Differences Between Sexes in Digestive Efficiency of the White Stork *Ciconia ciconia* under Experimental Conditions

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Sex differences in digestive performance may be related to food contents, to body size as well as many other physiological traits. However, evidence for sex differences in the digestion of birds, especially in the case of predators, is scarce. Therefore we studied digestive efficiency, and also body size, intestine length and food selection of the wild white stork (*Ciconia ciconia*), under experimental conditions in the Poznań Zoo. Altogether 29 individuals of this species were investigated (9 males, 20 females). During 5-day-long experimental cycles, the diet of the birds consisted of mammals, birds, fishes and insects. The mean daily wet food intake (weight of the food eaten) during the experiment was $272.8g \pm 89.3$ g for males and $342.7g \pm 157.4$ g for females, but the difference between sexes was not significant (P = 0.226). The mean digestive efficiency showed a significant difference, i.e. in male white storks it amounted to $70.87\% \pm 14.43\%$, whereas in females this value was $77.53\% \pm 3.99\%$ (P = 0.049). Digestive efficiency was slightly influenced by changes in body weight of storks during the experiment. Correlation coefficients between sexes also differed significantly (P = 0.037). The study showed that the digestive efficiency is positively correlated with the quantity of food intake and body weight.

Key words: Daily wet food intake, digestive efficiency, food selection, intestine length, white stork, sexual dimorphism.

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Avian digestion is a subject of interest to biologists because of the factors that mediate bird interactions and their environments (KARASOV 1990). Digestion is important at an individual level as well as at population and community levels through affecting the resource removal rate, and possibly by constraining the rate of production (KARASOV 1990; HILTON *et al*. 1999). Generally, digestive system efficiency is related to: (1) digest retention time; (2) rates of hydrolysis, fermentation and absorption; and (3) surface length and volume of the digestive tract (KARASOV 1990; BARTON & HOUSTON 1993; HILTON *et al*. 1999).

Bird digestion may also show sexual differences (MARKMAN *et al*. 2006). However, evidence for sex differences in digestive performance is limited and only one experimental study exists for the Palestine sunbird (*Nectarinia osea*) which forages on nectar, a rather simple liquid food source. Findings for this species are not necessary applicable to birds with a more complex diet. Moreover, information on sexual differences in digestive processes does not exist (see also KARASOV 1996; HILTON *et al*. 1999). A good example of a bird foraging on a different food source is the white stork (*Ciconia ciconia*). The white stork diet contains various, relatively small vertebrates and large invertebrates, and food choice depends on seasonal life cycle stage and habitat (PINOWSKA *et al*. 1991; MUZINIĆ & RASAJSKI 1992; TSACHALIDIS & GOUTNER 2002; ANTCZAK *et al*. 2002). The above mentioned results are based on pellet analysis or direct observations under field conditions. Therefore, due to lack of sex recognition (male and female white storks can be recognised only using molecular techniques and detailed measurements (see ĆWIERTNIA *et al*. 2006) and directional behavioural observations during copulation (SASVÁRI

et al. 1999; CHERNETSOV *et al*. 2006). However the authors did not provide data on food intake differences between males and females. Data on sex differences in digestibility are basic and useful for the estimation of demand at a population scale, which is important for protection of endangered species, such as the white stork (PROFUS 1986, 2006). Generally, sex differences in digestive processes may have various origins. Males and females may differ in energy requirements and food intake (e.g. RICKLEFS 1996; SASVÁRI *et al*. 1999). Also, sexes may differ in digestive functions (MARKMAN *et al*. 2006). Both food constraints and digestive process are frequently explained by differences in body size (RICKLEFS 1996; MARKMAN *et al*. 2006). However, sex differences in digestive process may not always be explained by differences in body size (MARKMAN *et al*. 2006). Data on both the digestibility and body mass of sexes is needed to fully understand this issue. Detailed research on the digestive efficiency and digestibility of different kinds of food in the white stork (and other bird species) is very difficult to obtain under field conditions due to logistic and technical problems (BARTON & HOUSTON 1993; DURANT *et al*. 2000; DURANT *et al*. 2004; PROFUS 2006), therefore studies in captivity are essential for understanding controlled conditions.

