TIME BUDGET, HABITAT USE AND BREEDING SUCCESS OF WHITE STORKS CICONIA CICONIA UNDER VARIABLE FORAGING CONDITIONS DURING THE BREEDING SEASON IN SWITZERLAND

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Following its extinction in 1950, the White Stork Ciconia ciconia was reintroduced to Switzerland. We analysed time budget, habitat use and breeding success of 28 breeding pairs at five sites in 1994. At two sites the adults were given extra food daily (SF), at the others no supplementary food was provided (NSF). During the first 20 days of life of the young, at least one adult stayed at the nest almost all the time. Later, adults left their young unguarded for increasing periods, NSF for longer periods than SF. Feeding rates of the young were higher in SF than in NSF. Outside the nest, SF spent more time foraging and less time flying than NSF. Foraging distances were larger in NSF than in SF. Overall breeding success was generally low in Switzerland in 1994 (1.2 versus 1.7 young per breeding pair 1965-98), mainly due to bad weather, and it did not differ significantly between NSF and SF. Furthermore, size and weight of the young did not differ between NSF and SF. Breeding success did not differ significantly between NSF and SF sites in years with an high overall reproductive output (1992, 1993). We conclude that surplus food did not enhance breeding output. It is yet unclear whether a long term breeding success of 1.7 young per breeding pair (1965-98) is sufficient to maintain a stable population.

Key words: Ciconia ciconia – foraging – breeding success – breeding population – supplementary feeding

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INTRODUCTION

In the 20th century, the population of the White Stork Ciconia ciconia sharply decreased, particularly in the western part of its range (review in Rheinwald et al. 1989). Census data document the decline of the native Swiss population from 140 breeding pairs in 1900 to its extinction in 1950 (Glut von Blotzheim 1962; Bloesch 1958, 1980); the causes of which are unknown. The multiple causes of the general decline invoke excess mortality during migration by collision and electrocution by power lines, hunting, droughts and locust control in wintering areas, and habitat loss and
climatic factors in the breeding areas (reviews in Dallinga & Schoenmakers 1987, 1989; Kanyamibwa et al. 1990; Bairlein 1991, Biber et al. 1995; Schulz 1999). White Storks are found in a wide range of open habitats with dry or wet grasslands, often near lakes or rivers. The majority of the western European population breeds in farmland, mostly below 700 m asl. (Aráujo & Biber 1997). The effect of habitat deterioration on population parameters of the White Stork during the phase of declining populations has been analysed (Dallinga & Schoenmakers 1987, 1989). Since the mid 1980s, the species has again increased in various parts of its range (Schulz 1995, 1999), especially in Spain (Bernis 1995; Marti 1999). In Switzerland, as in neighbouring France and Germany, and in The Netherlands, this increase is, at least for an important part, the result of reintroduction (Biber et al. 1995; Aráujo & Biber 1997). However, the positive trend did not go along with any obvious improvement of foraging habitats.

In 1948, just before the extinction of the population, a reintroduction project was launched in Switzerland with the goal of re-establishing the population in its former distribution. Young storks were imported first from different European countries and later in larger numbers from NW Africa. These young birds were raised by hand at the stork breeding centre Altreu and released once they were able to fly. Most of them disappeared from the rearing place after fledging and did not return. In order to avoid losses during dispersal and migration, in a second phase of the reintroduction programme, fledglings were kept in captivity until they reached sexual maturity at the age of normally three to four years (Bloesch 1980). The first breeding of a free-flying pair originating from the reintroduction project took place in 1960. Subsequently, more reintroduction centres were founded in areas regarded as suitable in Switzerland and neighbouring NE France and SW Germany, in The Netherlands and other countries. Since 1960 the number of free-ranging breeding pairs in Switzerland has increased, first slowly and then steeply. By 1990 the White Stork population had again reached the level of 1900. Having been kept in captivity for the first 1-3 years of their life and, therefore, prevented from migrating, most adults released in the wild afterwards stayed all year long in the breeding area, where they were provided with additional food. Originally, supplementary feeding was intended to bind the adults to the reintroduction centres; it was also argued that extra food was needed to ensure breeding success. Since the 1980s supplementary feeding has progressively been stopped at a growing number of breeding stations.

