CONDITION-DEPENDENT PARENTAL EFFORT AND
REPRODUCTIVE PERFORMANCE IN THE WHITE STORK
*CICONIA CICONIA*

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Relationships between the parental quality and reproductive performance have been studied in many birds, but not in Ciconiiformes so far. We hypothesised that parental condition of White Storks *Ciconia ciconia* affects both parental care and breeding success. To examine our hypothesis we assessed body mass of White Stork parents and their offspring and recorded breeding performance and parental activity in Hungary during 1992-97. Sex-related differences in parental care were found: females incubated longer than males, males compensated for reduced incubation by females, males delivered more food than females. Condition-related differences in parental effort were found, with heavier females laying more eggs and incubating longer than lighter females. Heavy males and females delivered more food to their offspring than light males and females. Parental condition was positively correlated to clutch size and provisioning rate (and therefore the survival of last hatched chicks to fledge), but hatching success was not related. Light parents raised small broods, but with chicks of relatively high body mass while heavy parents raised large broods of lighter chicks. In years with many cold days during the breeding period, White Storks produced fewer but heavier offspring than in mild years. Body mass of parents increased during the period of chick provisioning, suggesting that parents favour their own future survival in that period.

Key words: *Ciconia ciconia* - cost of reproduction - offspring quality - parental condition - sex-related differences in care

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INTRODUCTION

Monogamy combined with biparental care is common in birds (Lack 1968; Skutch 1976; Oring 1982), often with females displaying greater levels of parental effort than males. There is considerable interspecific variation in relative contributions by males and females with parental care (Wittenberger & Tilson 1980; Oring 1982; Mock 1985). In addition, responses by partners to changes in levels of parental care by their mates also vary widely. In some cases, increased parental care by the male has little or no detectable effect on levels of care provided by his mate (Slagsvold & Lifjeld 1988; Whittingham 1989). In other studies, parents were found to fully or partly compensate for reductions in input by their mates (Weatherhead 1979; Wanless et al 1988; Wolf et al. 1990). Coulson (1968) introduced and evaluated the concept of individual quality in precocial Black-legged Kittiwakes *Rissa tridactyla*, by using body mass and wing length as indicators of individual quality. In several similar studies, body mass has been used to estimate the stress due to reproduc-
tive effort in both non-passerines and passerines (Bryant 1979; De Steven 1980; Korpimäki 1989). The relationship between reproductive performance and parental effort has not previously been elucidated in field studies of storks (Ciconiiformes). The White Stork *Ciconia ciconia* is a single-brooded species that often nests on man-made objects. In this study we recorded body mass of both sexes, the number of eggs laid and hatched, the number of fledglings, the length of the incubation period, chick growth (body mass) and feeding frequency by both parents. In addition, we recorded the ambient temperature and estimate its effect on parental activity and breeding performance. We focused our study on the following questions: Is there a relationship between parental care and parental condition or between parental condition and productivity? Are there differences in parental care provided by males and females? Can intra-seasonal reproductive costs be detected by body mass loss by the parents during the breeding season? And finally, is there a year effect on (A) parental activities, (B) productivity or (C) presumed reproductive cost?

**METHODS**

White Storks were studied during 1992-97 in Kis-kunság National Park, 50 km south of Budapest (47°08'N; 19°07'E). Each season, breeding performance and parental activity were recorded in nine to twelve pairs. We evaluated year effects resulting from the number of cold days in three separate periods: during egg-formation (20 days before the last egg was laid), incubation (between clutch completion and hatching of the first chick), and chick provisioning (20 days after the first chick hatched). Daily temperatures were provided by the Central Institute of Meteorology in Budapest. Days with a mean ambient temperature of at least 5°C below the long-term average for that day (compiling data over the past 100 years) were recorded as 'cold days'. Days in which the mean temperature did not drop below the long-term average were classified as mild. We distinguished mild and cold periods of incubation and chick provisioning for each breeding pair. The median was calculated between the lowest and highest number of cold days recorded during either period. The number of cold days below the median reflected mild periods and the number of cold days above the median reflected cold periods. Changes in parental body mass were related to mild and cold periods of incubation and chick provisioning. Parental activities were recorded both on cold and mild days.

