INTRODUCTION

Among the topics concerning the White Stork that require closer attention are the mechanisms by which the sizes of populations are regulated. In the 1970s and 1980s the species suffered a serious decline in numbers in many parts of its range; only in a few regions have White Stork populations shown significant long-term fluctuations or a tendency to increase in recent years (Profus 1993, 1994, Jakubiec & Guziak 1998, Peterson et al. 1999).

Intraspecific competition and its influence on reproduction in the White Stork population have been relatively well described by Wojciechowski & Ogrodowczyk (1978), Górski et al. (1980), Wojciechowski (1992), Wojciechowski & Markowski (1992) and Ptaszyk (1994). The evident competition observed in the last ten years is thought to be the result of a crisis of biotope conditions (Wojciechowski 1992, Wojciechowski & Markowski 1992).

Some authors consider food to be the deciding factor as regards breeding success, and hence, the trends in population size (e.g. Mrugasiewicz 1972, Górski et al. 1980, Profus 1986, Struwe & Thomsen 1991). Dallinga & Schoenmakers (1989) show that the changes in the numbers of storks in Europe since the 1950s have generally been related to food resources. In the Obra river valley (Western Poland), for example, the total numbers of fledglings produced in the local stork population were correlated with the density of the Common Vole Microtus arvalis (Tryjanowski & Kuźniak 2002).

The White Stork’s home range, its use of its foraging habitat, and the impact of the feeding habitat on dietary composition were investigated by Pinowska...
However, little attention has been paid to the biotope structure. Like other environmental factors, this can affect both the mechanisms of number regulation and the intensity of intraspecific competition. The study of this issue is addressed in the present paper.

STUDY AREA

Observations were carried out in part of the Kolno Upland (Jedwabne district, Łomża province, NE Poland) adjoining the Biebrza river valley and in part of the valley itself within the southern basin of the river. The study area included c. 2 km wide stretches of land on either side of the river, between the villages of Ruś — at the confluence of the Biebrza with the Narew — and Klimaszewnica.

The main part of the study area was situated in Kolno Upland on the western, elevated, riverside of Biebrza. It is a mosaic-like farmland landscape with several small villages, undeveloped agriculture on poor sandy soils. Main land use form include small arable fields with various crops, orchards and fellow land. Patches of woodland meadows, pastures and forests lie usually along the small tributaries of the Biebrza.

The eastern part of the study area included some villages and farmland but is mainly the Biebrza flood plain. Its vegetation consists of wet meadows (Molinio-Arrhenterea), some of which are mown for hay or grazed by horses and cattle, and of sedge moor (Caricetum). In places willow bushes (Salix sp.) grow among the sedges. In the river valley there are many ox-bow lakes and water-filled depressions. In spring, the flood plain of the Biebrza is inundated, in places up to a distance of c. 2 km from the river channel. The floodwaters recede late, usually in June sometimes even in early July. In a few places along the edge of the river valley there are small forests and peat bogs.

METHODS

The fieldwork was conducted in July of the years 1994–1997. 20 villages in 1994–1995 and 24 in 1996–1997, located on either side of the river and the area of valley were monitored.

During the censuses the location of nests, the number of occupants (parent birds and young, if any) and the breeding success was noted for each one. The international standard symbols (Schüz 1952, Jakubiec 1985) were used for describing the White Stork’s parameters of reproduction:

- HO — unoccupied nest,
- HE — nest occupied by one bird,
- HPa — nest occupied by a pair,
- HPo — nest occupied by a pair, no breeding success
- Hpm1–5 — nest with 1, 2...5 nestlings,
- JZG — number of nestlings in all nests,
- J Za — average number of nestlings in HPa type nests,
- JZm — average number of nestlings in Hpm type nests.

For all nests in 1996 and 1997, the following habitats were distinguished and mapped in an area of 1 km radius around the nests: 1) peat bog, wet meadows, 2) green crops, pastures, 3) root-crops, 4) cereal crops, 5) woodlands, 6) water bodies, 7) built-up areas and roads.

The 1-km radius territory established in this study seemed optimal for the analysis of the formulated problem, as the biotopes favourable to the White Stork were located close to the occupied sites and the study area was optimal for the species. Evidence for this was provided by the high reproduction parameters in the population (J Za > 2.3 and JZm > 2.5). For foraging, the birds most often penetrate the area close by the nest (Löhmer et al. 1980, Ożgo & Bogucki 1999). According to Ożgo & Bogucki (1999), the actual geometric centre of the White Stork’s feeding territory was some 400 m away from the nest; moreover, 53% of feeding areas were up to 800 m away. Alonso et al. (1994) showed that White Storks foraged mainly within a radius of 1300 m around the nest, and Dziewiati (1992) in Lower Saxony noted that 80% of foraging sites were located up to 1 km from the nest.

