Bird assemblages as bio-indicators of water regime management and hunting disturbance in natural wet grasslands

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Abstract

Responses of the waterbird community to the management regime of a wet grassland system (primarily small changes in the water regime but also hunting disturbance) in a large floodplain lake, Grand-Lieu, were studied during three consecutive years (winter and spring in 1998–2000). These temporarily flooding grasslands (1100 ha) constituted a very important feeding area by supporting large flocks of waterbird species (52 regular spp., totalling up to 14250–22850 birds). A global similar seasonal pattern in the presence of waterbird species was recorded whatever the year. The March–May period was a key phase with the maximum species richness (42–48 spp.) and the maximum abundance (30–40% of the total according to year, essentially Anseriformes). Late in spring Ciconiiformes and to a lesser extent some waders exploit this feeding area. Nevertheless some changes in bird assemblages were exhibited according to the management regime (a decreasing spring water level from 1998 to 2000, and an exceptional hunting ban in January 2000, instead of an usual stop in late February). The hunting disturbance clearly limited diurnal accessibility of ducks to wet grasslands in January and February 1998 and 1999. Also, the duck population in flooding grasslands increased by 55–65% in January 2000 when hunting was prohibited and in the same time the richness species grew from 14–19 spp. up to 23 spp. in 2000. The overall impact of a high spring water level on waterbirds as in 1998 and to a lesser extent in 1999 (with respectively 54 and 35 cm of mean water level against 25 cm in 2000) was an increase in diving fish-eating birds and larger flocks of resting gulls. Conversely these conditions, notably a reduced period with a spring water level under 25 cm in spring (20 days in 1998–1999 instead of 40 days in 2000) were adverse to numerous ground-feeding waterbirds (Ciconiiformes and waders) that require shallow waters. This study showed that limitation of human disturbance and moderate flooding of wet grasslands can increase their attractiveness for numerous species of high conservation status.

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1. Introduction

Wetlands play an important role in biodiversity because they are attractive to many species due to their large habitat diversity and their great productivity providing nutrients and other resources (Weller, 1988; Elmberg et al., 1994). Birds are among the most conspicuous of wetland animals and various species are extremely sensitive to large hydrological changes (Kushlan, 1986a; Crowder and Bristow, 1988; Pyrovetsi and Papastergiadou, 1992). Creation of reservoirs demonstrated immediate effects on waterbird communities (Hunter et al., 1987; Bildstein et al., 1994) and water conditions are among the main factors affecting the composition and the abundance of waterbird communities directly and indirectly (Dister et al., 1990; Briggs et al., 1998; Osiejuk et al., 1999). Water level fluctuations influence the physical structure of habitats (zonation of vegetation), the availability and accessibility of food (Claussen, 2000) and the presence of safe roosting or breeding sites (Green and Robins, 1993; Guillemain et al., 2000). All these characteristics determine habitat selection by waterbirds (Sanders, 1999) and especially by migrant birds that depend largely on the presence of well functioning wetlands along their

flyways (Ens et al., 1994; van Eerden, 1997; Madsen, 1998a,b; Ntiamo-Baidu et al., 1998).

Human disturbances, especially hunting, can interfere with these factors and limit the accessibility to resources (e.g. Madsen, 1998a). However, the relative effect of hunting has not been assessed in relation to other parameters influencing the use of wetlands by waterbirds. Moreover, the detailed response of different taxonomic groups of waterbirds to low seasonal changes in water level has rarely been assessed (Elphick and Oring, 1998). Indeed, the studies of natural wetlands that have established relationships between water level and bird population changes concerned essentially responses either of specific groups, Ciconiiformes or ducks (Marion, 1989; Dubowy, 1996; Dimalexis and Pyrovetsi, 1997; Kingsford and Johnson, 1998; Duncan et al., 1999) or of the whole community (Hunter et al., 1987; Crivelli et al., 1995; Briggs et al., 1997; Hertzman and Larsson, 1999) exclusively to large water depth fluctuations or drainage, while small variations in water level on flooding surrounding grasslands have been little studied. Also, most of previous studies have described the responses on a taxonomic basis rather than on an ecological basis.

