Assemblage Type 1	2	3	4	5	F	df	P
Fine gravel	0.53	1.04	0.33	0.20	0.16	4.52	4, 42	0.004
DOM	0.062	0.043	0.048	0.038	0.045	4.03	4, 42	0.005
Phosphate-P ($\mu g/l^{-1}$)	23.9	15.7	10.6	11.6	12.8	3.64	4, 79	0.009
Medium gravel	0.77	0.91	0.33	0.18	0.26	3.88	4, 42	0.009
Coarse sand	1.77	1.56	0.27	0.58	0.64	3.80	4, 42	0.010
Area (ha)	6.3	5.1	8.4	10.7	6.4	3.45	4, 100	0.011
Nº invertebrate taxa	25.8	19.4	22.6	24.6	23.6	3.40	4, 42	0.017
Depth (m)	2.04	1.83	2.28	2.99	2.51	3.20	4, 42	0.022
Average TRS	8.38	8.09	7.78	8.24	8.38	2.97	4, 42	0.030
Plant abundance	6.78	3.53	5.40	6.45	5.93	2.82	4, 42	0.037
Nº plant taxa	3.0	1.9	2.6	2.7	3.0	2.67	4, 42	0.045

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abundance with lake size in all 12 species considered (Table 4). The linearity of the relationship (regression slope) was similar between assemblage types (non-significant interaction term) in eight species, but the assemblage main effect was highly significant in each case, indicating differences between the lake groups in terms of the value of a given unit of habitat or open water. In the remaining four species, there were differences between the assemblage types in the slope of regression (significant interaction term), suggesting even more profound differences between the lake groups. The ANCOVA models explained much of the variance in waterfowl numbers, so that it can be seen that lake size and the lake characteristics related to the differences in assemblage types (see Table 3) account for much of the value of these lakes for wintering waterfowl.

Regression models for waterfowl densities are summarised in Table 5. Assemblage type on its own was significant for all species except goldeneye. In six species, the models with assemblage type included more environmental variables than those without, suggesting that when differences between lakes are accounted for, more environmental factors are identifiable. In great crested grebe, wigeon and tufted duck, better models (larger R^2) were identified when assemblage type was included, but with a smaller number of environmental variables, indicating a great deal of consistency and predictability about their occurrence in different assemblages. Conversely, in gadwall and goldeneye, the model was poorer (smaller R^2) for being constrained to include assemblage type, suggesting that the interpretation of the assemblage types in which these species occurred is not particularly meaningful in terms of real biological communities. Overall, the models with both assemblage type and environmental variables were very successful in accounting for the densities of individual species on lakes, explaining up to 95.7% of the variance.

The contributions of the variables to the models are summarised according to ecological group of waterfowl in Figure 3. These results do not bear detailed interpretation, partly because correlations between the variables make their effects difficult to construe. However, the following points emerge: a) dabbling species generally favoured the most organically-rich lakes - high in DOM, detritus and dissolved nitrates (see Fig. 3a); b) diving species benefited from an abundance of aquatic invertebrates over gravelly substrata (see Fig. 3b); c) diving waterfowl appeared more susceptible to the effects of water-based recreation than any other group of species; d) grazing species were favoured by the use of lakes for both coarse and game fishing (see Fig. 3c); e) more than any other group, grazing waterfowl occurred on lakes with little marginal and other vegetation; f) fish-eating species favoured the deeper lakes (see Fig. 3d); g) fish-eating species were positively associated with some water-based recreational activities, but were adversely affected by the use or management of lakes for game fishing.

Models for waterfowl densities identified using a reduced set of environmental variables but constrained to include assemblage type are summarised

Table 4. Summaries of ANCOVA models explaining wintering waterfowl numbers in terms of assemblage types and lake size. Lake size expressed as area for diving and fish-eating species and perimeter length for dabbling and grazing species. Where the interaction term is not significant, the R^2 and the P-values for lake size and assemblage type are for a model excluding this term.

