Digestibility of prey by the White Stork (*Ciconia ciconia*) under experimental conditions

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Food composition of the White Stork *Ciconia ciconia* has been widely studied by pellet analysis throughout Europe, but the effect of digestibility on pellet contents has remained unclear. We studied the effect of digestion on the composition of pellets (N= 480) under experimental conditions in Poznań Zoological Garden in 2004–2005. Twenty-four captive wild-born White Storks were fed mammals, birds, amphibians, fish, insects and earthworms. Only the remains of mammals, birds and insects were found in the regurgitated pellets. Bones were present in 13.1% of pellets. Three chosen osteological pellet components (skulls, mandibles and innominate bones) were analyzed to determine the amount of bone loss by digestion. The digestive efficiency was greater than 95%. Based on a literature review, we compared results of pellet analyses with methods not affected by digestion (direct observations and prey remains). The invertebrate: vertebrate ratio in the White Stork diet differed significantly between methods. Prey biomass rather than the number of prey items should be considered a better reflection of the diet.

1. Introduction

Food acquisition is one of the major factors determining ecological continuity of species and populations (Kendeigh *et al.* 1977, Walsberg 1983). However, the effectiveness of the use of food resources is determined by a variety of physiological and ecological factors (Newton 1998). Thus, research on food composition may play a vital role in determining foraging habitats and in the restoration of threatened species (Fasta-Bianchet & Apollonio 2003). Food resources and their availability, both on breeding and wintering areas, are key factors in understanding the population dy-

namics of the White Stork *Ciconia ciconia*, the focal species of this paper (e.g., Profus 1991, 2006, Struwe & Thomsen 1991, Tryjanowski & Kuźniak 2002, Tryjanowski *et al.* 2005, Ciach & Kruszyk 2010, Kruszyk & Ciach 2010).

The diet composition of White Storks has usually been assessed on the basis of direct observations under field conditions (e.g., Pinowska & Pinowski 1989, Pinowski *et al.* 1991, Struwe & Thomsen 1991, Dolata 2006) or pellet and food remains analysis (e.g., Pinowski *et al.* 1991, Antczak *et al.* 2002, Kosicki *et al.* 2006). However, both methods produce biased results due to difficulties in counting and identifying prey items (Pinowski

et al. 1991) and the fact that prey found under/in nests represent only those components that are rejected, such as items too large and hence difficult to swallow (Kosicki et al. 2006). Pellet analysis is the most frequently used method, where most of the components of pellets are easy to identify (e.g., Sziji & Sziji 1955, Pinowski et al. 1991, Boukhamza et al. 1995, Barbaud & Barbaud 1997, Antczak et al. 2002, Tsachalidis & Goutner 2002). Nevertheless, this method also has its limitations (Raczyński & Ruprecht, 1974, Marchesi & Pedrini 2002, Lewis et al. 2004, Tornberg & Reif 2007). High digestive efficiency by the White Stork, including digestion of vertebrate cartilage and bones (Sziji & Sziji, 1955, Schulz 1998, Antczak et al. 2002, Kwieciński et al. 2006a), could make this method inaccurate in identifying the precise diet of this species. Until now the scale of error made during determination of the qualitative and quantitative composition of White Stork diet on the basis of pellet analysis has not been shown. Experiments in which the kind and quantity of ingested food is controlled can reveal this error. Hitherto such an experiment has been conducted only in one species of the Ciconiiformes, namely the American Bittern Botaurus lentiginosus (Rhoades & Duke 1975), and for a few species of owls (Strigiformes) and birds of prey (Falconiformes) (Raczyński & Ruprecht 1974, Dodson & Wexlar 1979, Barton & Houston 1993).

The aim of the present paper was to investigate the digestibility of a number of basic prey items by the White Stork under experimental conditions, to check for respective sexual differences and compare findings with those available in the literature.

2. Material and methods

2.1. Study individuals

The experimental study was conducted in the Poznań Zoological Garden in 2004–2005 (May, June). We tested a total of 24 wild-born White Stork individuals (five males and seven females in 2004 and four males and eight females in 2005) acquired by the zoo due to various traumas, mostly wing injuries (Kwieciński *et al.* 2006). All White Storks were adults determined on the basis of beak and leg colour. Males weighed (mean ± SD) 3230

 \pm 0.360 g and females weighed 2797 \pm 0.340 g. Their sex was determined by using DNA techniques (Ćwiertnia *et al.* 2006). During research, all storks were individually marked with colour rings. The birds were kept inside individual cages of ca. 10 m² in size. The boxes were wire-netted to allow the birds visual contact with other individuals.