The objectives of the present study are to identify firstly the patterns in the use of a wetland system by the whole waterbird community during a 3-year period, and secondly the effect of the management regime of the ecosystem (primarily small changes in the water regime, but also hunting disturbance) on the species assemblages. We compared the response of the different species groups, mainly Ciconiiformes, Anseriformes and Charadriiformes, recorded on flooded wet grasslands over three consecutive years (winter and spring) with partially controlled water regimes and an opportunistic exceptional hunting ban imposed during one of these years. The role of the water level on the breeding populations of the waterbird community in the different habitats of the lake will be addressed in another paper and will complement management recommendations made in the present study.

Practical management applications are discussed to define the optimum management regime for preserving or enhancing the value of the wetland as feeding habitat for the whole waterbird community and more specifically for some species of high conservation status.

2. Materials and methods

2.1. Study site

The Lac de Grand-Lieu is a shallow, turbid, eutrophic natural freshwater ecosystem in Western France (47°05’ N, 1°39’ W). This lake constitutes one of the most important bird areas in France supporting large numbers of wintering and migrating ducks and Fulica atra (about 20 000 birds) and breeding populations of ducks and heron species, the latter representing also one of the main European breeding populations and the largest colonies in France for Ardea cinerea, Egretta alba, Platalea leucorodia and Threskiornis aethiopicus (Rocamora and Yeatman-Berthelot, 1999; Marion et al., 2000). The whole wetland is designated a Special Protection Area under the EC Birds Directive and a Ramsar Site (Deceuninck et al., 2000).

The wetland is of value because of its diversity of habitats for waterbirds, with four major complementary functional units (see Marion et al., 1994, for a more detailed description). The lake covers 4000 ha in summer and 6300 ha in winter, by flooding adjacent peaty wet grasslands used mainly as pastures. About 20 km of the lake margin (2000 ha) are covered by a floating peat fen, which becomes progressively exposed in summer. Most of the permanently central flooded area of the lake is covered from April to October by about 1400 ha of floating macrophytes. The central open water region without floating or emergent plants except small patches of submerged macrophytes covers about 600 ha.

The wet grasslands of the Lac de Grand-Lieu can be considered as ecotonal habitats, as described by Dobrowolski (1997), and represent the principal feeding area of the wetland for wintering and migrating waterbirds. The grassland consists of level fields intersected by drainage channels. Human activities like mowing and grazing prevent the growth of trees and have formed fields with a heterogeneous vegetation structure dominated by Phalaris arundinacea, Glyceria maxima, Carex spp. or Eleocharis spp. The present study focuses on the use of the southwest unit by the waterbird community, the largest and most important part of the wet grasslands for waterbirds.

2.2. Water regime

A drainage channel flows from the lake to the Loire estuary 25 km away and a sluice gate regulates the water level of the lake, essentially during the hydrological storage period (mainly in winter) by discharging the water surplus to the outlet. In the past, pressure from the farming community for land drainage in spring contributed to reductions in water level and duration of flooding. During our study, three different water levels were recorded: a high water level in 1998, a low water level in 2000 and an intermediate one in 1999 (Fig. 1). Such a difference, occurring between three consecutive years in the same site, limits variations due to long term changes in population dynamics of birds related to other factors.

The water level is described by using a local depth measure (Buzay scale = 0.47 m above French Geographic Level NGF). The mean level of the wet grasslands is 1.89 m Buzay (Marion and Marion, 1975), with
a relatively slow variation (SD = 0.10 m). Thus a mean water level of 2.14 m Buzay corresponded to a real mean water level of 25 cm on the grasslands. For each year we calculated the length of time that the level was below this mean threshold of 25 cm commonly defined as the maximum feeding depth for the majority of waterbird species, especially Ciconiiformes and Charadriiformes (Owen and Black, 1990; Ntiamoa-Baidu et al., 1998).

2.3. Bird census

All waterbirds (here defined as Podicipediformes, Pelecaniformes, Ciconiiformes, Anseriformes, Gruidae, and Charadriiformes) were censused on the southwest wet grasslands from eight fixed-observation points covering 1100 ha (the other 300 ha, with many trees, not being used by large numbers of birds). For each observation point, waterbird species were counted individually or in units of 10 when flocks were larger than 100. When we encountered very large flocks of resting ducks (> 1000), we first counted them in units of 100 and then we counted each duck species in units of 10 to control both methods (Reeber, 2000). Given the open nature of the wet grassland system studied these counts were likely to estimate absolute abundance accurately for most species. Nevertheless some species for which this was unlikely to be true (common snipe Gallinago gallinago and little grebe Tachybaptus ruficollis) are not considered here. Birds seen flying overhead were not included so that they were not counted again at another station.