	P-values			
Species	Lake Size	Assemblage	Assemblage × Lake Size	R^2 (%)
Great crested grebe	<0.001	<0.001	0.400	66.5
Cormorant			0.015	41.0
Mute swan	<0.001	<0.001	0.697	53.7
Canada goose			0.040	46.9
Wigeon			0.009	58.4
Gadwall	<0.001	<0.001	0.682	55.8
Teal	<0.001	<0.001	0.143	44.4
Mallard	<0.001	<0.001	0.960	40.6
Pochard	<0.001	<0.001	0.802	55.9
Tufted duck	<0.001	<0.001	0.725	55.8
Goldeneye	<0.001	0.005	0.428	45.8
Coot			0.002	62.5

Table 5. Variation in wintering waterfowl densities explained by lake characteristics and/or assemblage types. Numbers of variables are the number of environmental variables included in the regression models. R^2 is the coefficient of determination, adjusted for degrees of freedom. P is the significance of the model using assemblage types only.

	Without Assemblage Type		With Assemblage Type		Assemblage Type Only	
Species	R^2 (%)	№ Variables	R^2 (%)	№ Variables	R^2 (%)	P
Great crested grebe	46.3	5	51.7	2	27.8	0.004
Cormorant	65.8	7	92.5	22	20.4	0.010
Mute swan	30.0	4	40.0	4	16.3	0.024
Canada goose	52.2	6	73.2	12	22.3	0.007
Wigeon	47.7	8	76.6	3	67.9	<0.001
Gadwall	60.9	11	36.6	1	34.8	<0.001
Teal	77.4	9	95.7	21	16.9	0.022
Mallard	65.0	7	83.9	14	37.0	<0.001
Pochard	57.3	6	68.0	7	23.8	0.005
Tufted duck	66.9	10	73.2	8	39.0	<0.001
Goldeneye	39.3	4	28.5	2	0.0	0.561
Coot	60.0	8	66.2	9	27.2	0.002

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Table 6. Summaries of regression models for wintering waterfowl densities on lakes. All models include terms for assemblage types. The signs indicate the direction and significance of regression coefficients: (+)/(-), 0.15>P>0.05; +/-, P<0.05; ++/--, P<0.01; +++/---, P<0.001.

Environmental Variable	Wigeon	Cormorant	Tufted duck	Mallard	Canada goose	Pochard	Great crested grebe	Gadwall	Coot	Teal	Goldeneye	Mute swan
Recreation			--	-	(+)	--					(-)	(+)
Invert. abundance			(+)	(+)		(+)				+		+
Depth	(+)	++	(+)							(-)		
Conductivity		(-)						(-)		(+)	--	
Invert. taxa			+		+++					-		
Indentedness		--		--		-						
Plant abundance					--	++					(+)	
Open water TRS					(+)	-			--			
Nº islands		+++		+								
Alkalinity							---			(-)		
Phosphate		+						+				
pH		---										
R^2 (%)	68.7	58.8	57.6	51.7	50.1	48.7	46.4	40.2	40.0	32.4	27.9	26.3

in Table 6. Smaller amounts of variance were explained than by full models (see Table 5), for all species except gadwall, but some important effects were highlighted. The most important of these was the strong impact of water-based recreation on densities of the two *Aythya* species (pochard and tufted duck). Some effects of potential food supply were also apparent: tufted duck favoured lakes with greater diversity and abundance of aquatic invertebrates, whilst pochard also favoured lakes with abundant aquatic plants. There were also some spurious correlations, however, such as the strong positive association between Canada goose densities and aquatic invertebrate diversity, which seems unlikely to be a causal relationship. The trophic and base-status of lakes appears to be relevant for some species. Densities of pochard and coot declined with increasing eutrophication, as measured by the average TRS-values for open water plants, whilst cormorant and gadwall appeared to be favoured by increasing dissolved phosphate levels. Great crested grebe and, to a lesser extent, teal densities were negatively correlated with alkalinity, whilst cormorant showed a strong negative association with pH. The model for cormorant highlights some other factors which may be important in defining habitat for this species: lake islands may be important disturbance-free resting areas, whilst the effects of water depth may be related to the fish populations of lakes and the ease of foraging.

Discussion

Waterfowl communities

Biological communities are composed of organisms which interact or are mutually dependent (Lincoln & Boxshall 1987). The extent to which wintering waterfowl recorded together on a lake constitute a community in this sense is arguable. Different species may have overlapping requirements for habitat and food, hence may be expected to compete, but interspecific interactions are rarely observable (Owen & Black 1990) and resource partitioning through behavioural or morphological adaptations may reduce direct competition (e.g. Lack 1945). However, spatial constraints on occupancy may apply even when there is no direct trophic dependence on a habitat, as in the case of waterfowl roosting on a lake, for which it may be simply a disturbance-free stretch of water. We are thus justified in considering patterns of variation in the assemblages of waterfowl using wetlands and in attempting to determine the ecological basis for such variation.