2.2. Feeding experiment

The feeding experiment lasted for 10 days for each individual. To reduce the stress caused by separation as well as close contact with humans, four to five birds took part in the single experiment simultaneously. Each individual was tested only once (ten days) during the research. The birds were fed with a diet consisting of six types of prey: mammals (captive-bred domestic mouse Mus musculus, shrews Sorex species, bank vole Clethrionomys glareolus, water vole Arvicola terrestris, pine vole Pitymys subterraneus, field vole Microtus agrestris, common vole Microtus arvalis, harvest mouse Micromys minutus, striped field mouse Apodemus agrarius, yellow-necked mouse Apodemus flavicollis and wood mouse Apodemus sylvaticus); birds (one-day-old chicks of Gallus gallus, and young chicks of Partridge Perdix perdix and Pheasant Phasianus colchicus); amphibians (brown frogs Rana temporaria, moor frog Rana arvalis); fish (sprat Sprattus sprattus, perch Perca fluviatilis, roach Rutilus rutilus, crucian carp Carassius carassius); insects (crickets Acheta domesticus, Gryllus bimaculatus and coleopterans of the family Carabidae [Carabus nemoralis, Carabus granulatus] as well as smaller beetles of the families Silphidae, Neerophoridae and Tenebrionidae) and annelids (earthworms Lumbricus species). The experimental diet was based on published data on the White Stork diet in the wild (Cramp & Simmons 1988, Pinowska & Pinowski 1989, Pinowska et al. 1991, Pinowski et al. 1991, Antczak et al. 2002). The food was presented in shallow, plastic containers on the basis of the 'Cafeteria test' the same time every day, i.e., at about 4 PM (Rychlik & Jancewicz 2002). Food items were counted and weighed separately for each food type using a Pesola balance to the nearest 0.2 g every day before presentation to each individual. The same protocol was followed in weighing uneaten food (for details, see Kwieciński *et al.* 2006a, b). Mean mass of each prey type and their percentage contribution to the overall diet, and the mean number of eaten prey items is presented in Table 1. Water was available *ad libitum* and changed daily. Before each experimental trial, White Storks were fasted for 24 hours to enable digestion of previously taken food and passing previously formed pellets.

The pellets of each individual were collected daily at 24 hours after food supply. Each pellet was weighed using a Pesola balance to the nearest 0.01 g of fresh mass. The pellets were stored at -20°C and were dried to a constant mass at 70°C, cooled in a desiccator and weighed using a Pesola balance to the nearest 0.01 g (Barton & Houston 1993). Water content (%) was calculated based on the difference between fresh and dry mass of the pellets. The pellets were subsequently soaked and washed through a sieve (1 mm mesh; see Antczak et al. 2002). The food remains were classified into four groups: osteological remains, insect remains (head capsules, fore legs, hind legs, elytrae, wings and mandibles), inorganic elements (stones) and fur. Due to their rare occurrence, other components (feathers, of which only one was found, seeds which were probably components of prey digesta) were not classified. The osteological remains were identified to class level (mammals, birds, etc.). Each classified group of bony remains was weighed using a Pesola balance to the nearest 0.01 g. The same protocol was followed for insect remains, stones and fur.

2.3. Pellet analysis

Pellet composition was expressed in (1) the mass of each component as a percentage of total fresh mass per pellet, and (2) the percentage of pellets containing each component. The effect of digestion on the osteological composition of the pellets was determined by analysing the numbers of skulls (craniums), mandibles (mandibulae) and innominate bones (ossa innominata). Apparent losses in prey skeleton and percentage of bones of prey digested by White Storks were calculated as the difference between the number of prey specimens eaten and the number of particular bony elements found in the pellets. This method is com-

Table 1. Food consumption of investigated White Storks (N = 24). The table shows mean daily number and mass \pm SD of food items consumed per White Stork individual, and the percentage contribution to the overall diet based on mass.

Таха	Number (n)	Mass (g)	Proportion in diet (%)	
Mammals	3.39 ± 1.78	73.81 ± 41.08	30.4	
Birds	4.66 ± 2.35	117.86 ± 57.72	48.5	
Amphibians	0.58 ± 0.96	4.88 ± 8.51	2.0	
Fish	3.43 ± 1.29	41.40 ± 15.04	17.0	
Insects	1.30±1.29	4.01 ± 3.62	1.6	
Earthworms	0.15±0.36	1.12 ± 2.77	0.5	

monly applied in determining losses in skeletons of eaten prey and allows for a comparison with results from similar studies of other bird groups, particularly owls and predatory birds (Raczyński & Ruprecht 1974, Dodson & Wexlar 1979, Kusmer 1990, Bocheński 2002).