The body mass of both parents was assessed in the first and fourth weeks of incubation and in the eighth week of the period of chick provisioning. After removing the eggs from the nest, a round base plate was positioned in the nest cup, with an electronic balance (± 10g) on top of it. A covering plate was then placed over the balance (Fig. 1). The balance was calibrated with known weights each time a measurement was taken after returning the eggs on the cover plate. Cables running from the balances were connected to monitors that were placed at 30-50m from the nests. Measurements were read for both parents when they
were sitting motionless during incubation. The two sexes were distinguished by their different body mass and positions during copulation. When chicks were older than 20 days the parents generally landed on the edge of the nests and regurgitated food into the centre of the cup and the chicks fed from there. We removed the chicks from the nests in order to measure the parents during the eight week of the period of chick provisioning. After removal of the chicks, the parents landed at empty nests and stepped into the cup where the electronic balance had been placed. Chicks were removed 60-90 minutes after delivery of the last feed and were weighed before placing them back into the nests, after their parents had been weighed. Once the parents had fed the chicks, the chicks were weighed again and the increases of their masses were subtracted from the masses of the parents. In this way we calculated the masses of the parents without the food delivered to chicks. We measured body mass and tarsus length of the chicks at 60-65 days of age.

We recorded the activities between 06:00h and 20:00h for those parents which were weighed. The number of pairs studied was equally distributed over the early (up to 15 days after the first egg was laid) and late (after the 15th day) incubation period. Critical for chick survival are the first two weeks of life (Tortosa & Redondo 1992). Hence, we chose three stages to record provisioning rates (frequency and mass of food delivered): when the first hatchlings were respectively 5, 10 and 15 d of age. Following the first feeding bouts seen after 06:00 h we would wait 90 min for small broods (2-3 chicks) and 60 min for large broods (4-5 chicks) before assessing chick body mass. Generally, within 15 min of assessing chick body mass, the parents returned to feed the chicks again. When the parents had finished provisioning the chicks, all offspring were again weighed, to establish the difference between individual body masses before and after feeding, reflecting the total amount of food delivered by the parents. After this, we would wait a further 60-90 minutes before making the next pair of measurements. We summed the differences between the ‘before’ and ‘after’ feeding measures made between 06:00h and 20:00h and considered this as the total quantity of food delivered to the brood in one day.

We measured the pairs and their offspring in the nests that were more than 500 m away from the nests studied in the previous year. Hence we presumed that all parents weighed during the study period were different individuals. Statistical analyses were carried out using SPSS statistical package.

RESULTS

Annual variations in breeding success

Clutch size varied between years, with females producing smaller clutches in years with a high number of cold days prior to egg-laying (ANCOVA: $F_{5,56} = 3.18, P = 0.013, b = -0.017$; Table 1). Hatching success and the number of cold days during incubation were not correlated ($F_{5,56} = 2.19, P = 0.075$). Chick provisioning also varied between years, with relatively low provisioning rates in cold periods following hatching (ANCOVA: $F_{5,56} = 4.91, P < 0.001, b = -0.014$). Fledging success was lower when the entire breeding season was characterised by a high numbers of cold days ($F_{5,56} = 4.28, P < 0.001, b = -0.131$).