A potential pitfall in the interpretation of species' roles in identified assemblages, and hence in the interpretation of assemblages as biological communities, is that short-term movements may change species distributions. In the present analysis there is a danger that wintering waterfowl assemblages identified from day-time surveys will not adequately represent trophic dependence on habitat, since many waterfowl species, particularly diving ducks, are known to feed at night. Observations of pochard and tufted duck in the Cotswold Water Park suggest that day-time feeding is adequate to account for at least the day-time fraction of the daily energy budget in these species (R. May & M.C. Bell, unpubl. data), but it is still probable that there are night-time movements between lakes.

The analysis of wintering waterfowl assemblages

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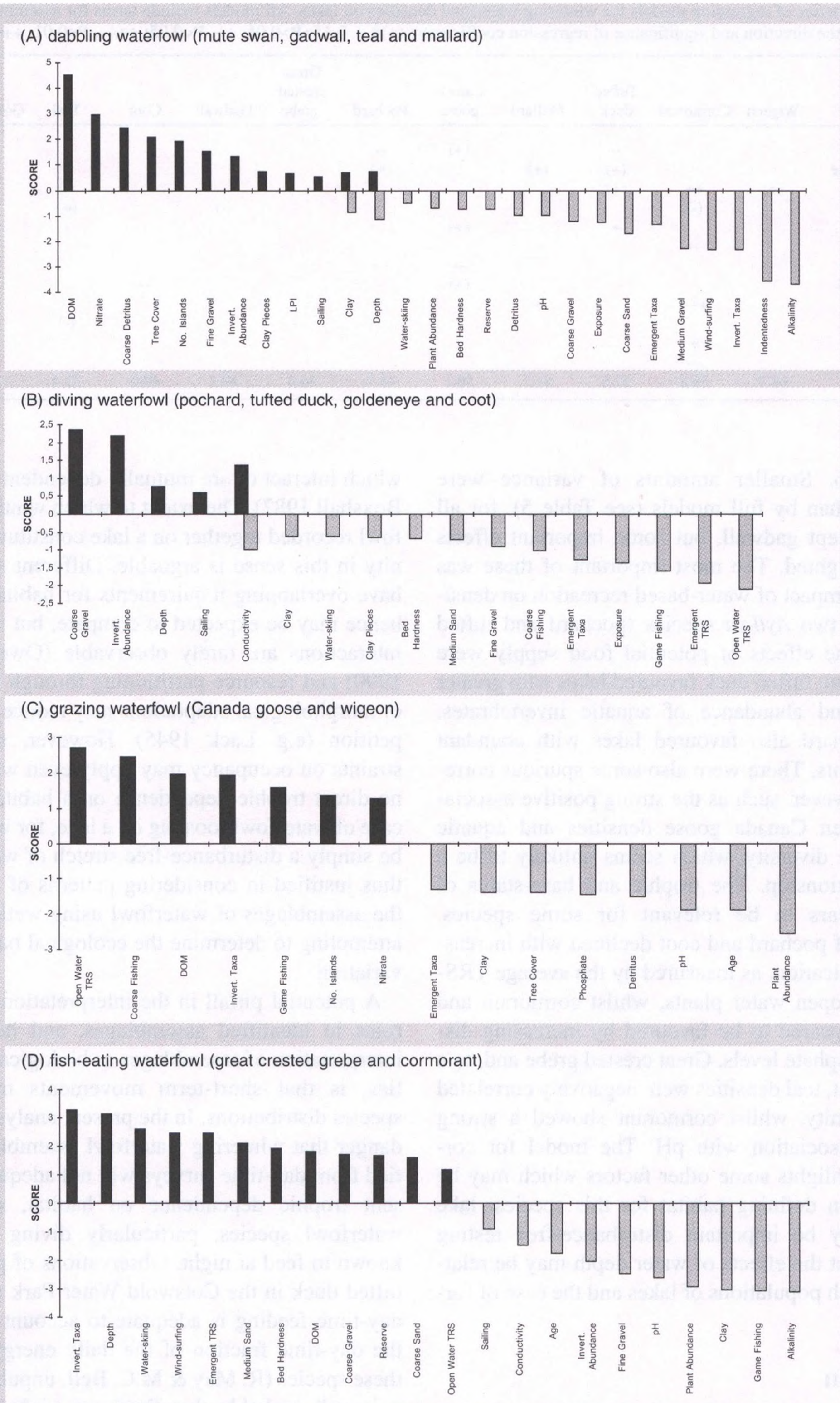