The first aim of the present study was to analyse habitat use and time budget of White Storks breeding in intensively cultivated farmland, as these sub-optimal habitats were thought to prevail in Switzerland, for comparison with the traits of populations studied in optimal habitats, i.e. extensively used grassland with wetland. The second aim was to assess possible positive effects of supplementary food on nest-guarding and foraging time patterns, feeding frequencies, foraging range, relative use of foraging habitats, breeding success and physical condition of nestlings just before fledging, of White Storks breeding under the given experimental conditions, in order to contribute to the decision on whether the supply of extra food as a management measure of the Swiss population is needed or not.

**STUDY SITES, MATERIAL AND METHODS**

**Study sites**

The field study was carried out in 1994, covering five groups of storks with variable conditions as to the provision with supplementary food in two regions Wynau and Zurich in central and northern Switzerland (Fig. 1). Altreu (A; 430 m asl) is the main centre of the White Stork reintroduction project in Switzerland. Seven pairs were selected (for easy access to the nests) out of the 48 pairs breeding in the village. Supplementary food (SF; mice, rats, fish and small chicken) was delivered near the nests daily at approximately the same time in
the evening. In Staad (S; 430 m), at four km distance from Altreu, all seven breeding pairs were surveyed; no supplementary food (NSF) was provided there. Grossaffoltern (G; 510 m; NSF; at 16 km distance from Altreu and 13 km from Staad) had five pairs, all were surveyed. At Hombrechtikon (H; 507 m; NSF) and Oetwil (O; 550 m; SF), 4 km apart from each other, five pairs out of seven were randomly selected in the study, the others were checked for breeding success only. At Oetwil, supplementary food was provided every day at variable times.

All breeding sites are surrounded by arable land, meadows and pastures. The productive soils are generally intensively cultivated (wheat, rye, barley and oats, turnip and potatoes, rape and maize). Most grasslands are nutrient-rich meadows. Habitats were mapped and their area calculated within a one km radius around the breeding sites. The average areas of habitat categories differed between sites. All but one site included only very small natural areas like wetlands. In Hombrechtikon the nests were on a farm by a small lake surrounded by a marsh with reed beds and sedges which were partly cut during the storks' breeding season.

In the result section, we give median values if data distributions were skewed. Weather data, i.e. temperature and rainfall, were obtained from two meteorological stations: Wynau meteorological station is about 40 km from Altreu, Staad and Grossaffoltern, and Zurich meteorological station is about 20 km from Oetwil and Hombrechtikon (from archives of the Swiss Meteorological Institute, Zurich 1992-1995).

**Observation method**

Each pair was surveyed once during the first 20 days of life of the young, once during the second and once during the third 20-day period (young storks leave the nest for the first time at the age of 54 - 70 days, Hancock *et al.* 1992). The activity of each pair was recorded during three different daytime periods (morning, midday, evening) on different days. The duration of an observation session was three hours at sites A, S and G, and four hours at O and H. During each observation session, both parents were followed by two observers who communicated by walkie-talkies; one recorded activities at or near the nest, while the other followed the storks by bicycle or by car when they flew off, and recorded their activities in foraging habitats. At site G only one observer alternately watched the birds at the nest and in the

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**Fig. 1.** Map of Switzerland with study areas in the region of Wynau (A = Altreu, G = Grossaffoltern, S = Staad) and Zurich (H = Hombrechtikon, O = Oetwil). Area above 600 meters asl shaded dark.
field. The field study was performed by Lionel Maumary and Laurent Vallotton at sites A and S, by Isabelle Steiner at site G and by Martin Moritz and David Schmid at sites H and O.

At the nest, the duration of nestguarding (presence of one or both parents on the nest or absence) was measured with a stop-watch and food provisioning events (regurgitating food on the nest) were recorded. The storks' landing spots after they had left the nest or moved from one site or habitat to another were recorded on a map (1: 25 000) on which the shortest distance to their nests was measured. Used foraging habitats (arable land, grassland, wetland, others), height of vegetation (4 categories: < 10 cm, 10 - 20 cm, 21 - 50 cm, > 50 cm) and farming activities (ploughing, spreading of manure, mowing, etc.) were recorded. The duration of all stork activities (in flight, foraging, resting) was measured with a stop-watch. Foraging was defined as the time a stork was pecking, walking or waiting in a hunting position (head and neck stretched forward). Resting was defined as the stork being immobile in a resting position (neck curved and head above back).

Relative habitat use of foraging storks was assessed by recording (a) the numbers of landings at foraging sites or moves on foot from one habitat type to another, and (b) the time spent foraging in a place until flying back to the nest or moving to another site or habitat. We compared the proportion of time spent foraging in different habitat types with the availability of these habitat types within a 1 km range around the nest. Prey items were counted and classified according to the following prey types and size categories: earthworms (Lumbricidae) of any length; prey other than worms: small (< 5 cm), large (> 5 cm); unknown (swallowing movement observed but prey type unidentified). No investigations on prey availability were performed.