2.4. Literature review

We reviewed the literature on the feeding habits of the White Stork in Europe in order to determine the effect of digestion on diet determination. Studies selected for numerical analysis met the following criteria. (1) Diet composition was estimated on the basis of a well-defined method. As we were mostly interested in digestive effects on food composition, the following methods were taken into account: prey composition established after digestion (pellet analyses: 32 studies), and those based on direct observations in the field and uneaten food remains found in nests (20 studies). (2) Food composition was expressed as a percent of a number and/or biomass of prey consumed (32 studies based on pellets, 20 studies for "non-digestion" methods, and in two studies using both methods). The studies included in the review evaluated between 23 and 103,042 (average 5883) prey items, with no significant difference in numbers between pellet and "non-digestion" methods (Student's ttest; t = 0.61, P = 0.544). Investigations from 29 localities in Europe met the above criteria (Appendix), covering a large part of the geographical range of the White Stork, from southern Denmark

Table 2. Number of vertebrate prey skulls (Cranium), mandibles (Mandibula) and innominate bones (Ossa innominata) found in pellets of captive White Stork males (N = 9) and females (N = 15), and percentages of undetected (digested) prey. Note that no amphibian or fish bones were found (i.e., were entirely digested). Sample sizes of analyzed male and female pellets are given in parentheses.

Sex/Bone type	No. prey eaten	Cranium		Mandibula		Ossa innom.	
		n	%	n	%	n	%
Males (225)	1,132	3	99.7	19	98.3	11	99.4
Females (255) Mammal bones	1,759	6	99.7	19	98.9	10	99.6
Males (225)	359	2	99.4	17	95.3	9	98.8
Females (255) Bird bones	454	6	98.7	19	95.8	10	98.9
Males (225)	421	1	99.8	2	99.5	2	99.8
Females (255) Amphibian bones	697	0	100.0	0	100.0	0	100.0
Males (225)	60	0	100.0	0	100.0	0	100.0
Females (255) Fish bones	78	0	100.0	0	100.0	0	100.0
Males (225)	292	0	100.0	0	100.0	_	_
Females (255)	530	0	100.0	0	100.0	_	-

to central Greece and from central Spain to western Belarus.

2.5. Statistical analyses

Between-sex similarities in diet composition were tested using Mann-Whitney U tests because the samples did not follow a normal distribution. Between-sex similarities in mammalian and avian bones in pellets were tested using chi-square test with Yates correction. Comparisons of pellet and "non-digestion" methods, based on data obtained from the literature, were carried out by first dividing detected diet components into two main categories: invertebrate and vertebrate remains. The first group covered mainly beetles (Coleoptera), orthopterans (Orthoptera) and earthworms (Lumbricidae), whereas the second group consisted mainly of voles (Microtidae), mice (Muridae), moles (Talpa europaea), scaled reptiles (Squamata) and frogs (Ranidae). Samples obtained from the pellet and "non-digestion" methods were then compared using an invertebrate: vertebrate ratio, based on both numbers found and on biomass, and subjected to Mann-Whitney U tests. All statistics were conducted following Zar (1999) and using SPSS for Windows.

3. Results

The White Storks regurgitated a total of 480 pellets (males 225, females 255). Males and females differed from each other significantly in terms of the mean number of regurgitated pellets (median 2.8 for males and 1.5 for females; Z = -2.74, P = 0.006), but not in pellet dry mass (mean \pm SD 5.10 \pm 2.02 g for males and 3.92 \pm 1.73 g for females; Z = -1.40, P = 0.161).

3.1. Pellet composition

The largest component of pellet fresh mass was water (65%) following by fur (33%), stones (1.3%), osteological remains (0.6%) and insects remains (0.1%). There were no statistically significant differences between the sexes in the mean mass of any particular pellet component (Mann-Whitney tests; P > 0.180 in all cases). Inorganic elements were found in 10% of pellets (males 8.9% and females 11.0% of pellets). Osteological remains were present in 13.1% of pellets (males: 11.0% and females 14.9% of pellets). Remains of insects were found in 13.5% of pellets (males 11.1% and females 15.7% of pellets).