Parental body mass and incubation sharing

Females spent more time incubating eggs than males, both in mild and cold seasons (ANOVA $F_{1,106} = 12.3, P < 0.001$ and $F_{1,106} = 9.60, P < 0.001$), while males spent more time guarding the nest than did females ($F_{1,106} = 14.1, P < 0.001$ and $F_{1,106} = 11.90, P < 0.001$; Fig. 2). There were no differences in foraging time between sexes in either mild or cold weather ($F_{1,106} = 2.80, P = 0.094$ and $F_{1,106} = 2.63, P = 0.183$). Females spent less time incubating on cold days than on mild days ($F_{1,106} = 5.19, P = 0.023$), while the opposite was true for males ($F_{1,106} = 5.12, P = 0.026$). Temperature did not affect the time females spent guarding the nest ($F_{1,106} = 2.38, P = 0.224$), but males spent less time on guard when temperatures were
Table 1. Number of cold days during the breeding season and breeding performance (mean ± SD), 1992-97.

<table>
<thead>
<tr>
<th></th>
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</tr>
</thead>
<tbody>
<tr>
<td>Number of pairs studied</td>
<td>11</td>
<td>10</td>
<td>12</td>
<td>9</td>
<td>9</td>
<td>11</td>
</tr>
<tr>
<td>Mean number of cold days before egg-laying</td>
<td>2.1 ± 0.5</td>
<td>3.7 ± 0.7</td>
<td>13.4 ± 0.8</td>
<td>8.8 ± 0.8</td>
<td>1.9 ± 0.7</td>
<td>11.5 ± 0.8</td>
</tr>
<tr>
<td>Mean number of cold days during incubation</td>
<td>11.6 ± 0.8</td>
<td>2.3 ± 0.5</td>
<td>2.1 ± 0.3</td>
<td>5.4 ± 0.7</td>
<td>9.0 ± 0.6</td>
<td>10.2 ± 0.5</td>
</tr>
<tr>
<td>Mean number of cold days after hatching</td>
<td>2.3 ± 0.5</td>
<td>2.0 ± 0.5</td>
<td>10.5 ± 0.8</td>
<td>11.8 ± 0.8</td>
<td>3.1 ± 0.3</td>
<td>11.3 ± 0.8</td>
</tr>
<tr>
<td>Total number of cold days</td>
<td>16</td>
<td>8</td>
<td>26</td>
<td>26</td>
<td>14</td>
<td>33</td>
</tr>
<tr>
<td>Clutch size</td>
<td>4.45 ± 0.62</td>
<td>4.47 ± 0.69</td>
<td>3.78 ± 0.71</td>
<td>4.34 ± 0.58</td>
<td>4.38 ± 0.61</td>
<td>3.91 ± 0.53</td>
</tr>
<tr>
<td>Hatching success</td>
<td>0.89 ± 0.12</td>
<td>0.89 ± 0.11</td>
<td>0.90 ± 0.09</td>
<td>0.97 ± 0.16</td>
<td>0.95 ± 0.16</td>
<td>0.90 ± 0.08</td>
</tr>
<tr>
<td>Feeding success</td>
<td>0.92 ± 0.09</td>
<td>0.90 ± 0.11</td>
<td>0.74 ± 0.09</td>
<td>0.79 ± 0.12</td>
<td>0.89 ± 0.08</td>
<td>0.76 ± 0.08</td>
</tr>
<tr>
<td>Number of fledglings</td>
<td>3.79 ± 0.74</td>
<td>3.84 ± 0.71</td>
<td>2.60 ± 0.59</td>
<td>3.12 ± 0.60</td>
<td>3.67 ± 0.69</td>
<td>2.71 ± 0.74</td>
</tr>
</tbody>
</table>

1Hatching success = number of eggs hatched of all eggs laid; 2Fledging success = number of young fledged of all young hatched.