The censuses were conducted at 5-day intervals in three consecutive years (1998–2000) from the fifth period of 5 days in January, noted Jan V, to the second period of 5 days in July, noted Jul II. Hunting activity on the wetland occurred from mid-July to the end of February in all years except 2000, when an exceptional ban was imposed in January (due to the Erika disaster) allowing the effects of disturbance on the waterbird community to be assessed. We combined data for the different fixed-observation points at each 5-day interval to test the overall effect of the two major local descriptors of the management regime (water level and hunting activity) on the waterbird community.

2.4. Data analysis

We used standard measures of species diversity to characterize the patterns of waterbird community in the wet grassland system: species richness and Shannon diversity (Guillory, 1999). A mean value of the Shannon diversity was calculated for each month from January to July. Annual frequencies of occurrence (% of species present in all the 5-day intervals) and monthly abundance were also defined.

The first step of the assemblage analysis was to classify species into groups, achieving this by a posteriori analysis of their abundance and distribution to identify species exhibiting similar patterns (Gawlick et al., 1998, and literature cited therein). We performed a Foucart’s Correspondence Analysis (CA) on a series of three contingency tables (one per year, counts at 5-day intervals for all species). This method (rarely used in ecology) represents a CA based on an average table called a compromise table (see Foucart, 1978, and Blanc et al., 1998, for more details of the method). We used three graphic representations: a graph linking consecutive 5-day intervals linked with a line according to years, a dendrogram based on a clustering procedure (Euclidian distances and then UPGMA of factorial coordinates—Unweighted Pair Group Method Algorithm), and plots of axes for each annual data set to identify species assemblages on the compromise plane (convex hull procedure). Analyses and graphics were performed using ADE-4 software (Thioulouse et al., 1997) and species with less than 10 birds recorded for each year were excluded from the matrices. Numbers of waterbirds were log (x + 1) transformed prior to analysis.

We used Wilcoxon signed rank tests (SYSTAT Software, 1998) to compare the mean abundance of each species between the three years to justify patterns of waterbird species in 5-day intervals and to determine the sensitivity of species groups to water regime. For each species the mean abundance was calculated for the same period of presence for the 3-year period, rather than the complete period of census. The comparisons were conducted according to the different water regime phases (Section 3). Finally some complementary comparisons of mean abundance were performed on the basis of numerical proportions of breeding population size of species feeding on the wet grasslands during the most variable period identified (Reeber, 2000). These latter tests were used to minimize the effect of possible variations in biogeographical population sizes, already reduced by the monitoring during three consecutive years.
3. Results

3.1. Water regime

The mean abundance patterns showed three major results on the use of the wet grassland system (Fig. 2). The maximum mean abundance of waterbirds was observed in March (from 11200 to 14800 respectively in 1999 and 2000, essentially Anseriformes and Gruiformes, Fig. 3) and represented from 30 (2000) to 40% (1998 and 1999) of the total annual abundance. The mean abundance was relatively lower in the other months, especially in the May–July period whereas the species richness was still high. At this period the wet grasslands were however largely used by Charadriiformes (41–46%) and Ciconiiformes (13–31%) which previously used this habitat little or not at all when the water level was higher (12–21% together). Finally the grasslands were more heavily used by the waterbird community in 2000, with more birds counted in almost all months (Fig. 2).

The Shannon diversity was relatively constant between months in 1998 with several similar values (Fig. 4), whereas this index increased in 1999 and 2000 from low values in the first 2 months (1.06–1.35) to the highest diversity in the May–July period (2.85–3.31). During the last 2 years reduced values were linked to dominance of *Fulica atra* in January and February, when it accounted for 65–70% of the total abundance (Fig. 3). The intermediate values were noted when the waterbird community was large but also composed of large flocks of Anseriformes (March and April). Finally the Shannon diversity reached a peak when the community was again diversified and more equilibrated.

3.2. Composition and biodiversity indices of the waterbird community

A total of 52 regular different waterbird species was recorded in the wet grasslands each year, except in 1999 with no *Tringa glareola* (Table 1). The most abundant waterbird species were Charadriiformes (27 species), Anseriformes (13) and Ciconiiformes (8). The different taxonomic groups included species that spend part of their life at the study site, some being always present, as well as migrant species making more temporary use of the wet grassland system, especially waders (10 species with a frequency of occurrence of less than 50%). There were great differences in the frequency of occurrence of waterbirds between the three years, notably among Charadriiforme species, but also among some Anseriformes.