Osteological remains consisted exclusively of

Table 3. Digestibility of invertebrates by captive White Stork males (N = 9) and females (N = 15). The columns show the number of items observed to be eaten, the number of items found in pellets, and the percent of items digested based on the two former values. Note that earthworm and orthopteran remains were not found (i.e., were entirely digested). Sample sizes of analyzed male and female pellets are given in parentheses.

Sex/remain type	No. eaten	No. found	% digested	
Earthworms				
Males (225)	26	0	100	
Females (255)	9	0	100	
Orthopterans				
Males (225)	72	0	100	
Females (255)	94	0	100	
Beetles				
Males (225)	91	64	29.7	
Females (255)	54	41	24.1	

fragments of mammal and bird skeletons. Elements of mammalian skeletons were found in 10.8% of pellets (males 9.8% and females 11.8% of pellets), whereas avian bones occurred in 2.3% of pellets (males 1.3% and females 3.1% of pellets). Males and females did not differ statistically significantly in terms of numbers of pellets containing mammalian bones (Chi-square test with Yates correction; df = 1; $\chi^2 = 0.231$, P = 0.63) or bird bones ($\chi^2 = 0.967$, Q = 0.33).

During the experiment, the median mass of bones in pellets of male storks was 0.26 g for mammalian and 0.18 g for bird bones (per stork over ten days), and for those of female storks the respective values were 0.00 g and 0.00 g, respectively. The sexes did not statistically significantly differ in mean mass of mammalian (Mann-Whitney test; Z = -0.209, P = 0.835) or bird bones (Z = -0.509, P = 0.610). Although birds constituted 48.3% and mammals constituted 30.2% of the diet by mass, bird bones amounted to only 11.5% of the total mass of recovered bones (Fisher's exact test; P < 0.0001)

3.2. Effect of digestion on pellet composition

Digestion efficiency of the analyzed bones was similar for both sexes. The storks digested between 95.3% and 100% of ingested bones, de-

pending on sex, prey taxa and the type of bone (Table 2). Skulls occurred in 1.2% of pellets (mammalian in 1.0%, avian in 0.2% of pellets). Mandibles were found in 4.8% of pellets (mammalian in 4.4% and avian in 0.4% pellets). Innominate bones were present in 2.7% of pellets (mammalian 2.5% and avian 0.2%). Fish and amphibians were digested entirely. Invertebrates were also digested to a high degree. Earthworms and orthopterans were digested entirely. However, for beetles 70.3% of ingested (and so expected) individuals were detected in pellets from male and 75.9% from female storks (Table 3).

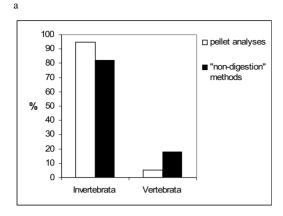
3.3. Comparison of pellet and "non-digestion" methods

According to the literature survey, invertebrates constitute on average 89.7% of all prey items (data from 53 studies, weighted by sample size), and vertebrates accounted for approximately 10.3% of all prey items. The invertebrate: vertebrate ratio, based on prey number in the White Stork diet, differed significantly between methods (Z=-3.57, P<0.001). The contribution of invertebrate prey in the diet based on pellet analyses was higher than that derived from "non-digestion" methods (Fig. 1a). However, the ratio based on consumed biomass did not reveal significant differences between the two methods (Z=-0.93, P=0.37; Fig. 1b).

4. Discussion

4.1. Pellet composition and digestive effect on pellet components

The findings of the present study demonstrate that White Storks digest their prey to a high degree, including prey bones, in agreement with published field investigations (e.g., Szijj & Szijj 1955, Schulz 1998). Similar to our results, Antezak *et al.* (2002) collected field data and found bones in 8% of White Stork pellets, whereas a fur analysis revealed that remains of *Microtus* voles occurred in 86.5% of pellets. Compared to other species, White Storks digest prey bones more efficiently than, for example, owls. Raczyński & Ruprecht



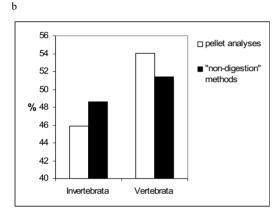


Fig. 1. Proportion of invertebrate and vertebrate prey as (a) numbers and (b) biomass in the White Stork diet as determined by pellet analysis and 'non-digestion' methods.