Figure 3. Contributions of lake characteristic variables to regression models for individual waterfowl species. Scores are t-values for regression coefficients, averaged across species, separately for positive and negative effects.

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in the Cotswold Water Park indicated that community structure depended on the ecological roles of the different species - largely a distinction between diving waterfowl assemblages, dependent on open water habitats, and dabbling waterfowl assemblages, more dependent on littoral habitats. A similar conclusion was drawn by Suter (1994) with respect to waterfowl wintering on Swiss lakes north of the Alps: species with similar food and feeding methods had similar distributions across the lakes. However, Suter (1994) found that distribution was more similar between species with similar food requirements but different feeding methods, such as coot and mute swan, than between species belonging to the same guild. In the present study, the distinction between diving and dabbling communities was very clear, although there were intermediate types.

The assemblages were also very distinct in terms of lake characteristics. Two main conclusions may be drawn from comparison of lakes between groups defined by assemblage types. Firstly, the findings support the notion that the scale of biotic diversity is reflected at all biotic levels within a lake. The poorest lakes for wintering birds were also the poorest for aquatic plants and benthic invertebrates. The converse appeared also to be true, although a diverse assemblage of dabbling waterfowl seemed to be a better indicator of generally high biotic diversity than a diverse assemblage of diving waterfowl. It is unclear, however, whether the link was causal, i.e. resulting from a dependence of birds on plants and invertebrates as a food resource, or systemic, i.e. reflecting a general effect of habitat diversity on all levels of biotic diversity. The modelling of lake characteristics important for individual species sheds more light on the existence of trophic links, at least for diving species.

The second conclusion concerns the link between the trophic status of lakes and the wintering waterfowl assemblage. Bell (1996) found a strong relationship between age and trophic status of lakes in the Cotswold Water Park, as measured by average Trophic Ranking Scores for open water plants, which implies a natural process of eutrophication occurring over a scale of a few decades. The eutrophication process appears to be driven by an interaction between the evolution of aquatic plant communities and the nutrient and base-status of the lake water. In terms of water chemistry, the trend is marked by an increased availability of dissolved phosphates. Lakes supporting the assemblage types in which diving waterfowl featured largely appeared to be at an earlier stage in the eutrophication process than those supporting assemblages dominated by dabbling species. These differences suggest that there is a relationship of wintering waterfowl community composition with a natural process of lake evolution towards increasingly eutrophic status, there being a parallel evolution from diving to dabbling assemblages. To a certain extent, this hypothesis is borne out by differences in age between lakes supporting different assemblage types: lakes supporting the diverse diving assemblage tended to be younger than all other lakes.

Several other workers have noted a relationship between the trophic status of lakes and wintering or breeding waterfowl (e.g. Rutschke 1987, Hoyer & Canfield 1994, Staicer, Freedman, Srivastava, Dowd, Kilgar, Hayden, Payne & Pollock 1994). Suter (1994) found that wintering diving duck in Switzerland tended to be associated with the less nutrient-enriched lakes, principally because their main food source, the zebra mussel *Dreissena polymorpha*, prefers less eutrophic waters; conversely, densities of fish-eating waterfowl were greatest on hypertrophic lakes, because of the abundance of cyprinid fish in these waters.

No effect of the recreational use of lakes on community structure was detected. That recreation can have profound effects on wintering waterfowl densities is apparent from this and other studies, both in the Cotswold Water Park (Fox et al. 1994) and more generally (Tuite et al. 1984). It appears that, at least in this study area, whilst water-based recreation can affect the numbers of birds using lakes (see below), it has little bearing on the types and relative proportions of different species, except inasmuch as recreation is correlated with habitat factors.