The monthly species richness patterns were generally similar between the 3 years (Fig. 2), with a maximum number of waterbird species from March to May (from 39 to 50) and fewer species in January and in July, especially in the two first years. The species richness pattern in 2000 was slightly different because of a high value in January (23 spp.) during the exceptional hunting ban followed by a resumption of hunting in February. This change in human disturbance induced a marked difference in curve pattern this year comparatively to the usual curves of the other years (see also mean abundance). The attractiveness of the wet grasslands was prolonged in 2000 since a larger number of species was recorded in July (30) than for 1998 (19) and 1999 (14). However the species richness was higher in February 1998 (35) than during the other years (26).
Table 1
Species of waterbirds recorded during census of the wet grassland system of the Lac de Grand-Lieu from 1998 to 2000 (scientific and common names)

<table>
<thead>
<tr>
<th>Scientific name</th>
<th>Common name</th>
<th>Species code</th>
<th>Frequency of occurrence (%)</th>
<th>Mean abundance</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Podicipediformes</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Podiceps cristatus</td>
<td>Great crested grebe</td>
<td>POCR 91.20–97.05</td>
<td>9.20±2.55</td>
<td>3.85±1.10</td>
<td>5.25±1.80</td>
</tr>
<tr>
<td>Podiceps nigricollis*</td>
<td>Black-necked grebe</td>
<td>PONI 8.80–47.05</td>
<td>2.85±1.95</td>
<td>0.45±0.45</td>
<td>0.65±0.85</td>
</tr>
<tr>
<td>Pelecaniformes</td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Phalacrocoracidae*</td>
<td>Great cormorant</td>
<td>PHCA 76.45–100</td>
<td>8.85±3.10</td>
<td>4.95±1.75</td>
<td>6.45±1.65</td>
</tr>
<tr>
<td>Ciconiiformes</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ardea alba**</td>
<td>Great white egret</td>
<td>EGAL 100</td>
<td>4.60±6.05</td>
<td>6.05±0.90</td>
<td>15.40±3.10</td>
</tr>
<tr>
<td>Ardea cinerea</td>
<td>Grey heron</td>
<td>ARCI 100</td>
<td>141.25±37.05</td>
<td>102.15±24.95</td>
<td>117.95±30.00</td>
</tr>
<tr>
<td>Ardea purpurea**</td>
<td>Purple heron</td>
<td>ARPU 55.88–61.75</td>
<td>7.85±2.45</td>
<td>6.85±2.85</td>
<td>12.10±4.80</td>
</tr>
<tr>
<td>Threskiornis aethiopicus</td>
<td>Sacred ibis</td>
<td>THAE 73.55–79.40</td>
<td>41.75±12.65</td>
<td>51.40±21.00</td>
<td>58.50±20.35</td>
</tr>
<tr>
<td>Platalea leucorodia**</td>
<td>Spoonbill</td>
<td>PLLE 5.90–61.75</td>
<td>1.20±0.95</td>
<td>0.25±0.40</td>
<td>3.85±1.35</td>
</tr>
<tr>
<td>Anseriformes</td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cygnus olor*</td>
<td>Mute swan</td>
<td>CYOL 76.45–100</td>
<td>11.35±2.15</td>
<td>8.35±2.55</td>
<td>15.25±4.30</td>
</tr>
<tr>
<td>Cygnus atratus</td>
<td>Black Swan</td>
<td>CYAL 8.80–64.70</td>
<td>–</td>
<td>–</td>
<td>–</td>
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<tr>
<td>Anser anser</td>
<td>Grey lag goose</td>
<td>ANAN 5.90–20.60</td>
<td>–</td>
<td>–</td>
<td>–</td>
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<tr>
<td>Tadorna tadorna</td>
<td>Shelduck</td>