Fig. 2. Percentage of time (% ± SD, sample size in parentheses) spent incubating, nest-guarding and foraging of White Stork parents during the incubation period in relatively mild and cold seasons.

low (F_{1,106} = 11.08, P < 0.001). Both parents devoted more time to foraging when the weather was cold (F_{1,106} = 8.96, P < 0.001 and F_{1,106} = 8.39, P = 0.003). Comparatively light females spent less time incubating their eggs than heavy females (F_{1,106} = 4.48, P = 0.035), but male body mass did not apparently influence the time spent incubating (F_{1,106} = 3.37, P = 0.067). Also, there was no correlation found between female body mass and the amount of the time spent guarding the nest (F_{1,106} = 3.27, P = 0.074), while lighter than average males spent less time on guard than heavy males (F_{1,106} = 4.73, P = 0.033). Multiple regression coefficients show an increase in time spent incubating with increasing body mass for females. For both parents, a decline in time spent incubating was found with increasing body mass of the partner (Table 2). Stage of incubation (early or late) did not affect the times spent incubating by either parent. The length of incubation increased with increasing daily mean temperature for females but decreased for males.
Table 2. Multiple regression coefficients between the proportion of time spent incubating and parental body mass, body mass of the mate, the stage of incubation and daily mean temperatures (* = \( P < 0.01 \), ** = \( P < 0.001 \)). Stage of incubation was calculated by series numbers, where 1 denoted the day when the first egg was laid.

<table>
<thead>
<tr>
<th></th>
<th>Female (n = 62)</th>
<th>Male (n = 62)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Own body mass</td>
<td>0.024**</td>
<td>0.011</td>
</tr>
<tr>
<td>Body mass of mate</td>
<td>-0.026*</td>
<td>-0.028*</td>
</tr>
<tr>
<td>Stage of incubation</td>
<td>0.146</td>
<td>0.201</td>
</tr>
<tr>
<td>Daily mean temperature</td>
<td>0.702**</td>
<td>-0.624**</td>
</tr>
<tr>
<td>( R^2 )</td>
<td>0.307</td>
<td>0.196</td>
</tr>
</tbody>
</table>

Chick provisioning (mass) in relation to parental body mass

The amount of food (mass) delivered when the earliest chicks were 10 days of age is presented in Fig. 3. Males delivered more food than females both on mild and cold days (ANOVA \( F_{1,58} = 5.46, \ P = 0.021 \) and \( F_{1,42} = 7.26, \ P = 0.015 \)), but both males and females delivered smaller quantities when temperatures were low (\( F_{1,50} = 7.76, \ P = 0.007 \) and \( F_{1,50} = 7.39, \ P = 0.009 \)). Individuals of either sex with above-average body mass delivered more food than lighter birds (\( F_{1,50} = 10.12, \ P < 0.001 \) and \( F_{1,50} = 12.05, \ P < 0.001 \)). Both females and males delivered more food to larger broods (4-5 nestlings) than to smaller broods (2-3 nestlings; \( F_{1,50} = 8.96, \ P = 0.005 \) and \( F_{1,50} = 9.42, \ P = 0.002 \)). The same trends were found in all comparisons when the first hatched chicks were respectively 5 and 15 days old (not presented here). Multiple regression coefficients indicated positive correlations between the amount of food (mass) delivered and parental body mass, brood size and daily mean temperatures in all three sampled chick stages (Table 3).

Effects of parental body mass and number of cold days on reproductive performance

Pairs in which both parents were heavier than average produced more fledglings, while pairs where both parents were lighter than average produced the least (\( F_{3,58} = 6.92, \ P < 0.001 \); Table 4). Most pairs consisted either of two relatively heavy or two relatively light individuals (\( \chi^2_3 = 41.8, \ P < 0.001 \)). Heavier females laid more eggs than lighter ones, and vice versa (Table 4).
Table 3. Multiple regression coefficients between the mass of food delivered and body mass of parents, brood size and daily mean temperature. *P < 0.05, **P < 0.01, ***P < 0.001.