Depending on the type of the habitat, the distance of foraging sites from the nest can vary. Pfeifer (1989) showed that in habitats sub-optimal for the White Stork only 35% of foraging sites lay within 1 km of the nest. Similarly, Struwe & Thomsen (1992) recorded that 62% of stork feeding areas were situated within a radius of 2.5 km from the breeding colony. However, the mean breeding success of these populations was very low: J Za = 1.2–1.5. In optimal habitats, the stork’s feeding area lies much closer to the nesting sites (Dziewiati 1992, Alonso et al. 1994, Ożgo & Bogucki 1999).

To explain the level of breeding success as defined by the number of fledglings, the step-
wise linear multiple regression method was used (Sokal & Rohlf 1995). In the regression models the following characteristics were used as independent variables: the surface area (%) of wet meadows (P1), green crops (P2), root crops (P3), cereal crops (P4), woodlands (P5), water bodies (P6), built-up areas and roads in the vicinity of the nest (P7), year of studies (Year), distance to the nearest nest (Dist. 1), distance to the nearest nest with breeding success (Dist. 2). Additionally, the variables P1–P7 were inserted in the regression models in the logarithmic /ln (1+x)/, square and arc sin transformations, in order to find possible curvilinear relations besides the linear dependencies.

The General Regression Model was based on Mallow’s Cp value criterion for the best-subset procedures ensured with sigma restriction of variables representing predictors. The model was then selected to yield a minimum value of the criterion, or a value that was acceptably small. The logistic binary regression model was used to explain the relationship between the breeding success of the White Stork and the structure of habitats in nesting territories (Afifi & Clark 1990). One level (binary value 0) represents pairs without breeding success (HPo), the other one (binary value 1) nests with nestlings (HPm1–5).

The differences in the proportions of the specified habitat types within the territories between the 1996 and 1997 seasons, and between the different types of nests were tested by ANOVA models for the arc sin transformed data. The ANOVA were used to test the variability of the level of breeding success in relation to the distance of nests to the edge of the Biebrza valley.

All the calculations were performed using SPSS PC+ and STATISTICA 6.0 software.

### RESULTS

#### Characteristics of the population studied

62 White Stork nests were found in the area covered by the census in 1994, and 95 nests in 1996. Most of them were sited in built-up areas. In some villages particularly large numbers of nests (12–15) were clustered together. A very small number of nests had been constructed on trees or haystacks, a long way from the villages.

In this White Stork population, the numbers of nests occupied varied from year to year. As compared with 1994–1996, a somewhat lower proportion of nests in 1997 was occupied by pairs of birds (HPa) or by single storks (HE), and the proportion of unoccupied nests (HO) was higher (Table 1).

Broods with three (HPm3) nestlings made up the highest proportion of nests with breeding success (Table 2). In 1994 the proportions of HPm4 and HPm5 were high, while in 1995–1997 the proportion of broods with two (HPm2) nestlings among the nests with differing breeding success was also high (Table 2). In 1997 there were no nests with five offspring (HPm5); moreover, a remarkably low proportion of broods with four young (HPm4), and an increase in the frequency of nests with one nestling (HPm1) were observed (Table 2). This situation was reflected by the number of fledglings. The breeding success measured by the JZm and JZa indices was also higher in 1994–96 than in 1997 (Table 2).

The average breeding success of pairs with nests located at a distance of less than 100m to the nearest wet meadows in the river valley was higher in comparison with those pairs whose nest site was located farther away (ANOVA, F = 2.375, p = 0.022; Tukey test). Storks did indeed tend to

<table>
<thead>
<tr>
<th>Parameters</th>
<th>1994*</th>
<th>1995*</th>
<th>1996</th>
<th>1997</th>
<th>Mean per year</th>
</tr>
</thead>
<tbody>
<tr>
<td>% (n)</td>
<td>% (n)</td>
<td>% (n)</td>
<td>% (n)</td>
<td>% (n)</td>
<td></td>
</tr>
</tbody>
</table>

| Nests: Unoccupied (HO) | – | 10.0 (7) | 8.4 (8) | 13.1 (11) | 7.9 (6.5) |
| Occupied by one bird (HE) | 3.2 (2) | 1.43 (1) | 4.2 (4) | 1.2 (1) | 2.5 (2.9) |
| Occupied by a pair (HPa) | 96.8 (60) | 88.6 (62) | 87.4 (83) | 85.7 (72) | 89.6 (69.25) |
| Total number (HO + HPa + HE) | 62 | 70 | 95 | 84 | |