(1974) showed that owls digest between 5.3% and 78.6% of mammalian bones. This difference might be due to differences in the pH of stomach between storks and owls, but the pH of the gastric juice of the White Stork is not known. Duke et al. (1975) found that the pH of owl stomachs during digestion was 2.35, whereas that of diurnal raptors was 1.6. This result was reflected in differences in bone contents between pellets of owls and diurnal raptors: owl pellets contained distinctly more bones than those of diurnal raptors. We suspect that the pH of stork gastric juice is very low and quite similar to that of a diurnal raptor. We also suggest that small stones (diameter up to 1 cm), observed in White Stork pellets, may act as gastroliths. Thus, they could contribute to the fragmentation of swallowed food and increase the effectiveness of digestive enzymes through peristaltic movements of the stomach (Antczak *et al.* 2002, Z. Kwieciński, unpublished data).

Bones of birds tend to be thinner and lighter than those of mammals, in turn being more susceptible to chemical digestion and less likely to be present in pellets (Duke et al. 1973). Indeed, in the present study, bony remains of birds occurred less frequently and at a lower recovery rate than those of mammals. Higher digestion efficiency of avian bones may result not only from specificity of their structure but also that, as in our experiment, all prey birds were juveniles. Raczyński and Ruprecht (1974) showed that owls digest bones of juvenile mammals more efficiently than those of adult mammals. Perhaps the same applies to the digestion of avian skeletons. In field studies, bird remains have been found in 2.5% (Antezak et al. 2002) and 1.0% of examined pellets (Pinowski et al. 1991). In the light of the present results, the pellet-analysis based hypothesis that the proportion of birds in the diet would be very low or marginal (Pinowska & Pinowski 1989, Pinowski et al. 1991) becomes questionable. White Storks can and do utilize available avian prey, such as Whitewinged Tern (Chlidonias leucopterus) nestlings (Profus 2006).

Amphibians are traditionally considered a common component of the White Stork diet, and based on the present data are digested by this species almost entirely. Consequently, their remains rarely appear in pellets (Pinowski *et al.* 1991). Indeed, our experiment showed that no amphibian remains were found in the studied pellets. Similarly, these remains were not found by Antczak *et al.* (2002), and Pinowski *et al.* (1991) discovered amphibian remains in only 0.8% of pellets (N = 669), although direct observations suggested that this prey was commonly eaten by storks.

Fish remains were not detected in our examined pellets, although fish constituted 17.3% of the diet by mass. Thus, the efficiency of White Stork in digesting fish bones appeared very high. In other studies based on pellet analysis, these remains were often not found (Pinowski *et al.* 1991, Antczak *et al.* 2002). On the other hand, the absence of fish remains in pellets collected in natural conditions may also result from the fact that White Storks capture this type of prey only sporadically (Krapivny 1957, Pinowski *et al.* 1991, Kosicki *et al.* 2006).

A lack of earthworm and orthopteran remains in the pellets was probably associated with a very low contribution of both insects (1.6%) and earthworms (0.5%) to the food mass eaten by the investigated storks. However, the relatively high detection rate of beetles in the pellets probably resulted from the hardness of beetle exoskeletons and consequent low digestibility. Antezak et al. (2002) found earthworm remains in over 87% and insect remains in 100% of pellets, and their share of the diet mass averaged 11.5% and 22.8%, respectively. In other studies, the contribution of earthworms to food mass varied between 0 and 20% (see review in Schulz 1998). These differences are probably due to different methods applied in specifying the diet composition as well as variation in hunting-habitat types and hence different availability of prey (Pinowski et al. 1991, Antezak et al. 2002).

The finding that males regurgitated a greater number of pellets per day than females did, whereas the mean mass of pellets did not differ significantly between sexes, might be associated with differences in foraging strategies between the sexes. During the breeding season, males can invest more time for foraging (Sasva'ri & Hegyi 2001). Thus, emptying the stomach and intestines faster may be advantageous to them in enabling them to take prey items more often (Hilton et al. 1999, Barton & Houston 1993). This hypothesis may be supported by Kwieciński & Tryjanowski (2009) who showed that male White Storks have shorter digestive tracts than females have, resulting in a more rapid flow rate of digesta (Hilton et al. 1999).