<table>
<thead>
<tr>
<th>Age of first hatched chick</th>
<th>5 days (n = 52)</th>
<th>10 days (n = 52)</th>
<th>15 days (n = 48)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body mass of female</td>
<td>0.033*</td>
<td>0.041**</td>
<td>0.029***</td>
</tr>
<tr>
<td>Body mass of male</td>
<td>0.039**</td>
<td>0.049***</td>
<td>0.054***</td>
</tr>
<tr>
<td>Brood size</td>
<td>0.018*</td>
<td>0.022*</td>
<td>0.034**</td>
</tr>
<tr>
<td>Daily mean temperature</td>
<td>0.129*</td>
<td>0.218**</td>
<td>0.240**</td>
</tr>
<tr>
<td>$R^2$</td>
<td>0.124</td>
<td>0.197</td>
<td>0.218</td>
</tr>
</tbody>
</table>

Table 4. Condition of White Stork pairs expressed as body mass relative to the average body mass of either sex (g ± SD) and the number of fledglings produced (productivity, n ± SD).

<table>
<thead>
<tr>
<th>Condition of pairs</th>
<th>Body mass</th>
<th>Productivity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Both parents above average (n = 28)</td>
<td>Female 3782 ± 412</td>
<td>3.89 ± 0.77</td>
</tr>
<tr>
<td></td>
<td>Male 4143 ± 326</td>
<td></td>
</tr>
<tr>
<td>Heavy female, male below average (n = 9)</td>
<td>Female 3531 ± 366</td>
<td>3.00 ± 0.87</td>
</tr>
<tr>
<td></td>
<td>Male 3640 ± 294</td>
<td></td>
</tr>
<tr>
<td>Light female, male above average (n = 4)</td>
<td>Female 2979 ± 304</td>
<td>3.50 ± 0.58</td>
</tr>
<tr>
<td></td>
<td>Male 3952 ± 402</td>
<td></td>
</tr>
<tr>
<td>Both parents below average (n = 21)</td>
<td>Female 2849 ± 217</td>
<td>2.62 ± 0.80</td>
</tr>
<tr>
<td></td>
<td>Male 3424 ± 329</td>
<td></td>
</tr>
</tbody>
</table>

Table 5. Multiple regression coefficients between body mass of parents at the onset of incubation and the number of cold days and breeding performance expressed as clutch size, hatching success, provisioning rates and number of fledglings (*P < 0.01, **P < 0.001; n = 62 in each relationship).

<table>
<thead>
<tr>
<th>Clutch size</th>
<th>Hatching success</th>
<th>Provisioning rate</th>
<th>Fledglings</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body mass of female</td>
<td>0.005**</td>
<td>0.011</td>
<td>0.015*</td>
</tr>
<tr>
<td>Body mass of male</td>
<td>0.003*</td>
<td>0.008</td>
<td>0.009**</td>
</tr>
<tr>
<td>Number of cold days</td>
<td>-0.043**</td>
<td>0.037</td>
<td>-0.029**</td>
</tr>
<tr>
<td>$R^2$</td>
<td>0.218</td>
<td>0.029</td>
<td>0.197</td>
</tr>
</tbody>
</table>

than lighter hens, but clutch size was also negatively affected by the number of cold days (Table 5). Multiple regression coefficients did not indicate a relationship between parental mass, the number of cold days and hatching success. However, chick provisioning increased with increasing body mass in females and males, but declined with an increasing number of cold days. Body mass of both males and females was positively correlated with the number of fledglings, while increases in the number of cold days during the breeding period resulted in a decrease in the number of fledglings (all Table 5).
Table 6. Body mass (g ± SD) of chicks before fledging in relation to brood size and parental condition (expressed as body mass relative to the average body mass of either sex). Sample size, as the number of chicks, is shown in parentheses.