Breeding success:

| Nests occupied by a pair, no breeding success (HPo) | – | 5.7 (4) | 3.2 (3) | 4.8 (4) | 3.4 (2.75) |
| Nests with breeding success (HPm) | 96.8 (60) | 82.9 (58) | 84.2 (80) | 81.0 (68) | 86.2 (66.5) |

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nest close to the edge of the river valley (chi-square test: \( \chi^2 = 95.342, n = 122, df = 8, p < 0.001 \)). The average breeding success of pairs correlates significantly with the number of nests located at distances of up to 800 m between nest sites and the edge of the Biebrza valley (\( r = 0.955, df = 5, p = 0.011 \)) (Fig. 1–2).

Reproduction parameters in relation to the habitat structure

In 1996 and 1997 the greatest proportion of the nesting territories consisted of cereal crop, green crop and wet meadow habitats. Only a small part of the territories consisted of built-up areas and water bodies (Fig. 3). The variation in the percentages of these habitat types in the nesting territories between 1996 and 1997 was not statistically significant (ANOVA). However, the proportions of these habitat types did vary significantly between the nests (ANOVA models, \( F = 7.935 \) to \( 392.525, p < 0.001 \)).

The mean breeding success of stork pairs was significantly related to the distance from the nearest occupied nest (Fig. 4). Where the distances between two HPa nests were short (to 600 m), the mean numbers of fledglings were significantly lower than in the nests located at longer distances \( (y = 2.26 + 0.018x; R^2 = 0.03, df = 144, F = 4.93, p = 0.028) \). Where the distances of between 600 and 1100 m separated the nests, mean numbers of nestlings were smallest, and the dependence of breeding success on inter-nest distance was not significant. In that part of the population where the distances between pairs were greater than

Table 2. Productivity parameters of the White Stork population studied. Data from 24 (20*) villages.

<table>
<thead>
<tr>
<th></th>
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</thead>
<tbody>
<tr>
<td>Pairs with fledged young</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HPm1</td>
<td>1</td>
<td>4</td>
<td>3</td>
<td>6</td>
<td>3.5</td>
</tr>
<tr>
<td>HPm2</td>
<td>11</td>
<td>15</td>
<td>25</td>
<td>25</td>
<td>19.0</td>
</tr>
<tr>
<td>HPm3</td>
<td>25</td>
<td>26</td>
<td>37</td>
<td>32</td>
<td>30.0</td>
</tr>
<tr>
<td>HPm4</td>
<td>14</td>
<td>10</td>
<td>12</td>
<td>5</td>
<td>10.25</td>
</tr>
<tr>
<td>HPm5</td>
<td>6</td>
<td>3</td>
<td>3</td>
<td>–</td>
<td>3.0</td>
</tr>
<tr>
<td>Fledged young (JZG)</td>
<td>184</td>
<td>167</td>
<td>227</td>
<td>172</td>
<td>–</td>
</tr>
<tr>
<td>Young per pair (JZa)</td>
<td>3.06</td>
<td>2.69</td>
<td>2.73</td>
<td>2.39</td>
<td>2.72</td>
</tr>
<tr>
<td>Young per pair with fledged young (JZm)</td>
<td>3.06</td>
<td>2.88</td>
<td>2.84</td>
<td>2.53</td>
<td>2.83</td>
</tr>
</tbody>
</table>

Fig. 1. Relationship between breeding success (average number of fledglings) and distance between the nest sites and the edge of the river valley.

Fig. 2. Regression (solid line) of the breeding success (average number of fledglings per nest) on the distance between the nest site and the edge of the river valley. 95% confidence interval is indicated by dotted lines. The regression equation is: \( y = 2.8038 - 0.0025x + 0.000001x^2 \).
There was a significant positive correlation between the inter-nest distance and the number of fledglings ($y = -0.873 + 0.0024x$, $R^2 = 0.98$, df = 3, $F = 114.94$, $p = 0.002$). These relations demonstrate the effect of competition between pairs, probably in two different environments: 1) birds whose nests were located at short distances from one another inhabited the river; 2) the birds inhabiting the upland, where the river valley did not strongly influence the breeding success of pairs.