Estimations of the daily food intake and calculation of the energetic value of certain elements of stork diet under field conditions were given by PROFUS (1986, 2006). The data presented are based on direct observation of only one nest, and the results are extrapolated onto the energy requirements of the local population. We primarily fed the storks a diet quite similar to the natural diet under field conditions that captive storks readily feed on. Therefore, this study was aimed to assess digestive efficiency in the white stork under experimental conditions and to determine its daily dietary requirements. The basic scheme of this study follows standard procedures and is based on results of research conducted on other carnivorous species, such as birds of prey and owls (BARTON & HOUSTON 1993). Males and females were kept under the same conditions and obtained the same food during the experiment. We tested the prediction that there is no difference in digestive efficiency.

Additionally, because digestive processes may be related to body mass as well as intestine length (KARASOV 1990, 1996; RICKLEFS 1996), we also included these factors in our study.

Material and Methods

The study was conducted in the Poznań Zoo in 2004-2005 (May, June), on wild-born birds (released in the wild after completion of experiments)

(KWIECIŃSKI *et al*. 2006a). All storks were adults (3-5 years old). Their sex was determined by using DNA techniques (FRIDOLFSSON & ELLEGREN 1999; details in: ĆWIERTNIA *et al*. 2006). Our experiment was carried out on 29 individuals: 9 males and 20 females. All storks were individually marked with colour rings. During the experiment, the observer was not aware of the sex of individual birds, because information on this came some months later. The birds were kept inside individual cages of ca. 10 m^2. The boxes were wire-netted to allow visual contact amongst individuals. The lower 40 cm was made of plastic sheeting to prevent droppings from falling into neighbouring cages. The floor was covered with plastic foil (2 mm thick) to allow easy and reliable collection of faeces. The experiment took 5 days; the birds were fed with a diet regularly provided to captive individuals under zoo condition. It consisted of domestic mice *Mus musculus* (captive-bred); one-day-old chicks *Gallus gallus;* fish (sprat *Sprattus sprattus;* perch *Perca fluviatilis*) and insects (crickets *Acheta domesticus, Gryllus bimaculatus*). Water was available *ad libitum* and changed daily (storks drink water). To reduce the stress caused by separation as well as by close contact with humans, 4-5 birds took part in the experiment simultaneously. Before each experiment, storks were fasted for 24 hours to enable digestion of previously taken food and the passage of previously formed pellets. The food was presented in shallow, plastic containers on the basis of the 'Cafeteria test' at the same time of the day, i.e. about 4 PM (RYCHLIK & JANCEWICZ 2002). The food items (separately: mammals, birds, etc.) were weighed every day on a Pesola scale to the nearest 0.2 g. The same protocol was followed in weighing food remnants, pellets and faeces. The pellets were collected separately from each individual, weighed and put into plastic bags, each labelled with the bird code and date. The faeces were collected into 100-ml plastic containers, weighed and labelled. Subsequently the faeces were watered and analysed under a stereomicroscope (magnification 5×) to identify the undigested particles.

The percentage of digestive efficiency (DE) was calculated on the basis of the formula developed by BARTON and HOUSTON (1993), slightly modified to fit the stork research. White storks not only intake water from food, but also soak each item in water before eating. Moreover, sometimes the birds spilled some of the available water during the experiment. Therefore we couldn't preciously calculate water intake by storks.

$$\text{DE} = 1 - (\frac{\text{faeces (g)} + \text{pellet (g)}}{\text{food intake (g)}}) \times 100\%$$

The quantity of the food presented to birds on the first day of the experiment was 100 g of each com-

ponent of the diet for every bird tested (initial food ratio). During subsequent days the quantity of food was regulated individually by the birds themselves. The quantity of consumed items as well as leftovers determined an increase or decrease of the diet components during the experiment (i.e. if storks consumed all mammal prey during one day, the quantity of mammal food was increased on the next day). The mean daily food intake was calculated on the basis of the difference between the weight of the food provided and left uneaten by storks (in grams). The mean production of faeces and pellets, as well as mean digestibility efficiency were estimated.

During the 5 days of the experiment, the birds were weighed twice, on the first and on the last day of the experiment, with a Pesola scale to the nearest 5.0 g. Thus we obtained initial and final body weights (BARTON and HOUSTON 1993).

Data on intestine length were collected from dead (mainly euthanized) individuals due to serious problems with legs and wings after collision with electrical wires and delivered to the zoo. It should be noted that these birds were not used for the experiment (STIVENSON 1933).