<table>
<thead>
<tr>
<th>Condition of pair</th>
<th>Number of chicks in the brood</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
</tr>
<tr>
<td>Both parents above average</td>
<td>3431 ± 325 (27)</td>
</tr>
<tr>
<td>Heavy female, male mass below average</td>
<td>3464 ± 260 (6)</td>
</tr>
<tr>
<td>Light female, male mass above average</td>
<td>3440 ± 296 (6)</td>
</tr>
<tr>
<td>Both parents below average</td>
<td>3510 (1)</td>
</tr>
</tbody>
</table>

Body mass and length of tarsus of chicks before fledging

Only pairs in which both parents weighed above average raised five chicks. One or two chicks were raised by the pairs where the body mass of males were below the mean (Table 6). The heaviest chicks were found in broods of only 1-2 while the lightest chicks were in broods of 5 nestlings ($F_{4,200} = 5.29, P < 0.001$). When comparing chick body mass in broods of the same size, there were no differences that related to the body mass of parents (broods of two chicks: $F_{1,18} = 3.57, P = 0.092$; broods of three chicks: $F_{3,74} = 2.29, P = 0.084$; broods of four chicks: $F_{3,72} = 2.31, P = 0.077$). The average mass of all chicks reared in broods of particular sizes showed that light parents raised more small broods with heavier chicks, while heavier parents produced larger broods but with lighter chicks ($F_{3,201} = 4.67, P = 0.004$). Chicks were also comparatively large (tarsus length) in pairs where both parents were light (mean ± SD 237.6 ± 22.4 mm, $n = 55$) and smaller where both parents were heavy (223.9 ± 20.7 mm, $n = 109$). In comparison, in pairs where the female weighed above average and where the male was lighter than average, chick tarsus length amounted to 226.9 ± 30.1 mm ($n = 27$); the reverse, with female below average and the male being relatively heavy, chick tarsus length amounted to 229.0 ± 27.7 mm ($n = 14$; $F_{3,201} = 5.83, P < 0.001$).

Changes in body mass in females and males

The body mass of male and female White Storks increased slightly when the incubation took place during a mild spell (Fig. 4). However, nor for parents in which the subsequent period of chick provisioning turned out to be relatively mild ($t_1 = 1.17, n.s. and t_2 = 0.98, n.s.$), nor for parents facing a cold period of chick provisioning ($t_1 = 0.88, n.s. and t_2 = 1.07, n.s.$), was the body mass gain significant. Both parents gained mass during relatively warm ($t_1 = 3.43, P < 0.01$ and $t_2 = 4.29, P < 0.001$) and cold periods of chick provisioning ($t_1 = 2.53, P < 0.02$ and $t_2 = 2.90, P < 0.02$). As a consequence, the parents had a higher body mass at the end of the breeding season than at the start (Females in mild and cold periods of chick provisioning: $t_1 = 4.17, P < 0.01$ and $t_2 = 3.61, P < 0.01$; males in mild and cold periods: $t_1 = 4.02, P < 0.01$ and $t_2 = 3.25, P < 0.01$). The mass of parents declined when the incubation period was
cold (followed by a mild period of chick provisioning: $t_1 = 2.96, P < 0.01$ and $t_2 = 3.41, P < 0.01$; followed by a cold period of chick provisioning: $t_3 = 3.63, P < 0.01$ and $t_4 = 4.69, P < 0.001$). These parents regained their original body mass both in warm ($t_5 = 4.32, P < 0.001$ and $t_6 = 3.15, P < 0.02$) and in cold subsequent periods of chick provisioning ($t_7 = 4.19, P < 0.01$ and $t_8 = 3.29, P < 0.01$), with no significant difference between body mass at the start and at the end of the breeding season (in mild subsequent periods of chick provisioning: $t_9 = 1.17, \text{n.s.}$ and $t_{10} = 1.66, \text{n.s.}$; in cold periods of chick provisioning: $t_{11} = 0.94, \text{n.s.}$ and $t_{12} = 1.36, \text{n.s.}$).