The correlation between breeding success and the habitat structure of the nesting territories was poor, as most nests were located in an optimal habitat. Generally, however, a significant positive correlation was found between the number of nestlings raised and the proportion of wet meadows and peat bogs in the nesting territories (Table 3). The breeding success of pairs with more than two nestlings was related to the area of water bodies in the nesting territories (Table 4). In territories

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**Table 3. Variability in the number of nestlings in nests explained by the best subset of multiple regression calculated using Mallow’s Cp value.**

<table>
<thead>
<tr>
<th>Effect</th>
<th>Parameter</th>
<th>SE</th>
<th>t</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Log (proportion of wet meadows)</td>
<td>0.24722</td>
<td>0.09836</td>
<td>2.513</td>
<td>0.0129</td>
</tr>
<tr>
<td>Log (proportion of low crops)</td>
<td>-0.45736</td>
<td>0.20199</td>
<td>-2.264</td>
<td>0.0248</td>
</tr>
<tr>
<td>Proportion of meadows ^ 2</td>
<td>-0.00051</td>
<td>0.00020</td>
<td>-2.584</td>
<td>0.0106</td>
</tr>
<tr>
<td>Proportion of high crops ^ 2</td>
<td>-0.00049</td>
<td>0.00018</td>
<td>-2.766</td>
<td>0.0063</td>
</tr>
<tr>
<td>constant</td>
<td>5.65558</td>
<td>1.20486</td>
<td>4.694</td>
<td>0.0001</td>
</tr>
</tbody>
</table>

**Table 4. Breeding success in relation to habitat structure of nesting territories.**

<table>
<thead>
<tr>
<th>Effect</th>
<th>b</th>
<th>SE of b</th>
<th>t</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model: pairs with &gt; 2 fledglings</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>proportion of water bodies</td>
<td>0.07880</td>
<td>0.02336</td>
<td>3.374</td>
<td>0.0011</td>
</tr>
<tr>
<td>constant</td>
<td>3.04137</td>
<td>0.08327</td>
<td>36.521</td>
<td>0.0001</td>
</tr>
<tr>
<td>Model: pairs with &lt; 3 fledglings</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>proportion of water bodies</td>
<td>0.03137</td>
<td>0.03252</td>
<td>0.966</td>
<td>0.3382</td>
</tr>
<tr>
<td>constant</td>
<td>1.45158</td>
<td>0.13748</td>
<td>10.559</td>
<td>0.0001</td>
</tr>
<tr>
<td>Model: pairs with &lt; 3 fledglings</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>proportion of wetlands</td>
<td>0.01568</td>
<td>0.00736</td>
<td>2.131</td>
<td>0.0368</td>
</tr>
<tr>
<td>constant</td>
<td>1.31117</td>
<td>0.14358</td>
<td>9.145</td>
<td>0.0001</td>
</tr>
</tbody>
</table>

Fig. 3. Average proportions of habitat types distinguished in nesting territories.

Fig. 4. Relationship between the average breeding success in two adjacent nests and the distances between nests.
of type HPm3-5 nests the proportion of water bodies was significantly higher in comparison with the territories of type HPm2 nests (ts = 2.144, df = 115, p = 0.0017, arc sin data transformation).

In the case of pairs with low breeding success (HPo + HPm1–2), there was no correlation, although the numbers of fledglings did correlate positively with the proportions of wetlands in the territories (Table 4). The territories of pairs without nestlings (HPo) cover a significantly small proportion of wetlands (8.10%) in comparison with the pairs with one nestling (HPm1) — 16.63%. The different proportions of wetlands in the types of nests compared were significant (ts = 2.009, df = 38, p = 0.026; arc sin data transformation). Results of logistic regression explaining the impact of habitat structure in nest territories on the breeding success showed significant relation between share of wetlands and breeding success (Table 5).

### DISCUSSION

The White Stork population inhabiting the study area has enjoyed a relatively high breeding success in comparison with other regions of Poland, especially in the last twenty years (e.g. Wojciechowski & Markowski 1992, Bogucki 1994a, Ptaszyk 1994, Indykiewicz et al. 1998). The average breeding success as measured by the JZm index was higher than the average for Central Europe (Profus 1991). The average value of the JZa index was distinctly higher than the expected value for a stable White Stork population (Wojciechowski 1992). In comparison with other regions of Poland (Profus 1991, Wojciechowski 1992, Bogucki 1994b), the population studied here was characterised by a higher and dominant proportion of HPm3-type broods. Exceptionally, the percentage of nests without nestlings (HPo) was lower than in other regions of Poland or Europe (Profus 1991).