The number of nestlings was checked daily or every second day from hatching of the first young to fledging. Breeding success is expressed as the number of fledglings per pair. The number of fledged young in relation to the number of hatched nestlings was defined as survival rate of nestlings. Body mass, winglength and length of tarsometatarsus of nestlings were measured (methods described in Svensson 1992) when the young were ringed at the age of about 45 days.

RESULTS

Time budget

During the first 20 days after hatching, the nestlings in all stork sites were guarded by one or both parents throughout the full observation time in 87% of all observation sessions (n = 74, 28 stork pairs, Fig. 2A). Overall, in 18.3% of observation time (median) both parents were at the nest together. Maximum time a brood was left unguarded was 27 minutes in three hours in one case (i.e. 15% of this 180 min. observation session). In the age class 21-40 days, the brood was sometimes left alone for slightly longer periods, but still in 87% of all observation sessions at least one adult was present at the nest during the full observation time. The median duration with both parents present decreased to 11.9% of observation time (n = 74, 24 pairs, Fig. 2B). Chicks older than 40 days were left alone for significantly longer periods (median 15.3% of the observation duration; n = 78, 23 stork pairs, Fig. 2C). In a few cases, especially when the young were about to leave the nest, they remained unguarded for as long as three to four hours. The median time both adults stayed at the nest together decreased sharply to 1.1% of observation time. But even then at least one of the parents was present on the nest during the full duration of observation time in 76% of the cases; the nest-guarding parent usually waited for its mate to come back before flying off. While there was very little variation between sites in the first and second age-class, significant differences in nest guarding appeared in the third nestling age-class (Kruskal-Wallis test: $H_{4,78} = 15.2$, $P < 0.005$, Fig. 2C). In particular, at sites Altreu and Oetwil with supplementary food, the proportion of time both parents stayed at the nest was higher and the percentage of time no adult was present
In three study sites it was difficult to follow adult storks in the field for topographical reasons. We, therefore, consider only the two sites Altreu and Staad where the storks' position was known in 94% and 100% of time, respectively. Their activity could be identified during 85% and 88% of total observation time (A: 58 observation sessions, 7 stork pairs; S: 54 observation sessions, 7 pairs). Main activities outside the nest were foraging (means 68% and 51% of the time in A and S, respectively) and flying (means 12% and 25%). During the rest of the time, the storks were resting (10% and 12%) or their activity was unknown (10% and 12%). There was a significant difference in the storks' time budget between the two sites: at A with access to supplementary food the adults spent more time foraging than at S (median 80% versus 60%); on the other hand, NSF spent more time in flight (median 16% versus 6%; Kruskal-Wallis test: $H = 9.8, P < 0.005$). The difference was largest in the second and third age-class in the evening, when supplementary food was delivered to the storks in A and part of the adults from S flew to A (4 km one way) to get their share.

The overall mean feeding rate was $0.73 \pm 0.51$ provisioning per hour ($n = 226$; median = 0.67). Maximum duration of an observation session without any feeding was 243 minutes; maximum observed provisioning rate was 7 feedings in 180 minutes. Feeding rates differed significantly between sites (Kruskal-Wallis test: $H_{4,146} = 13.7, P < 0.01$; for pooled morning and midday records, excluding evening records, see below). This difference appears to be mainly due to the difference between sites A and S (Fig. 3). Provisioning frequencies increased significantly with brood-size (Kruskal-Wallis test: $H_{3,225} = 38.6, P < 0.001$; Fig. 4), but did not change significantly with nestling age-classes or time of the day, except for one case: provisioning rates were much higher in the evening at site A when extra food was delivered (mean provisioning rate 1.2 per hour, median 1.0) than in the morning and at midday (means 0.7 and 0.9, median 0.67 in both cases).
Table 1. Relative habitat use of White Storks within a 1 km range around their nests at the five study sites (excluding feeding on supplementary food).