Wintering waterfowl and habitat

The diversity of waterfowl species and ecological types recorded on lakes in the Cotswold Water Park suggests that there is a corresponding diversity of waterfowl habitats. Inevitably, there must be overlaps in the ecological requirements of the different species such that the abundance of individual species should not be considered in isolation. The suitability of a lake for one species will be affected by the presence of other species, either because the species compete for the same resources or simply because there are spatial limits on the occupancy of different habitats. It can be shown that the reduction in the capacity of a unit of habitat to support a particular species caused

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by the presence of a second species may be modelled statistically in terms of interactions between the amount of habitat and the abundance of the second species.

We tried to account for the presence of other species by considering lake suitability for a species within groups of lakes defined by assemblage types. The proportions of the different species present should be relatively similar between lakes within assemblage types, so that the effects of interspecific interactions may be assumed to be effectively constant. A further justification of this approach is that the ecological requirements of a species may differ between assemblage types; a species may be present as a roosting member of one assemblage, for example, whilst a feeding member of another, thus presenting two different types of relationship with habitat factors.

It was clear from these analyses that a great deal of variation in numbers of individual species was explicable in terms of lake size and assemblage type. Wintering waterfowl assemblage type appeared to summarise a great deal about the nature of lakes, such that within groups of lakes supporting similar assemblages, lake size is a good correlate of the amount of suitable habitat for assemblage members. The success of models including assemblage type implies that the pattern of lake use by waterfowl stems from more than just the sum of individual habitat preferences; individual species may also have different ecological roles in different assemblages.

The importance of lake size was not unexpected; Suter (1994), for example, found relationships of wintering waterfowl numbers on Swiss lakes with either lake area or perimeter length, depending on waterfowl guild. These results were parallelled in the present study: in preliminary analyses we found that abundance was most strongly related with lake area in those species dependent on open water habitats (diving and fish-eating waterfowl) and with lake perimeter length in those species dependent on littoral habitats (dabbling and grazing waterfowl). However, even in some of the diving and fish-eating species, non-linearity in the relationship of numbers with area suggested that not all units of lake habitat are of equal value.

Over and above the effects of lake size and the lake characteristics summarised by assemblage types, it was clear that habitat factors defining the availability of food for wintering waterfowl were of great importance in determining numbers and that the human use or management of lakes was an important modifying factor. Water-based recreation appeared to be an important factor reducing the suitability of lakes, particularly for diving waterfowl. In some species, however, human management of lakes appears to be beneficial: management of lake shores for angling benefits the grazing species, particularly where the removal of marginal vegetation facilitates movements between banks and the open water.

It is unclear whether waterfowl using the Cotswold Water Park are in any sense resource limited. Effects of food supply and other habitat factors on waterfowl numbers do not necessarily imply that numbers are at a sustainable maximum on any given lake, merely that birds are distributed according to the availability of resources. Nevertheless, the results of the modelling presented in this paper are of value in identifying some major determinants of waterfowl numbers, which may be of use in directing management of lakes for waterfowl.

Implications for management of lakes for wintering waterfowl

A natural process of eutrophication accompanied by changes in the nature of wintering waterfowl assemblages was identified which has considerable implications for the maintenance of conservation interest in the Cotswold Water Park. In the absence of intervention to halt or divert this process, a lake which is of great conservation interest for the numbers of diving duck in winter is likely to evolve into one of lesser interest in the future, 20 to 30 years hence. Measures which are applied to protect this conservation interest may very well become misplaced. In the case of wintering waterfowl, it is unlikely that an important lake will become totally uninteresting in the future: any sizeable stretch of water in the region will support some waterfowl, if only for roosting, simply because there is a paucity of other open water in the region. It may well be the case, however, that conditions will no longer favour the concentrations of diving duck for which the Cotswold Water Park is renowned.

In the short term, shifts in conservation interest are unlikely to be a problem, since enough new gravel pits are excavated to ensure the availability of habitat at all stages of evolution. If the planned extension of gravel extraction in the upper Thames valley takes place (Gloucestershire County Council, Upper Thames Plan), there should be a supply of new habitat well into the future. To ensure maximum conser-

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vation benefit from this habitat creation requires a flexible conservation strategy, however, and a recognition by both conservationists and planners that conservation and the human-use of lakes in the Cotswold Water Park can coexist if planned with due regard to the likely changes and shifts in conservation interest. In the longer term, there needs to be research into methods of maintaining the conservation value within individual lakes. Habitat management may have a crucial role to play in ensuring that the Cotswold Water Park continues to be of outstanding importance for national and international nature conservation.