**DISCUSSION**

**Sex- and condition-related differences in parental care**

Sex-related differences in parental care by White Storks can now be summarised as follows. Females are responsible for a greater proportion of incubation than males, but males increased their contribution during cold weather when females spent more time foraging. Males spent more time guarding the nest than females, but spent more time foraging (and, hence, less time on guard) when the weather was cold compared to when it was mild. In females, there were no temperature-related differences in time spent on guard. Males delivered more food to their offspring than females, both in mild and cold weather. Condition-related differences in parental effort, as indicated by body mass, were that heavier females laid more eggs than light females. Heavier females spent more time incubating than light females, but no such relationship was found in males. Heavy males spent more time nest guarding than light males, but females did not demonstrate condition-related differences in this respect. Heavier parents delivered more food to the chicks than lighter individuals. Males responded to reduced parental effort by the fema-
les during incubation, but provided no compensa-
tion during chick provisioning. Since females
with low body masses spent less time and shorter
periods incubating than heavier females, the de-
gree of compensation by male storks with such
lighter mates was particularly high on cold days.
The higher rate of food provisioning of the chicks
by males could reflect a greater foraging success
by the larger and heavier sex and does not neces-
sarily indicate that these birds spent more time
foraging during the nestling period.

Parental condition and year affect clutch size
and the survival of the latest hatched chicks
Correlations between clutch size and food
supply have been demonstrated earlier both in
Passerines (Bryant 1977; Järvinen & Väisänen
1984) and Non-Passerines (Dijkstra et al. 1982;
We did not study food availability for White
Storks but presume that small clutches, laid by
females in years with a high proportion of cold
days prior to egg laying, were due to adverse
effects on food availability. Relationships
between body condition and clutch size have been
shown previously (Dijkstra et al. 1988; Korpimäki
1989; Sydeman et al. 1991) and was confirmed for
White Storks in the present study with positive
correlations between body mass and clutch size in
both sexes. Since most of the heavier than average
males mated with heavy females, while lighter
males tended to be paired with lighter females, it
is impossible to demonstrate a relationship
between male body mass and clutch size that is
independent of the effects of female body mass,
which is likely to be more relevant. The mate-
choice of sexes fell into the same categories for
body mass and, hence, we presume assortative
mating on basis of body condition. Hatching suc-
cess, was neither influenced by temperature nor
by parental condition during incubation but chick
provisioning was affected by both factors. Chick
mortality was highest during the first 15 days after
hatching (only four of 38 nestlings that died suf-
fered this fate after they reached 15 days of age:
$\chi^2 = 47.3, P < 0.001$.) Tortosa & Redondo (1992)
found that, as nestlings grew older, their diet
changed, so that by 20-30 days the young were
taking more substantial portions of food and beca-
me less vulnerable to starvation. The number of
fledglings of White Storks is therefore mainly
determined by two key phases of the nesting peri-
od: during egg-formation and while the nestlings
are still small.

Parents with poorer condition raised offspring
of higher quality
It is generally assumed that natural selection
works to optimise the number of recruits in a
breeding population, rather than the number of
independent nestlings (Smith & Fretwell 1974;
Brockelman 1975; Sibly & Calow 1986). Studies
on both Passerines (Garnett 1981) and Non-Pas-
serines (Murphy 1983; Coulson & Porter 1985)
have shown that the survival of fledglings
depends on their size and body mass. White
Storks do not feed their chicks after fledging (Tort-
tosa & Redondo 1992) and therefore high body
reserves may be important for chick survival in an
unfamiliar environment during the first few days
of dispersal after fledging. Light parents raised
smaller broods than heavy parents but, since the
chicks fledged from small broods were heavier
than those from large broods, it seems that parents
with poorer condition produced offspring of high-
er quality. In order to confirm this suggestion it
would be necessary to carry a study of recruitment
of marked offspring with different body mass at
fledging. We found fewer and heavier fledglings
in years with many cold days, suggesting that
White Storks produced (fewer) offspring of high-
er quality and better survival chances in breeding
seasons with adverse weather conditions than in
more favourable seasons.