<table>
<thead>
<tr>
<th>Site</th>
<th>Suppl. food</th>
<th>Grassland</th>
<th>Arable land</th>
<th>Wetland</th>
<th>Others</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>records n</td>
<td>records (%)</td>
<td>avail (%)</td>
<td>records (%)</td>
<td>avail (%)</td>
</tr>
<tr>
<td>Altreu</td>
<td>yes</td>
<td>155</td>
<td>51.0</td>
<td>18.0</td>
<td>40.0</td>
</tr>
<tr>
<td>Staad</td>
<td>no</td>
<td>189</td>
<td>57.1</td>
<td>24.0</td>
<td>31.2</td>
</tr>
<tr>
<td>Grossaffoltern</td>
<td>no</td>
<td>153</td>
<td>58.8</td>
<td>32.0</td>
<td>29.4</td>
</tr>
<tr>
<td>Hombrechtikon</td>
<td>no</td>
<td>291</td>
<td>70.5</td>
<td>57.0</td>
<td>7.2</td>
</tr>
<tr>
<td>Oetwil</td>
<td>yes</td>
<td>230</td>
<td>72.2</td>
<td>36.5</td>
<td>17.4</td>
</tr>
</tbody>
</table>

Table 2. Numbers of foraging records in relation to vegetation height in foraging habitats. All records from all sites and from total foraging range are used.

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Records</th>
<th>Height of Vegetation (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>&lt;10 (%)</td>
</tr>
<tr>
<td>Meadows</td>
<td>607</td>
<td>59</td>
</tr>
<tr>
<td>Pasture</td>
<td>129</td>
<td>40</td>
</tr>
<tr>
<td>Arable land</td>
<td>250</td>
<td>80</td>
</tr>
<tr>
<td>Wetlands</td>
<td>67</td>
<td>2</td>
</tr>
</tbody>
</table>

Foraging

A total of 1384 records of distances to foraging sites were analysed. Excluding visits to supplementary feeding places in sites A and O (SF), the median distance for all pairs was 380 m ($n = 1159$; maximum distance was 4500 m), and 88% of records were within a 1 km radius around the nests. Foraging distances varied significantly between sites (Kruskal-Wallis test: $H_{4,1156} = 50.0, P < 0.001$, excluding foraging records from supplementary feeding places). Median distances were lower in SF sites A and O (300 and 284 m respectively, excluding visits to supplementary food at the breeding sites) than in NSF sites (650, 600 and 350 m respectively in sites S, G and H).

Including records from supplementary food reduced the median distance to 30 m in site A (49% of 368 records within 20 m from the nest), where food was delivered every evening. At the other SF site O, median distance did not differ.
excluding foraging on supplementary food, more than half of the records were from meadows and pastures which covered about one third of the total surface within a 1 km radius around the nests (Table 1). Arable land was used below its availability, except for sites H and O, where it covered a small part of the total area only. Wetlands were used as available. Throughout the breeding season, the quality of potential foraging sites changed due to plant growth and farming activities. These changes were not mapped systematically; thus, no comparisons with the available area were possible. However, during ploughing, mowing or spreading manure, storks quickly arrived to take advantage of the food that was temporarily made accessible by machines. Most foraging took place in low vegetation (< 10 cm; Table 2); tall vegetation was usually avoided, except for wetlands.

The possibilities to identify food items differed with site, habitat and topographic features (e.g., between 0 and 22% unidentified prey items; Table 3). Prey of small size accounted for about half of the items taken, with a minimum of 40% in site A and a maximum of 62% in site S. The other half was made up of worms (Table 3). Large prey items were taken in negligible numbers at all sites, except for fish, mice and small chicken delivered at feeding places.

**Breeding success**

The average number of fledglings per breeding pair and the nestling survival rate did not dif-

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**Table 3.** Total numbers of prey items taken during total recording time (excluding supplementary food). Prey categories: small = up to 5 cm; worms = usually earthworms; large = > 5 cm; undet. = undetermined prey, only swallowing movement of the storks recorded.

<table>
<thead>
<tr>
<th>Site</th>
<th>Suppl food</th>
<th>small</th>
<th>worms</th>
<th>large</th>
<th>undet.</th>
<th>total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Altreu</td>
<td>yes</td>
<td>1420</td>
<td>2103</td>
<td>2</td>
<td>0</td>
<td>3525</td>
</tr>
<tr>
<td>Staad</td>
<td>no</td>
<td>3291</td>
<td>2047</td>
<td>2</td>
<td>0</td>
<td>5340</td>
</tr>
<tr>
<td>Grossaffoltern</td>
<td>no</td>
<td>3590</td>
<td>2492</td>
<td>9</td>
<td>167</td>
<td>6258</td>
</tr>
<tr>
<td>Hombrechtikon</td>
<td>no</td>
<td>3479</td>
<td>1950</td>
<td>12</td>
<td>1516</td>
<td>6957</td>
</tr>
<tr>
<td>Oetwil</td>
<td>yes</td>
<td>3523</td>
<td>2284</td>
<td>9</td>
<td>873</td>
<td>6689</td>
</tr>
</tbody>
</table>
were better years both with respect to breeding success and weather. Except for Grossaffoltern and Hombrechtikon in 1992 and 1993, the breeding success was below 2.0 y bp\(^{-1}\) in all colonies (Table 5). Number of fledged young was positively correlated with temperature in May (Spearman \(R = 0.73, n = 20, P < 0.001\)) and negatively with precipitation in May (Spearman \(R = -0.55, n = 20, P < 0.02;\) Table 5).