Statistical analyses were conducted by using the package SPSS for Windows following the recommendations of ZAR (1999).

Results

Body mass and intestine length

Mean body mass of males (3230 ± 0.360 g, N = 9) was 12.5% higher than that of females (2870 ± 0.350 g, N = 20) ($t27 = -2.57$, P = 0.016). Mean in-

testine length of females (168.4 ± 5.41 cm, N = 5) was 15.4% higher than that of males (142.5 ± 11.90 cm, N = 4) ($t7 = 4.387$, P = 0.003).

Food intake and food selection

The mean daily wet food intake (weight of the food eaten) during the experiment was 272.8 ± 89.3 g for males and 342.7 ± 157.4 g for females. The difference between the sexes was not significant ($t_{27} = 1.24$, P = 0.226). Food intake affected changes in body weight during the experiment and this relationship was significant for both sexes (Figs 1 & 2). Changes in body weight did not differ between sexes during the experiment ($t_{27} = 1.18$, P = 0.247). However, the sexes did not differ significantly in proportion of used food type (birds, mammals, fishes and insects; $\chi^2 = 2.26$, P>0.20).

Digestive efficiency

The mean weight of faeces was 60.16 ± 21.21 g, which accounts respectively for 22.05% of the weight of consumed food in the case of the males, and 61.38 ± 27.58 g, which is 17.91% in the case of females ($t_{27} = 0.12$, p = 0.907). The mean weight of a fresh pellet was 12.21 ± 6.22 g, which constitutes 4.48% of the food consumed in males. For females this value amounted to 13.92 ± 9.09 g, or 4.06% of the food intake ($t_{27} = 0.51$, P = 0.615). Therefore, the mean digestive efficiency in male and female white storks was 70.87 ± 14.43% and 77.53 ± 3.99%, respectively, the obtained values differed significantly ($t_{27} = 2.07$, P = 0.049).

Digestive efficiency slightly influenced changes in body weight of storks during the experiment
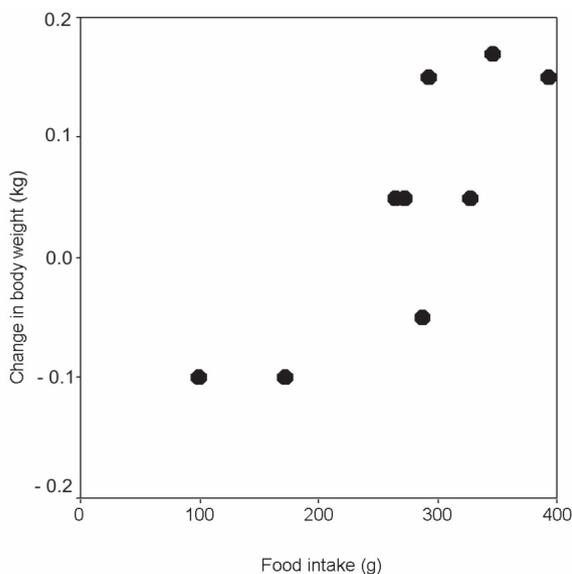

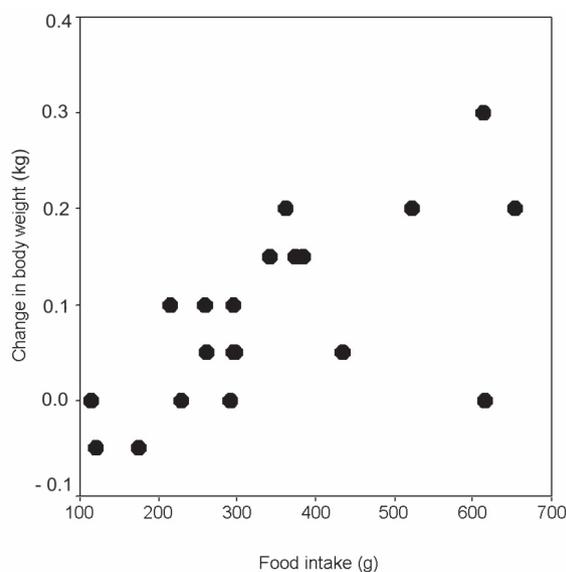Fig. 1. Relation between food intake and changes in body weight of male white storks (r = 0.833, N = 9, P = 0.005).