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References

Andrews, J. & Kinsman, D. 1991: Gravel pit restoration for wildlife. A practical manual. - Royal Society for the Protection of Birds, Sandy, 184 pp.

Barker, P.J. & Rushton, K.R. 1983: The interaction of a gravel aquifer with pits and rivers. Cotswold Water Park, Ashton Keynes section. Phase I. - Department of Civil Engineering Report, University of Birmingham, 97 pp.

Begon, M., Harper, J.L. & Townsend, C.R. 1986: Ecology. Individuals, populations and communities. - Blackwell, Scientific Publications, Oxford, 876 pp.

Bell, D.V. 1992: Cotswold Water Park nature conservation review. - Gloucestershire Wildlife Trust, Gloucester, 109 pp.

Bell, M.C. 1996: Gravel pit ecology in the Cotswold Water Park: A review of recent data collected by The Wildfowl & Wetlands Trust. - Research Report. The Wildfowl & Wetlands Trust, Slimbridge, 55 pp.

Burnham, K.P. & Anderson, D.R. 1992: Data-based selection of an appropriate biological model: the key to modern data analysis. - In: McCullough, D.R. & Barrett, R.H. (Eds.); Wildlife 2001: populations, Elsevier, London, pp. 16-30.

Davidson, N.C., Laffoley, D.d'A., Doody, J.P., Way, L.S., Gordon, J., Key, R., Pienkowski, M.W., Mitchell, R. & Duff, K.L. 1991: Nature conservation and estuaries in Great Britain. - Nature Conservancy Council, Peterborough, 422 pp.

Delany, S.N. 1993: Counts of waterfowl in the Cotswold Water Park: 1989/90-1992/93. - Report to English Nature. The Wildfowl & Wetlands Trust, Slimbridge, 19 pp.

Digby, P.G.N. & Kempton, R.A. 1987: Multivariate analysis of ecological communities. - Chapman and Hall, London, 206 pp.

Fox, A.D. & Bell, M.C. 1994: Breeding bird communities and environmental variable correlates of Scottish peatland wetlands. - Hydrobiologia 279/280: 297-307.

Fox, A.D., Jones, T.A., Singleton, R. & Agnew, A.D.Q. 1994: Food supply and the effects of recreational disturbance on the abundance and distribution of wintering Pochard on a gravel pit complex in southern England. - Hydrobiologia 279/280: 253-261.

Hilton, G., Bell, M.C. & Menendez, C.T. 1994: Summer waterbird populations of the Cotswold Water Park: results of the 1994 surveys. - Report to the National Rivers Authority (Thames Region) and Cotswold District Council. The Wildfowl & Wetlands Trust, Slimbridge, 73 pp.

Hoyer, M.V. & Canfield, D.E. 1994: Bird abundance and species richness on Florida lakes: influence of trophic status, lake morphology, and aquatic macrophytes. - Hydrobiologia 279/280: 107-119.

Kirby, J.S. 1995: Winter population estimates for selected waterfowl species in Britain. - Biological Conservation 73: 189-198.

Lack, D. 1945: The ecology of closely related species with special reference to cormorant (Phalacrocorax carbo) and shag (P. aristotelis). - Journal of Animal Ecology 14: 12-16.

Lance, G.N. & Williams, W.T. 1966: A generalized sorting strategy for computer classifications. - Nature, London 212: 218.

Liddle, M.J. & Scorgie, H.R.A. 1980: The effects of recreation on freshwater plants and animals: a review. - Biological Conservation 17: 183-206.

Lincoln, R.J. & Boxshall, G.A. 1987: The Cambridge illustrated dictionary of natural history. - Cambridge University Press, Cambridge, 413 pp.

Millett, M.C. 1992: Environmental determinants of wetland invertebrate communities. - PhD Progress Report to University of Wales College Cardiff. The Wildfowl & Wetlands Trust, Slimbridge, 19 pp.

Millett, M.C. 1993: Environmental determinants of wetland invertebrate communities. - PhD Progress Report to University of Wales College Cardiff. The Wildfowl & Wetlands Trust, Slimbridge, 45 pp.

Merritt, A. 1994: Wetlands, Industry and Wildlife. A manual of principles and practices. - The Wildfowl & Wetlands Trust, Slimbridge, 182 pp.