We compared breeding success before the extinction of the White Stork, and after the reintroduction (Fig. 5): storks had a significantly higher breeding success between 1929-48 (mean ± SD; 2.3 ± 0.5 young per breeding pair (y bp\(^{-1}\)), range 1.5 - 3.3 y bp\(^{-1}\), \(n = 20\) years) than between 1965-98 (1.7 ± 0.6 y bp\(^{-1}\), range 0.4 - 3.3 y bp\(^{-1}\), \(n = 34\) years; \(t\)-test: \(t_{52} = 3.7, P < 0.001\)). Furthermore, breeding pairs successfully rearing young had a higher output of young before extinction (data from 1934-48; 3.3 ± 0.4 y bp\(^{-1}\)) than in the 1990s (1990-98; 2.4 ± 0.5 y bp\(^{-1}\); \(t\)-test: \(t_{22} = 4.7, P < 0.001\)).

**Condition of nestlings**

18 nestlings from 12 SF nests were compared with 19 nestlings from 13 NSF nests. The youngest nestling was 40 days old, the oldest 54 at the time they were measured (median age: 44 days in SF and 46 days in NSF, Mann-Whitney \(U\)-test, \(Z = 1.50, n.s.\)). Body mass, wing length and length of tarso-metatarsus did not differ significantly between the two groups: body mass was 3248 ± 388 g (mean ± SD) for SF nestlings and 3087 ± 634 g for NSF nestlings (\(U\)-test, \(Z = 0.32, n.s.\)), tarso-metatarsus length was 210 ± 23 mm and 201 ± 33 mm, (\(Z = 0.27, n.s.\)), and wing length was 384 ± 56 mm and 389 ± 62 mm (\(z = 0.10, n.s.\)).

**DISCUSSION**

**Time budget**

The overall daytime activity pattern in our study is similar to that described by Böhning-Gaese (1992) and Lakeberg (1995): about 50 to 70% resting, including the time spent at the nest and the
Table 4. Breeding success at the five study sites in 1994. $HPa =$ total number of surveyed breeding pairs (= total number of breeding pairs per site, except for Altreu, where only the seven study pairs were considered out of the total 48 breeding pairs); $HPm =$ total number of breeding pairs with fledged young; $JZa =$ number of fledglings per breeding pair; $JZm =$ number of fledglings per successful breeding pair; Survival (%) = fledged young per hatched nestling.

<table>
<thead>
<tr>
<th>Sites</th>
<th>Suppl. food</th>
<th>$HPa$</th>
<th>$HPm$</th>
<th>hatched</th>
<th>fledged</th>
<th>$JZa$</th>
<th>$JZm$</th>
<th>Survival (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Altreu</td>
<td>yes</td>
<td>7</td>
<td>6</td>
<td>26</td>
<td>12</td>
<td>1.7</td>
<td>2.0</td>
<td>46</td>
</tr>
<tr>
<td>Oetwil</td>
<td>yes</td>
<td>7</td>
<td>4</td>
<td>12</td>
<td>4</td>
<td>0.6</td>
<td>1.0</td>
<td>33</td>
</tr>
<tr>
<td>Staad</td>
<td>no</td>
<td>7</td>
<td>6</td>
<td>21</td>
<td>11</td>
<td>1.6</td>
<td>1.8</td>
<td>52</td>
</tr>
<tr>
<td>Grossaffoltern</td>
<td>no</td>
<td>5</td>
<td>3</td>
<td>16</td>
<td>5</td>
<td>1.0</td>
<td>1.7</td>
<td>31</td>
</tr>
<tr>
<td>Hombrechtikon</td>
<td>no</td>
<td>7</td>
<td>4</td>
<td>25</td>
<td>6</td>
<td>0.9</td>
<td>1.5</td>
<td>24</td>
</tr>
</tbody>
</table>