4.2. Biases in the methods of diet analysis

The observed high digestive efficiency makes results from pellet analysis difficult to interpret. Our experiment showed considerable underestimation in frequency and biomass assessment of diet composition determined on the basis of pellet analysis. Compared to "non-digestion" methods, pellet analysis overestimated the number of invertebrate prey and underestimated the vertebrate prey. However, in terms of determined biomass, both methods gave similar results. Apart from the three most popular methods that we compared, other

diet assessment methods have been used in studies on the White Stork. These include stomach analyses, a leather cap put on chicks' beaks, and continuous video recording (see review in Kosicki *et al.* 2006). However, such methods are limited to single studies, or may be even prohibited for ethical reasons. Different methods differ in their results on diet composition (c.f. Rosenberg & Cooper 1990). Disparity between results derived from different methods of diet investigation have also been found for other species, such as the Red-backed Shrike (*Lanius collurio*; Tryjanowski *et al.* 2003, Goławski 2006), several species of diurnal raptors (e.g., Lewis *et al.* 2004, Tornberg & Reif 2007) and owls (e.g., Marchesi & Pedrini 2002).

The varying digestibility of different prey types can significantly limit the usefulness of pellet analyses. Thus, it is necessary to simultaneously use complementary methods, such as analyses of food remains along with direct observations. An additional methodological problem has recently arose due to a novel behaviour of the White Stork in Central Europe: foraging on rubbish dumps (Ciach & Kruszyk 2010, Kruszyk & Ciach 2010). Some rubbish are easy to detect but hard to quantify, whereas others, such as carrion and meat scrapes, are undetectable by current methods.

4.3. Conclusions

Our experiment showed that the value of White Stork pellet analysis may be limited, as it does not always produce an accurate estimate of the diet composition. Additionally, differences between results obtained from pellet analysis and methods not affected by digestion (analysis of prey remains, and direct observations) provide additional evidence against treating pellet analysis as a sole method. Therefore, in order to determine diet composition and predict the impact of food sources on local populations, both methods should be used simultaneously.

It is difficult to judge if one method is better than the others for accurate and detailed dietary studies of the White Stork. Hence, it is desirable to apply multiple methods simultaneously. If only one method can be used in a study (for economic, labour, or other reasons), the method chosen should be based on the goals of investigation. Finally, as our method comparisons indicated, prey biomass produces more accurate data than prey numbers in estimating diet composition.

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Kattohaikaran ravinnon sulayuus koeolosuhteissa

Kattohaikaran (*Ciconia ciconia*) ravintokoostumusta on Euroopassa tutkittu paljon oksennus- ja ulostepellettejä analysoimalla, mutta ravinnon sulavuuden vaikutus pellettien sisältöön on huonosti tunnettu. Tutkimme pellettien (*N* = 480) koostumusta kokeellisesti Poznańin eläintarhassa 2004–2005. Ruokimme 24 luonnossa syntynyttä, tarhattua kattohaikaraa nisäkkäillä, linnuilla, sammakkoeläimillä, kaloilla, hyönteisillä ja kastemadoilla. Oksennuspalloista löytyi vain nisäkkäiden, lintujen ja hyönteisten jäänteitä. Luita löytyi vain 13,1 % palloista.

Selvitimme myös ruuansulatuksen vaikutusta luiden häviämiseen analysoimalla kolme luukomponenttia (kallot, leukaluut ja nimeämättömät luut); häviäminen ylitti 95 %. Lisäksi vertailimme julkaistujen pellettianalyysien tuloksia menetelmiin, joissa ruuansulatus ei vaikuta tuloksiin (suorat havainnot ja saaliin jäänteet). Selkärangattomien ja -rankaisten suhde kattohaikaran ravinnossa vaihteli merkitsevästi menetelmien välillä. Ravinnon biomassa kuvannee ravintoa paremmin kuin syötyjen saalispartikkelien määrä.

References

- Antczak, M., Konwerski, S., Grobelny, S., Tryjanowski, P. 2002: The food composition of immature and nonbreeding white storks in Poland. — Waterbirds 25: 242–428.
- Barbaud, C. & Barbaud, J.C. 1997: Le re'gime alimentaire des poussins de cigogne blanche *Ciconia ciconia*, en Charente-Maritime: importance des insects. — Alauda 65: 259–262.
- Barbaud, C., Barbaud J.C., Barbaud M, Delord K. 2002: Recent changes in the feeding diet of white stork (*Ci*-