Fig. 2. Relation between food intake and changes in body weight of female white storks (r = 0.651, N = 20, P = 0.002).

Fig. 3. Effect of digestive efficiency on changes in body weight of male white storks (r = 0.595, N = 9, P = 0.091).

Fig. 4. Effect of digestive efficiency on changes in body weight of female white storks (r = 0.344, N = 20, P = 0.137).

(Figs 3 & 4), and correlation coefficients between sexes differed significantly (P = 0.037). However the digestive efficiency in males was not significantly different from that of females when we used body mass as a covariate (ANCOVA, $F_{1,26}$ = 1.63, P = 0.213).

Discussion

Under field conditions the male and female white stork diet consists of items such as chicks, mice, crickets and fish (PINOWSKA et al. 1989; PINOWSKA et al. 1991; ANTCZAK et al. 2002; TRYJANOWSKI & KUŹNIAK 2002; PROFUS 2006). Moreover, the diet of white stork is diverse, this species consumes a number of invertebrate and vertebrate species and has an ability to switch to numerous and even new food sources (TSA-CHALIUDIS & GOUTNER 2002; NEGRO et al. 2000; TORTOSA et al. 2002).

The daily dietary requirement of captive birds proved to be at least 50% lower in comparison to wild birds (PROFUS 1986; 2006; SASVÁRI et al. 1999). However, PROFUS (1986, 2006) estimated daily food requirements based on theoretical equations for establishing field metabolic rate which was not proven experimentally. On the other hand, comparisons were also made difficult because other studies did not provide information on sex differences in food intake (PINOWSKA et al. 1989; PINOWSKI et al. 1991; ANTCZAK et al. 2002; TRY-JANOWSKI & KUŹNIAK 2002; PROFUS 2006; TSA-CHALIUDIS & GOUTNER 2002; NEGRO et al. 2000; TORTOSA et al. 2002).

Digestive efficiency in the white stork was similar to other carnivorous and piscivorous birds (HILTON et al. 1999) and generally supports the hypothesis that this species should have an effective digestive system, in accord to the results of examining damage to unconsumed food in pellets (ANTCZAK et al. 2002). Our data suggest that storks (both sexes) that eat more food experience a positive change in body mass (KWIECIŃSKI et al. 2006b). However, digestive efficiency affects the changes in body mass in different ways for males (generally positive) and females (generally negative). Although male and female body components and body size differed through the year (HALL & GWINER 1987), this is unlikely to explain differential mass change during this short-term experiment. Therefore, a simple explanation would be to look for a link between digestibility and body mass. Suggested explanations favour taking into account sexual differences according to ecological constraints. On the other hand, mechanical explanations are simpler and suggest that digestive efficiency is associated with body size, and differences between sexes occur because they differ in body mass as well.

Digestive efficiency is dependant on the nutrient content of the food, intestine surface, volume and enzyme activity (KARASOV 1990, 1996). In our experimental study, birds of both sexes received the same kind of food and we did not detect significant differences between males and females. Therefore, we suspect that digestion efficiency is related mainly to intestine length, differing significantly between sexes. Interestingly, this is in opposition to RICKLEFS (1996) prediction that the

bigger sex (males) has a shorter intestine. HILTON *et al.* (1999) in a study of raptors suggests that species with a relatively short intestine may effectively control digestion efficiency. A similar situation may apply to the white stork.

It should be emphasized that body mass strongly influenced and masked differences in digestion efficiency between the sexes. Mature males and females differ in body mass and intestine length, and digestive efficiency is a consequence of these two factors. A positive correlation between digestive efficiency and changes in body size in males and a lack of this relationship in females suggest different ecological strategies during foraging. Females should more effectively digest and control their body condition for egg production and a generally higher parental effort (HALL & GWINNER 1987). Moreover, at least during the breeding season, especially at the time of chick development (May-June, same period as in the experiment), males have more time for foraging, and therefore lower digestibility may be easily recompensated by access to more food, and hence the diet of males would be more diverse. However, to our best knowledge this hypothesis has not been tested.

In conclusion, the differences between males and females in digestive efficiency and especially the opposite direction of the effect of digestion on changes in body mass call for: (1) a description of the gastro-intestinal system of both sexes, and (2) information on diet segregation between sexes which entails more detailed field studies on marked individuals.

Acknowledgements

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