Sites with suppl. food:
- Altreu: $7 \times \text{yes} = 14$
- Oetwil: $7 \times \text{yes} = 10$
- Staad: $7 \times \text{no} = 62$
- Grossaffoltern: $5 \times \text{no} = 22$
- Hombrechtikon: $7 \times \text{no} = 13$

Sites without suppl. food:
- Altreu: $7 \times \text{no} = 19$
- Oetwil: $7 \times \text{yes} = 13$
- Staad: $7 \times \text{no} = 62$
- Grossaffoltern: $5 \times \text{no} = 22$
- Hombrechtikon: $7 \times \text{no} = 13$

Table 5. Breeding success at the five study sites, 1992 to 1995 in comparison with monthly mean temperatures ($°C$) and sum of precipitation (mm) for May. Meteorological stations: Wynau, about 40 km from Altreu, Staad and Grossaffoltern; Zurich, about 20 km from Oetwil and Hombrechtikon (from archives of the Swiss Meteorological Institute, Zurich 1992 - 1995). $JZa =$ number of fledged young per breeding pair; number of breeding pairs are mentioned in brackets.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Altreu</td>
<td>yes</td>
<td>1.5</td>
<td>(47)</td>
<td>1.7</td>
<td>(45)</td>
</tr>
<tr>
<td>Staad</td>
<td>no</td>
<td>1.9</td>
<td>(12)</td>
<td>1.5</td>
<td>(6)</td>
</tr>
<tr>
<td>Grossaffoltern</td>
<td>no</td>
<td>2.7</td>
<td>(3)</td>
<td>3.0</td>
<td>(3)</td>
</tr>
<tr>
<td>Mean temperature Wynau ($°C$)</td>
<td></td>
<td>12.8</td>
<td></td>
<td>13.5</td>
<td></td>
</tr>
<tr>
<td>Mean of precipitation Wynau (mm)</td>
<td></td>
<td>80</td>
<td></td>
<td>93</td>
<td></td>
</tr>
<tr>
<td>Hombrechtikon</td>
<td>no</td>
<td>3.3</td>
<td>(6)</td>
<td>2.0</td>
<td>(7)</td>
</tr>
<tr>
<td>Oetwil</td>
<td>yes</td>
<td>1.0</td>
<td>(3)</td>
<td>1.1</td>
<td>(7)</td>
</tr>
<tr>
<td>Mean temperature Zurich ($°C$)</td>
<td></td>
<td>12.8</td>
<td></td>
<td>14</td>
<td></td>
</tr>
<tr>
<td>Mean of precipitation Zurich (mm)</td>
<td></td>
<td>78</td>
<td></td>
<td>113</td>
<td></td>
</tr>
</tbody>
</table>
time resting in the field, and 30 to 50% foraging including the time spent in flight.

The fact that during the first 20 days of life of the nestlings at least one parent stayed on the nest nearly all the time in both SF and NSF fits general knowledge (e.g. Hancock et al. 1992), whereas the time both parents remain at the nest together is poorly documented (4.5 and 1.5 hours per day, in two pairs, Böhning-Gaese 1992). The shift in the adults' activity from predominantly nest guarding to more foraging as the young grow larger has been described by several authors (e.g. Löhmer et al. 1980; Struwe & Thomsen 1991). The lack of any difference in nest guarding and food searching time between NSF and SF during the first 20 days may be explained by the fact that supplementary food consisted of relatively large items (mice, rats, fish, small chicken) which are inadequate for small chicks; thus, both groups had to gather small prey items in the fields.

Food provisioning rates as observed in the present study are in the same range as for other populations of White Storks in N Germany (0.5, Struwe & Thomsen 1991) and Spain (about 0.5, Tortosa & Redondo 1992); Lakeberg (1995) recorded between 9 and 16 provisionings per day (approximately 0.5 - 1 provisioning per hour). A positive correlation of provisioning rate with the number of young in the nest, as found in our study, was reported by Schulz (1989), Struwe & Thomsen (1991) and Tortosa & Redondo (1992).

The provisioning rate is influenced by the quality of foraging habitats (Struwe & Thomsen 1991) and by the distance of these habitats from the nest. In this respect, the artificial feeding places are optimal and, accordingly, the highest provisioning rates in SF were recorded in the evening when supplementary food was provided during a short time. However, provisioning rate was also higher in SF than NSF when considering morning and midday records only, possibly as a consequence of shorter foraging flights (see below).