<td>TATA 11.75–44.10</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Anas penelope</td>
<td>Wigeon</td>
<td>ANPE 55.90–61.75</td>
<td>343.00±219.00</td>
<td>357.00±249.50</td>
<td>431.00±204.00</td>
</tr>
<tr>
<td>Anas strepera*</td>
<td>Gadwall</td>
<td>ANST 73.55–79.40</td>
<td>109.00±82.00</td>
<td>120.00±83.50</td>
<td>151.00±96.00</td>
</tr>
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<td>Anas platyrhynchos</td>
<td>Mallard</td>
<td>ANPL 94.12–100</td>
<td>64.50±13.50</td>
<td>31.55±9.00</td>
<td>33.00±7.30</td>
</tr>
<tr>
<td>Anas acuta</td>
<td>Pintail</td>
<td>ANAC 44.10–50.00</td>
<td>132.15±92.00</td>
<td>83.50±73.50</td>
<td>202.50±135.00</td>
</tr>
<tr>
<td>Anas clypeata*</td>
<td>Shoveler</td>
<td>ANCL 82.35–88.25</td>
<td>970.00±820.50</td>
<td>1006.50±730.70</td>
<td>2077.00±1403.00</td>
</tr>
<tr>
<td>Anas querquedula*</td>
<td>Garganey</td>
<td>ANQU 67.35–79.40</td>
<td>27.65±12.50</td>
<td>21.15±8.85</td>
<td>24.95±11.00</td>
</tr>
<tr>
<td>Anas crecca*</td>
<td>Teal</td>
<td>ANCR 20.60–32.35</td>
<td>5.85±6.55</td>
<td>0.85±0.65</td>
<td>3.30±2.00</td>
</tr>
<tr>
<td>Aythya ferina*</td>
<td>Pochard</td>
<td>AYFE 35.30–52.95</td>
<td>7.05±5.05</td>
<td>4.35±3.90</td>
<td>8.35±11.50</td>
</tr>
<tr>
<td>Aythya fuligula*</td>
<td>Tufted duck</td>
<td>AYFU 8.80–29.40</td>
<td>1.70±1.50</td>
<td>1.00±1.65</td>
<td>5.50±8.95</td>
</tr>
<tr>
<td>Gruiformes</td>
<td></td>
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</tr>
<tr>
<td>Fulica atra</td>
<td>Coot</td>
<td>FUAT 100</td>
<td>1647.50±412.80</td>
<td>1809.40±456.00</td>
<td>3104.55±769.00</td>
</tr>
<tr>
<td>Charadriiformes</td>
<td></td>
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<td></td>
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<tr>
<td>Himantopus himantopus*</td>
<td>Black-winged stilt</td>
<td>HIHI 26.45–67.65</td>
<td>3.40±1.60</td>
<td>1.65±1.35</td>
<td>60.50±19.55</td>
</tr>
<tr>
<td>Charadrius dubius</td>
<td>Little ringed plover</td>
<td>CHDU 29.40–61.75</td>
<td>5.30±7.05</td>
<td>4.60±3.25</td>
<td>18.80±13.00</td>
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<tr>
<td>Charadrius hiaticula</td>
<td>Ringed plover</td>
<td>CHHI 23.55–50.00</td>
<td>–</td>
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<td>–</td>
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<tr>
<td>Pluvialis apricaria*</td>
<td>Golden plover</td>
<td>PLAP 8.80–26.45</td>
<td>5.70±4.70</td>
<td>0.25±0.25</td>
<td>0.15±0.15</td>
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<tr>
<td>Pluvialis squatarola</td>
<td>Grey plover</td>
<td>PLSQ 14.70–26.45</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Vanellus vanellus*</td>
<td>Lapwing</td>
<td>VAVA 97.05–100</td>
<td>230.80±139.30</td>
<td>88.80±38.70</td>
<td>122.15±37.20</td>
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<td>Calidris alpina</td>
<td>Dunlin</td>
<td>CAAL 38.25–52.95</td>
<td>1.85±1.15</td>
<td>2.75±1.55</td>
<td>6.85±2.90</td>
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<tr>
<td>Phaenicurus fulignatus*</td>
<td>Ruff</td>
<td>PHPU 41.20–64.70</td>
<td>32.45±36.10</td>
<td>50.35±39.75</td>