- conia ciconia) chicks in Charente Maritime (West France). Alauda 70: 437–444.
- Barton, N.W.H. & Houston, D.C. 1993: A comparison of digestive efficiency in birds of prey. Ibis 135: 363–371.
- Baudoin, G. 1973: Analyse de pelotes de rejection des cigognes (*Ciconia ciconia*) nicheuses á Hachy en 1972.
 Aves 10: 113–121.
- Bocheński, Z.M. 2002: Owls, diurnal raptors and humans: signatures of avian bones. In Biosphere to Lithosphere 9th ICAZ Conference (ed. Terry O'Connor): 31–45. Durham.
- Boehning-Gaese, K. 1992: Zur Nahrungsoekologie des Weissstorchs (*Ciconia ciconia*) in Oberschwaben: Beobachtungen an zwei Paaren. — Journal of Ornithology 133: 61–71.
- Boukhamza, M., Righi, M., Doumandii, S., Hamdine, W. 1995: Diet of the white stork *Ciconia ciconia* in the Kabyle region, Algeria. — Alauda 63: 199–207.
- Ciach, M. & Kruszyk, R. 2010: Foraging of white storks Ciconia ciconia on rubbish dumps on non-breeding grounds. — Waterbirds 33: 101–104.
- Ćwiertnia, P., Kwieciński, Z., Kwiecińska, H., Wysocki, A., Tryjanowski, P., Olsson, O. 2006: Sexing of white storks Ciconia Ciconia based on biometric measurements. — In The white stork in Poland: studies in biology, ecology and conservation (ed. Tryjanowski, P., Sparks, T.H. & Jerzak, L.): 423–429. Bogucki Wyd. Nauk, Poznań.
- Dodson, P. & Wexlar, D. 1979: Taphonomic investigation of owl pellets. Paleobiology 5: 275–284.
- Dolata, P.T. 2006: "Close to the storks" project of the white stork's *Ciconia ciconia* on-line nest monitoring, some examples and possibilities of such project's utility for the scientific researches. In The white stork in Poland: studies in biology, ecology and conservation (ed. Tryjanowski, P., Sparks, T.H., Jerzak, L.): 437–448. Bogucki Wyd. Nauk, Poznań
- Dolderer, P. 1956: Käfer und andere Beutetiere als Zeugen für das Jagdrevier des Weissen Storches. Aus die Heimat 64: 21–27.
- Duke, G.E., Ciganek, J.G., Evanson, O.A. 1973: Food consumption and energy, water, and nitrogen budgets in captive great horned owls (*Bubo virginianus*). — Comparative Biochemistry and Physiology 44A: 283–292.
- Duke, G.E., Jegers, A.A., Loff, G., Evanson, O.A. 1975:Gastric digestion in some raptors. Comparative Biochemistry and Physiology 50A: 649–656.
- Dziewiaty, K. 1992: Feeding ecology of the white stork Ciconia ciconia in the Dannenbrger Elbmarsch (Lower Saxony). — Vogelvelt 113: 133–144.
- Fasta-Bianchet, M. & Apollonio, M. 2003. Animal behavior and wildlife conservation. Island Press, Washington.
- Goławski, A. 2006: Comparison of methods for diet analysis and prey preference: a case study on the red-backed shrike *Lanius collurio*. Ornis Fennica 83: 108–116.