**Foraging**

Foraging distances were in the same range as described in other studies, e.g. for floodplains of the river Elbe ('Elbtalauen') (Niedersachsen, Germany: 64% within 1000 m, maximum 2.3 km, n = 1355, Dziewiaty 1992) or in Save-Auen, Croatia (mostly within 1 km, maximum 2 to 3 km, Schneider 1988); according to the high breeding success, these two regions offer optimal habitats. For central Spain, Alonso et al. (1994) report a mean foraging distance of 1.3 km with a maximum distance of 12.5 km from the nest site. In general, foraging distances and home ranges are highly variable: maximum distances in central and northern Europe lie between one and eleven km, home ranges are between 100 and 3500 ha (review in Lakeberg 1995). Foraging distances found in our study indicate home ranges of mainly less than 1000 ha, close to values from optimal habitats. Excluding foraging on supplementary food, median distances were still significantly shorter in SF than in NSF, suggesting that the storks at SF sites were able to minimise their flight expenditure.

**Foraging, habitat use and diet**

Preferred feeding habitats in Europe are dry or wet meadows (Carrascal et al. 1993; Dziewiaty 1992). On the breeding grounds in Switzerland, intensively cultivated farmland is the rule, and regularly manured grassland is most often used by storks for foraging. Wet meadows are rare and temporary. Grassland was also the predominant foraging habitat in most other studies: Niedersachsen, Germany (74 - 85% of landings, Dziewiaty 1992, 1994), Oberschwaben, Germany (> 95% of foraging time spent on grassland which covered 11 - 18% of the study area, Böhning-Gaese 1992), Sievershausen, Germany (Löhmer et al. 1980) and Poland (Pinowska & Pinowski 1989). Alonso et al. (1991) showed that foraging habitat preferences depend on prey density and accessibility. The latter is influenced by vegetation height and density. Short vegetation and shortly mown meadows are favoured by foraging storks in most studies.

Wetlands other than wet meadows are rather little used, even in regions with large natural wetlands like the floodplains of the 'Elbtalauen' (Dziewiaty 1992). Wetlands were not preferably exploited in our study, in spite of the abundance
of frogs, like in site H, perhaps because the vegetation density and water depth inhibited free access to this otherwise profitable prey. Thomsen & Struwe (1994) showed that amphibians are an important and predictable food source in N Germany when meadows dry out in late spring.

The striking point in the storks’ diet in our study was the near absence of vertebrate prey, such as voles, that are often mentioned as an important prey, e.g. by Creutz (1988), who underlines the importance of rodent abundance as a factor influencing breeding success of White Storks. The contribution of voles to the diet of the White Stork is highly variable from year to year in the same region: e.g. 70% of total prey mass in one year and less than 5% in the following year on the same study plot in northern Germany (Thomsen & Struwe 1994; Thomsen 1995). In another four-year study in S Germany, rodents accounted for less than 5% of total prey biomass in the minimum year and almost 90% in the maximum year (Lakeberg 1995). According to Sackl (1987), vertebrates are only profitable prey at high densities because the specific hunting method ‘wait and peck’ is more time consuming and less efficient than the “walk and peck“ method used for invertebrates. However, 3% vertebrate prey by number may contribute 61% of prey mass (Thomsen & Struwe 1994). Vertebrate prey may make up as much as 25% of prey numbers (Pinowska & Pinowski 1989). In other studies earthworms contributed up to 90% of prey items (Württemberg, Germany, Hornberger 1953) or up to 84% of total prey mass (S Germany, Lakeberg 1995). In the Elbe floodplains (Niedersachsen, Germany), known as holding one of the ‘largest’ White Stork populations, earthworms were the main prey in spring; only 7% of 3212 prey items were vertebrates, most of them small rodents (Dziewiaty 1992). In Central Balkan, another region with optimal White Stork habitats, earthworms form an important part of the diet of nestling during the first 20 days of life (Muzinic & Rasajski 1992). The mass proportion of vertebrates rose from 15% in April to more than 90% in July in N Germany (Struve & Thomsen 1991).

Breeding success and physical condition of the young

Burnhauser (1963) suggested that a breeding success of 2 young per breeding pair (y bp\(^{-1}\)) and year is sufficient to maintain a stable population; according to Bairlein & Zink (1979) 2.8 y bp\(^{-1}\) are required, given an adult mortality of 24% per year. However, these values have to be taken with caution: the last c. 10 pairs of the White Storks breeding in Switzerland had a breeding success of 2.3 y bp\(^{-1}\) and this did not halt the decline to extinction by 1950. Obviously other factors, such as survival during migration and in the winter quarters, but also population size and density may affect population dynamics. After reintroduction in the early 1960s, the overall breeding success of the Swiss White Stork population was about 1.7 y bp\(^{-1}\), with a considerable variation from year to year. During our study in 1994, it was rather poor with 1.2 y bp\(^{-1}\). Therefore, it remains an open question whether the breeding success of the local Swiss Stork population is sufficient to maintain a stable population surviving in the future. Analyses of adult and juvenile survival are hardly needed to tackle this question.