<td>87.15±20.20</td>
</tr>
<tr>
<td>Limosa limosa*</td>
<td>Black-tailed godwit</td>
<td>LILI 41.20–61.75</td>
<td>39.15±22.60</td>
<td>14.75±15.70</td>
<td>13.85±11.20</td>
</tr>
<tr>
<td>Numenius arquata</td>
<td>Curlew</td>
<td>NUAR 8.80–17.65</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Numenius phaeopus</td>
<td>Whimbrel</td>
<td>NUPH 11.75–23.55</td>
<td>6.90±9.15</td>
<td>3.40±4.75</td>
<td>11.80±9.35</td>
</tr>
<tr>
<td>Tringa erythropus</td>
<td>Spotted redshank</td>
<td>TRER 20.60–26.45</td>
<td>–</td>
<td>–</td>
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<tr>
<td>Tringa totanus*</td>
<td>Redshank</td>
<td>TRTO 70.60–76.45</td>
<td>17.85±4.40</td>
<td>17.05±4.15</td>
<td>43.75±19.60</td>
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<td>Tringa nebularia</td>
<td>Greenshank</td>
<td>TRNE 29.40–50.00</td>
<td>12.25±9.00</td>
<td>9.30±7.05</td>
<td>19.60±15.20</td>
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<tr>
<td>Tringa ochropus</td>
<td>Green sandpiper</td>
<td>TROC 5.90–35.30</td>
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<td>–</td>
<td>–</td>
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<tr>
<td>Tringa glareola</td>
<td>Wood sandpiper</td>
<td>TRGL 0–14.70</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Actitis hypoleucos*</td>
<td>Common sandpiper</td>
<td>ACHY 14.70–32.35</td>
<td>0.85±0.80</td>
<td>0.30±0.25</td>
<td>2.80±1.95</td>
</tr>
<tr>
<td>Larus melanocephalus*</td>
<td>Mediterranean gull</td>
<td>LAME 41.20–58.80</td>
<td>3.45±1.10</td>
<td>4.05±1.20</td>
<td>4.00±2.55</td>
</tr>
<tr>
<td>Larus ridibundus</td>
<td>Black-headed gull</td>
<td>LARI 100</td>
<td>1122.00±203.50</td>
<td>752.00±150.00</td>
<td>734.00±127.50</td>
</tr>
<tr>
<td>Larus minutus*</td>
<td>Little gull</td>
<td>LAMI 17.65–47.05</td>
<td>5.75±9.90</td>
<td>0.25±0.15</td>
<td>12.90±16.15</td>
</tr>
<tr>
<td>Larus canus</td>
<td>Common gull</td>
<td>LACA 26.45–55.90</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>
The biological integrity and ecological value of a wetland can be judged by the occurrence and the number of waterbird species that represent a high nature conservation value (Owen and Black, 1990; van Eerden, 1997). The presence of 26 species of high conservation value out of a total of 52 species (Table 1) showed that the temporarily flooding grasslands of the Lac de
Grand-Lieu are really an important ornithological wetland by supporting numerous wintering, migrating and breeding waterbird species. These wet grasslands constituted a very important feeding area for wintering ducks, breeding Ciconiiformes, and a stop over migrating site for waders, while few waterbirds nest on these marsh grasslands. The March–May period was generally a key phase with the maximum biodiversity (42–48 spp. from a total of 52 spp.) and the maximum abundance recorded (30–40% of the total bird sightings, peaks of 14,250–22,850 birds according to years). However some differences were noted between years, and 2000 was characterized by many waterbirds foraging in the wet grasslands in most of the months and by a rich and equilibrated community until summer.