Parents favour own survival against the num-
ber of chicks during the feeding effort
In studies of European Tree Sparrows Passer
montanus (Sasvári & Hegyi 1994), Lapwing
Vanellus vanellus and Black-tailed Godwit Lim-
sa limosa (Hegyi & Sasvári 1998) it was shown
that only females paid intra-seasonal costs during
the breeding season. We did not find sex-related differences in the mass loss in White Storks, however. Both females and males lost mass during cold incubation periods but these losses were replenished by the end of breeding season during chick provisioning. European Tree Sparrows are wintering residents remain in areas where they breed in spring and summer. Lapwings and Black-tailed Godwits stop tending their young in May and June, to leave the breeding area in October and November. White Storks are a single brooded species, with a long breeding period lasting from the time of their arrival after migration until the end of summer. The time between fledging and the onset of autumn migration, during which the birds must build up fat reserves sufficient to complete their migration, is short. Apparently for that reason begin parent birds to increase their body mass before the end of the breeding season. Increases in body masses were found during chick provisioning, even during adverse weather conditions. We believe that chick mortality and the increase in body mass of the parents during the chick provisioning may reflect a selection process in favour of the survival of the parents and their own future reproductive success.

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SAMENVATTING

Het verband tussen de kwaliteit van oudervogels en hun broedsucces is al bij veel vogelsoorten onderzocht, maar tot dusverre niet bij ooievaars en verwanten. In het hier beschreven onderzoek wordt verondersteld dat er een direct verband bestaat tussen de conditie (geme- ten als het lichaamsgewicht) van Ooievaars *Ciconia ciconia* bij aanvang van het broedseizoen en zowel de mate van geleverde broedzorg als het uiteindelijke broedsucces. Om dit verband aan te tonen werden in een Hongaarse populatie in het Nationale Park Kis- kunság (50 km ten zuiden van Boedapest) tussen 1992 en 1997 elk jaar van negen tot twaalf broedparen de broedzorg en de conditie van ouders en jongen bestudeerd. Er werden aanzienlijke verschillen in broedzorg tussen beide partners gevonden: wijfjes spendeerden veel meer tijd aan broeden dan mannetjes, maar mannetjes compenseerden dit wanneer hun partner (noodge- dwongen) minder aandacht had voor het legsel. Manne- tjes voerden altijd veel meer voedsel aan dan wijfjes en spendeerden meer tijd aan de bewaking van het nest. Inderdaad werden verschillen in broedzorg gevonden tussen vogels van verschillende conditie: zware wijfjes (verondersteld in een relatief goede conditie te zijn) legden meer eieren en besteedden meer tijd aan het bebroeden daarvan dan lichte wijfjes; zowel zware mannetjes als zware wijfjes brachten meer voedsel aan voor de jongen dan lichte individuen. Er bestond een positief verband tussen broedzorg en voedselaanvoer en daarmee tussen dit verband en de overleving van de laatst uitgekomen jongen, maar er was geen verband met het uitkomstsucces van de eieren. Lichte ouders brachten een klein aantal jongen groot, maar hun kuikens waren relatief zwaar, terwijl zware ouders grotere legsels verzorgden en grootbrachten, maar hun kuikens waren lichter. In broedseizoenen met veel koude dagen produceerden alle Ooievaars minder jongen, maar de uitvliegende kuikens hadden een hoger lichaamsgewicht dan in milde jaren. Het lichaamsgewicht van beide ouders nam toe gedurende de broedtijd, waaruit afgeleid kan worden dat de Ooievaars hun eigen overle- ving en daarmee hun toekomstig broedsucces niet in de waagschaal stelden. De periode tussen het uitvliegen en de wegtrek is kort, zodat de tijd benodigd voor het voedende opvatten van de oudervogels nog tijdens de jongen- zorg een aanvang moest nemen.

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