The long-term breeding success in Switzerland is relatively low compared to other European areas, with an average of about 2 y bp\(^{-1}\) (range 0.8 to 3.4 y bp\(^{-1}\), Bauer & Glutz von Blotzheim 1966, and 1.5 to 2.8 y bp\(^{-1}\), Bezzel 1985). The long-term average in Bergenhusen, N Germany, is 1.5 y bp\(^{-1}\) (Struve & Thomsen 1991) and 2.8 y bp\(^{-1}\) in the Save-Auen in Croatia (Schneider 1988).

The factors influencing breeding success of the Swiss population are poorly understood, although weather has been shown to play a role. Most of the nestling losses occurred during two periods of wet and cold weather. Critical periods are when the young are only a few days old when thermo-regulation is still incomplete (O’Connor 1984) and later when the young are too big to be protected by adults. The young storks are very sensitive to cold and rain until they are 20 to 25 days old, when they have developed their second down feathers which give a better insulation. In N Germany, 44% of all young of 17 nests died dur-
ing a cold spell with rain in 1989 (Struwe & Thomsen 1991), which is similar to what happened in our study area in 1994. As in our study, reproductive success in Spain was inversely correlated with the number of days with precipitation in May (when the young are small) (Carrascal et al. 1993).

Conclusions
The fact that no difference between SF and NSF could be shown in breeding success, body mass, wing length and length of tarsometatarsus of the young leads to the following tentative conclusions: (a) additional food did not improve the reproductive output significantly in a year with adverse weather conditions. (b) White Storks are able to reproduce in intensively cultivated farmland without or with limited access to supplementary food, foraging and feeding their young almost exclusively on earthworms and other small prey. Either food was not a limiting factor or the overall (weather related) high losses of nestlings could not be prevented even with surplus food. These provisional conclusions need to be confirmed by a larger sample size and in years with differing weather conditions. (c) It is yet unclear whether a breeding output of 1.7 y bp1 is sufficient to maintain a stable Swiss White Stork population in the future.

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SAMENVATTING

In 1950 stierf de Ooievaar *Ciconia ciconia* in Zwitserland als broedvogel uit. Vanaf het midden van de jaren zestig werden pogingen ondernomen om deze soort te herintroduceren. In dit artikel worden de gegevens over tijdsbudget, biotoopgebruik en broedsucces van 28 broedparen op vijf plaatsen in 1994 besproken. Op twee plaatsen werden tijdens het broedseizoen Ooievaars bijgevoerd, op de drie andere plaatsen niet. Gedurende de eerste 20 dagen na het uitkomen van de jongen was er steeds ten minste een van de ouders op het nest aanwezig. Daarna werden de kuikens steeds meer alleen gelaten; de niet-bijgevoerde paren waren vaker afwezig dan de bijgevoerde paren. Ook kregen de jongen van niet-bijgevoerde paren minder voedsel dan de jongen van bijgevoerde paren. Als ze niet bij het nest waren, spendsden niet-bijgevoerde ouders een groter deel van de tijd aan foerageren dan wel-bijgevoerde ouders, en de afstand van het nest waarop vogels voedsel zochten was ook het grootst bij niet-bijgevoerde paren. In 1994 werden er in Zwitserland maar weinig ooievaars vliegvlug (gemiddeld 1,2 jongen vergeleken met een gemiddeld broedsucces van 1,7 jongen per paar in 1965-98). Dit was vooral het gevolg van het slechte weer; het broedsucces verschilde niet tussen bijgevoerde en niet-bijgevoerde paren. Er waren geen verschillen tussen de grootte en het gewicht van kuikens uit beide groepen. Aangezien er zelfs in jaren met een gemiddeld hoog broedsucces (1992, 1993) geen verschillen bestaan tussen wel en niet-bijgevoerde paren, levert bijvoeren geen verhoogd broedsucces op. Dat is jammer want het is niet zeker of de gemiddelde productie van 1,7 uitgevlogen jongen per paar per jaar voldoende is om de Ooievaarsstand in Zwitserland op peil te houden. TP)

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