4.2. Relationships between patterns of the waterbird community and the management regime

The multivariate analysis exhibited a relatively similar seasonal pattern of use of the flooded grasslands by waterbirds whatever the year. Both migrating behaviour (early vs late species) and breeding behaviour (species with long breeding season vs short late breeding season or regular territorial feeding inducing small dispersed birds vs opportunist social feeding with large flocks of birds) appear to be the main factors determining this pattern of use of the habitats. Nevertheless some changes in bird assemblages, notably the formation of group 6 in 1999 and 2000 from a large set of species, associated with comparisons of mean abundance within and between years, revealed the effect of the management regime (water level and hunting disturbance) of the wet grasslands.

Although regional and/or continental-wide factors can influence the fluctuations in abundance recorded among waterbird populations which is particularly true for migratory species whose population sizes depend on survival and reproduction in different geographical areas, sometimes very far apart (Kushlan, 1986b; Duncan et al., 1999), most of the changes in abundance of these species could probably be attributed to hunting and water regime factors. The monitoring during three consecutive years reduces the effect of possible variations in biogeographical population sizes. In any case tests performed on numerical proportions of the breeding population on the lake that fed on the wet grasslands avoid this eventual biogeographical device (Table 3). Moreover habitat selection is known to be strictly related to the availability and accessibility of food (Clausen, 2000) and the presence of safe roosting or breeding sites (Green and Robins, 1993; Guillemain et al., 2000) which are mainly governed by the hydrological and disturbance conditions in wetlands (Ferns et al., 1989). The changes in location of 5-day intervals in January 2000 (Fig. 5B,C with an unusual stop of hunting), corresponding mainly to the presence of large flocks of *Fulica atra*, showed the weight of the hunting disturbance. An optimal use of feeding resources by ducks was prevented when wet grasslands were insecure during the hunting season (January–February).
Fig. 5. Results of the Foucart’s Correspondence Analysis on the three-year contingency tables (5-day intervals-species abundance). (A) Plots of samples (5-day intervals) on the first two axes of the compromise table identifying trajectories of the 3 years. (B) Dendrogram of 5-day intervals exhibiting the different levels of clustering. 1998 in dotted line, 1999 and 2000 respectively in black solid plain and bold lines. (C) Coordinates and grouping of the waterbird species on the compromise plot of the two axes (see Table 1 for species codes).
Table 2
Level of significance of the difference between the abundance of species during the three years and for the two different phases of water regime (respectively Jan V–March VI and Apr I–Jul II) using Wilcoxon’s signed rank test a

<table>
<thead>
<tr>
<th>Comparison of mean abundance</th>
<th>Phase 1</th>
<th>Phase 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Podicipediformes species</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Podiceps cristatus</em></td>
<td>**</td>
<td>ns b</td>
</tr>
<tr>
<td><em>Podiceps nigricollis</em></td>
<td>**</td>
<td>*</td>
</tr>
<tr>
<td>Pelecaniformes species</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Phalacrocorax carbo</em></td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Ciconiiformes species</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Bubulcus ibis</em></td>
<td>*</td>
<td>+**</td>
</tr>
<tr>
<td><em>Egretta garzetta</em></td>
<td>*</td>
<td>ns</td>
</tr>
<tr>
<td><em>Egretta alba</em></td>
<td>+**</td>
<td>+**</td>
</tr>
<tr>
<td><em>Ardea cinerea</em></td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td><em>Ardea purpurea</em></td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td><em>Threskiornis aethiopicus</em></td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td><em>Platalea leucorodia</em></td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Anseriformes species</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Cygnus olor</em></td>
<td>ns</td>
<td>+**</td>
</tr>
<tr>
<td><em>Anas penelope</em></td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td><em>Anas strepera</em></td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td><em>Anas platyrhynchos</em></td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td><em>Anas acuta</em></td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td><em>Anas clypeata</em></td>
<td>ns</td>
<td>+**</td>
</tr>
<tr>
<td><em>Anas querquedula</em></td>
<td>*</td>
<td>ns</td>
</tr>
<tr>
<td><em>Anas crecca</em></td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td><em>Aythya ferina</em></td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td><em>Aythya fuligula</em></td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Gruiformes species</td>
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<td></td>
</tr>
<tr>
<td><em>Fulica atra</em></td>
<td>ns</td>
<td>+**</td>
</tr>
<tr>
<td>Charadriiformes species</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Himantopus himantopus</em></td>
<td>ns</td>
<td>+**</td>
</tr>
<tr>
<td><em>Charadrius dubius</em></td>
<td>+**</td>
<td>+*</td>
</tr>
<tr>
<td><em>Pluvialis apricaria</em></td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td><em>Vanellus vanellus</em></td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td><em>Calidris alpina</em></td>
<td>ns</td>
<td>+*</td>
</tr>
<tr>
<td><em>Philomachus pugnax</em></td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td><em>Limosa limosa</em></td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td><em>numenius phaeopus</em></td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td><em>Tringa totanus</em></td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td><em>Tringa nebularia</em></td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td><em>Actitis hypoleucus</em></td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td><em>Larus melanocephalus</em></td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td><em>Larus ridibundus</em></td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td><em>Larus minutus</em></td>
<td>+**</td>
<td>ns</td>
</tr>
<tr>
<td><em>Larus argentatus</em></td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td><em>Larus fuscus</em></td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td><em>Chlidonias niger</em></td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td><em>Chlidonias hybridus</em></td>
<td>ns</td>
<td>ns</td>
</tr>
</tbody>
</table>

a The “+” and “−” signs indicate the direction of the difference between two years. No test was performed for some species not recorded during phase 2.

b ns, Not significant.