The conglomerated distribution of the Biebrza valley population, with its distinct tendency towards nest concentration along the edge of the valley, and the high breeding success parameters of pairs inhabiting the terrain adjoining the edge of the valley, demonstrated that the area provided optimal conditions for reproduction in the White Stork population. The distribution of nests, and their associated territories, were spatially related to the distribution of certain habitat types able to provide abundant food for the storks. The largest concentrations of nests were located in villages lying near vast complexes of wet meadows, green crops, and pastures, and also in villages situated in the valleys of small rivers in the Biebrza catchment area. The habitat types specified above are commonly regarded as the most optimal feeding areas for the White Stork.

Ptaszyk (1994) stated that the density of breeding pairs of White Storks in the Wielkopolska region of Poland varied distinctly and depended, among other factors, upon the proportions of meadows or pastures. In areas with a low proportion of these habitats, densities were very low or storks did not breed at all. The highest densities were noted in valleys of large and medium-size rivers and in lake districts with abundant wet meadows, ponds and low peat bogs (Ptaszyk 1994). Indykiewicz (1998) demonstrated a significant relationship between the percentage of meadows and pastures in farmland and the number of breeding pairs in the Bydgoszcz region. Also Aunins et al. (2001) showed that on Latvian farmland the White Stork exhibits a distinct preference for habitats located close to river valleys.

Based on their observations of feeding White Storks in the Masuria (Mazury) region, Pinowski et al. (1991) showed that the habitats clearly preferred by this species for feeding are wet meadows, pastures and fields of root crops (vegetation height up to 40 cm). In Pomerania, Ożgo & Bogucki (1999) showed that the habitats visited most often in search of food were meadows, grassland and fields; male birds additionally frequented water bodies.

The relationships demonstrated by this study, variously distributed in groups of birds with different levels of breeding success, may be an
indicator of the non-homogeneity of the population investigated here. The effects of these diverse relationships very probably overlap in the two groups: 1) in the birds inhabiting the area along the edge of the Biebrza valley — the close proximity of the water-filled depressions exerted the greatest influence on breeding success; 2) in the birds whose nests were situated on the Kolno Upland, some considerable distance away from the valley’s edge, where the wet meadows lying close by the nests had a similar influence on breeding success.

ACKNOWLEDGMENTS

I wish to sincerely thank Dr. Zbigniew Wojciechowski and Dr. Tomasz Janiszewski (Łódź University) for interesting me in this problem, and their comments on this work. Many thanks also go to my colleagues Barbara Wasielska, Jolanta Osiewicz, Agnieszka Szwarc, Aneta Werner, Ewa Gardocka and Robert Gawroński for their very efficient assistance with the field work.

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STRESZCZENIE

[Struktura środowiskowa terytoriów gniazdowych i parametry rozrodu bociana białego — przykład z Wysoczyzny Kolneńskiej i doliny Biebrzy]  
Badania prowadzono w latach 1994–1997 na części Wysoczyzny Kolneńskiej (powiat Jedwabne) przylegającej do doliny Biebrzy oraz na obszarze tej doliny w pasie ok. 2 km szerokości. Kontrolowano od 62 do 95 gniazdnocznikowi i powierzchni zbiorników i cieków wodnych (Tab. 3 i 4). Związki te odmienne układały się w różnych grupach ptaków wyróżniających z uwagi na wielkość sukcesu lęgowego mogły wskazywać na niejednorodność badanej populacji. Wyróżniają się w niej dwie grupy — ptaki zasiedlające obszar krawędziowy doliny Biebrzy i te, których gniazda położone były na terenie wyżyny w znacznej odległości od krawędzi doliny.

Związek między przeciętną liczbą odchowywanych młodych a udziałem powierzchni podmokłych ląk i powierzchni zbiorników i cieków wodnych w rewirach bociana był wyraźnie zaznaczyony jedynie w grupie ptaków o wysokim sukcesie rozrodczym (HPm3–5). W całości populacji jak również u par z mniejszą liczbą odchowywanych młodych zależności takiej nie stwierdzono (Tab. 4). Terytoria par bez sukcesu lęgowego (HPo), miały w rewirach istotnie mniejszy udział terenów podmokłych.