Owen, M. 1983: The importance of artificial habitats for wildfowl in Britain. - Proceedings of a symposium on the

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subject of wildlife on man-made wetlands, ARC Wildfowl Centre, Great Linford, England, pp. 73-97.
Owen, M. & Black, J.M. 1990: Waterfowl ecology. - Blackie, Glasgow, 194 pp.
Owen, M., Atkinson-Willes, G.L. & Salmon, D.G. 1986: Wildfowl in Great Britain. - 2nd Edition. Cambridge University Press, Cambridge, 613 pp.
Palmer, M. 1989: A botanical classification of standing waters in Great Britain. - Research and survey in nature conservation No. 19. Nature Conservancy Council, Peterborough, 20 pp.
Pollitt, M.S. 1995: Waterfowl monitoring in the Cotswold Water Park. Report on midweek winter counts in 1994-95. - Report to the Joint Nature Conservation Committee. The Wildfowl & Wetlands Trust, Slimbridge, 27 pp.
Pöysä, H. 1984: Temporal and spatial dynamics of waterfowl populations in a wetland area - a community ecological approach. - Ornis Fennica 61: 99-108.
Pöysä, H. & Virtanen, J. 1994: Habitat selection and survival of Common Goldeneye (Bucephala clangula) broods - preliminary results. - Hydrobiologia 279/280: 289-296.
Ramsar Convention Bureau 1990: Proceeding of the fourth meeting of the Conference of Contracting Parties (of the Ramsar Convention). Montreux, Switzerland, 27 June to 4 July 1990. Volume I. - Ramsar Convention Bureau, Gland, 306 pp.
Ratcliffe, D.A. (Ed.) 1977: A nature conservation review. Volume 2. - Cambridge University Press, Cambridge, 320 pp.
Rose, P.M. & Taylor, V. 1993: Western Palearctic and south-west Asia waterfowl census 1993. - International Waterfowl & Wetlands Research Bureau, Slimbridge, 215 pp.
Rutschke, E. 1987: Waterfowl as bio-indicators. - In: Diamond, A.W. & Filion, F.L. (Eds.); The value of birds. ICBP Technical Publication No. 6, International Council for Bird Preservation, Cambridge, pp. 167-172.
SAS Institute Inc. 1988: SAS/STAT user's guide, Release 6.03 edition. - SAS Institute Inc, Cary, NC, 1028 pp.
Sillén, B. & Solbreck, C. 1977: Effects of area and habitat diversity on bird species richness in lakes. - Ornis Scandinavica 8: 185-192.
Sokal, R.R. & Rohlf, F.J. 1981: Biometry. - 2nd Edition. W.H. Freeman, San Francisco, 859 pp.
Staicer, C.A., Freedman, B., Srivastava, D., Dowd, N. Kilgar, J., Hayden, J., Payne, F. & Pollock, T. 1994: Use of lakes by black duck broods in relation to biological, chemical, and physical features. - Hydrobiologia 279/280: 185-199.
Stewart, N.F. & Church, J.M. 1992: Red Data Books of Britain and Ireland: stoneworts. - Joint Nature Conservation Committee, Peterborough, 143 pp.
Stroud, D.A., Mudge, G.P. & Pienkowski, M.W. 1990: Protecting internationally important bird sites. A review of the EEC Special Protection Network in Great Britain. - Nature Conservancy Council, Peterborough, 230 pp.
Suter, W. 1994: Overwintering waterfowl on Swiss lakes: how are abundance and species richness influenced by trophic status and lake morphology? - Hydrobiologia 279/280: 1-14.
Tuite, C.H., Hanson, P.R. & Owen, M. 1984: Some ecological factors affecting winter wildfowl distribution on inland waters in England and Wales, and the influence of water-based recreation. - Journal of Applied Ecology 21: 41-62.
Waters, R.J. & Cranswick, P.A. 1993: The Wetland Bird Survey 1992-93: wildfowl and wader counts. - British Trust for Ornithology/The Wildfowl & Wetlands Trust/Royal Society for the Protection of Birds/Joint Nature Conservation Committee, Slimbridge, 122 pp.
Webster, R. & Oliver, M.A. 1990: Statistical methods in soil and land resource survey. - Oxford University Press, Oxford, 316 pp.

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