0.05 < P < 0.01.

** P ≤ 0.01.
In January 1998 and 1999, ducks feeding on the hunted wet grasslands represented only 0.21% (25) and 0.16% (27) of the wintering population on the whole wetland, against 10.56% (1941) in January 2000 when hunting was prohibited (unpublished data). In February when hunting occurred, there were only 136, 46 and 227 ducks on the wet grasslands, respectively, in 1998, 1999 and 2000. The largest flocks were observed only and suddenly in March after the end of the hunting season. The increased attractiveness of the wet grasslands as feeding habitats which are subject to hunting. The pattern of use of flooding grasslands did not always correspond to taxonomy but to ecological responses of well-defined species assemblages. Morphological and behavioural adaptations like the tarsus length for Ciconiiformes or Charadriiformes (DuBow, 1996; Ntiamo-Aboit et al., 1998) or the neck length for dabbling ducks (Pöysä, 1983) and life history strategies like the diet composition and the foraging behaviour for instance for herons (Marion et al., 2000) are the likely mechanisms explaining variations in the use of the wet grasslands by birds according to suitability of feeding habitats.

The increased attractiveness of the wet grasslands as feeding habitats in 2000 for numerous Ciconiiformes is all the more true since the population size of these colonial species nesting in trees in the neighbouring floating peat fen has increased between years, notably for Egretta alba and Ardea cinerea (unpublished data). These long-legged herons are known to be favoured by high water levels in wetlands (Marion et al., 2000) and...
field observations indicated that particularly *Egretta alba* was often present in deep waters (about 40 cm).

In the present study, *Tringa totanus* and *Himantopus himantopus* were grouped with the summer migrant breeding Ciconiiformes. At low water levels, wet grasslands provide suitable habitats (Sanders, 1999). These two species and *Vanellus vanellus* were grouped with the summer migrant breeding *Vanellus vanellus* and *Himantopus himantopus* were grouped with the summer migrant breeding Ciconiiformes. At low water levels, wet grasslands provide suitable habitats (Sanders, 1999). These two species and *Vanellus vanellus* were grouped with the summer migrant breeding Ciconiiformes. At low water levels, wet grasslands provide suitable habitats (Sanders, 1999). These two species and *Vanellus vanellus* were grouped with the summer migrant breeding Ciconiiformes. At low water levels, wet grasslands provide suitable habitats (Sanders, 1999). These two species and *Vanellus vanellus* were grouped with the summer migrant breeding Ciconiiformes. At low water levels, wet grasslands provide suitable habitats (Sanders, 1999). These two species and *Vanellus vanellus*

4.3. Recommendations for management regime of wet grasslands for the waterbird community

Numerous studies have shown large changes in the use of wetlands by bird populations according to severe trends in water conditions, from total drought (Kushlan, 1986a; Catsadorakis et al., 1996; Sanders, 1999) to major flooding such as 2–5 m at Kerkin reservoir (Pyr-ovetsi and Papastergiadou, 1992; Crivelli et al., 1995). But when modest water level fluctuations occurred, the presence and pattern of many species at a site becomes less predictable (Elphick and Oring, 1998). The present study shows that, in relation to the semi-natural functioning of the ecosystem, it is essential to use appropriate management strategies to ensure and perhaps to enhance the value of the wet grassland system of the Lac de Grand-Lieu as feeding habitat for waterbirds. Any change in lake water regime needs to be monitored carefully in view of the rapid response of many species to the hydrological conditions.

The maintenance of a water regime close to that recorded in 2000 seems more favourable to the species of high conservation value (Table 4). A water level around 50 cm during winter until April ensured suitable conditions for large flocks of wintering and migrating Anseriformes. During the following months, the increased duration of a water level of less than 25 cm provided feeding areas for long-legged Ciconiiformes and also for short-legged waders. In this geographical area, the maintain of grasslands flooded until June is very important since numerous inland wet grasslands are exposed and the attractiveness of the wet grasslands of the Lac de Grand-Lieu is likely increased. In the same way, Fasola and Ruiz (1996 and literature cited therein) have shown the importance of rice fields in the Mediterranean Region as valuable replacements for lost natural habitats for a variety of waterbirds because of the long duration of flooding through winter and to a lesser extent as breeding sites.

Finally the water regime applied in 2000 for the Lac de Grand-Lieu favours early accessibility for livestock which is essential in maintaining the diversity of habi-

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**References**