- Haverschmidt, F. 1949. The life of the white stork. Leiden, Holland.
- Hilton, G.M., Houston, D.C., Barton, N.W.H., Furness, R.W. 1999: Ecological constraints on digestive physiology in carnivorous and piscivorous birds. — Journal of Experimental Zoology 283: 365–376.
- Kendeigh, S.C., Dolnik, V.R., Gavrilov, V.M. 1977: Avian energetics. In Granivorous birds in ecosystems (ed. Pinowski, J. & Kendeigh, S.C.): 127–204. Cambridge Univ. Press, London.
- Kosicki, J.Z., Profus, P., Dolata, P., Tobółka, M. 2006: Food composition and energy demand of the white stork *Ciconia ciconia* breeding population. Literature survey and preliminary results from Poland. — In The white stork in Poland: studies in biology, ecology and conservation (ed. Tryjanowski, P., Sparks, T.H. & Jerzak, L.): 169–183. Bogucki Wyd. Nauk, Poznań.
- Krapivny, A. 1957: Nestling food of the white stork in Bialowieza Primeval Forest. Vesci Akad. Nauk BSSR, Ser. Bijal Navauk 1: 91–98.
- Kruszyk, R. & Ciach, M. 2010: White storks, Ciconia ciconia, forage on rubbish dumps in Poland – a novel behaviour in population. — European Journal of Wildlife Research 56: 83–87.
- Kusmer, K.D. 1990: Taphonomy of owl pellet deposition.— Journal of Paleontology 64: 629–637.
- Kuźniak, S. 1994: The White Stork Ciconia ciconia in the Middle Obra Valley in 1983–1992. — Pracownia Zakładu Biologii i Ekologii Ptaków UAM 3: 119– 130. (In Polish with English summary).
- Kwieciński, Z., Kwiecińska, H., Ratajszczak, R., Ćwiertnia, P., Tryjanowski, P. 2006a: Digestive efficiency of the white storks *Ciconia Ciconia* under laboratory conditions. In The White Stork in Poland: studies in biology, ecology and conservation (ed. Tryjanowski, P., Sparks, T.H. & Jerzak, L.): 195–201. Bogucki Wyd. Nauk, Poznań.
- Kwieciński, Z., Kwiecińska, H., Ratajszczak, R., Ćwiertnia, P., Tryjanowski, P. 2006b: Food selection of the white storks *Ciconia Ciconia* under captive conditions. In The white stork in Poland: studies in biology, ecology and conservation (ed. Tryjanowski, P., Sparks, T.H. & Jerzak, L.): 185–193. Bogucki Wyd. Nauk, Poznań.
- Kwieciński, Z. & Tryjanowski, P. 2009: Differences in digestive efficiency of the white stork *Ciconia ciconia* under experimental conditions. Folia biologica (Krakow) 57: 193–198.
- Lakeberg, H. 1995: Feeding ecology of the white stork Ciconia ciconia in Oberschwaben (S-Germany): feeding area, time budget, development of the young, and territoriality. Ökologie der Vögel: 17 (Sonderheft): 1–87
- Lázaro, E., Chozas, P., Fernández-Cruz, M. 1986: Breeding population of the white stork (*Ciconia ciconia*) in Spain. National census 1984. Ardeola 33: 131–170
- Lewis, S.B., Fuller, M.R., Titus, K. 2004: A comparison of

- three methods for assessing raptor diet during the breeding season. Wildlife Society Bulletin 32: 371–385.
- Marchesi, L. & Pedrini, P. 2002: Biases associated with diet study methods in the Eurasian eagle-owl. Journal of Raptor Research 36: 11–16.
- Newton, I. 1998: Population limitation in birds. Academic Press, London.
- Pinowska, B. & Pinowski, J. 1989: Feeding ecology and diet of the white stork *Ciconia ciconia* in Poland. In Weißstroch – White Stork. International Council for Birds Preservation (ed. Rheinwald, G. *et al.*): 381– 396. Walsrode.
- Pinowski, J., Pinowski, B., de Graaf, R., Visser, J., Dziurdzik, B. 1991: Influence of feeding habitat on prey capture rate and diet composition of white stork *Ciconia ciconia* (L). Studia Naturae A 37: 59–85.
- Profus, P. 2006: Population changes and breeding ecology of the white stork *Ciconia ciconia* L. in Poland against a background of the European population. Synthesis.

 Studia Naturae 1: 501–155.
- Raczyński, J. & Ruprecht, A. 1974: The effect of digestion on the osteological composition of owl pellets. — Acta ornithologica 24: 24–38.
- Rékási, J. 1975: Analyse der in Weisstorchnesten (Ciconia ciconia) gesammelten Gewölle. — Aquila 80/8: 282– 283
- Rhoades, D.D. & Duke, G.E. 1975: Gastric function in a captive American bittern. Auk 94: 786–792.
- Rosenberg, K.V. & Cooper, R.J. 1990: Approaches to avian diet analysis. — Studies in Avian Biology 13: 80–90.
- Rychlik, L. & Jancewicz, E. 2002: Prey size, prey nutrition and food handling by shrews of different body size. — Behavioural Ecolology 13: 216–223.
- Sackl, P. 1987: Über saisonale und regionale Unterschiede in der Ernährung und Nahrungswahl des Weisstroches (*Ciconia ciconia*) im Verlauf der Brutperiode. — Egretta 30: 49–80.
- Samusenko, I. 2000: Preservation of white stork (*Ciconia ciconia* L.) population in Belarussian Polessia. Final Report, MAB Young Research Project.
- Sasvári, L. & Hegyi, Z. 2001: Condition-dependent parental effort and reproductive performance in the white stork *Ciconia ciconia*. — Ardea 89: 281–291.
- Schierer, A. 1962: Sur le régime alientaire de la Cigogne blanche (*Ciconia ciconia*) en Alsace (Premiere contribution: analyse de 24 pelotes de rejection). — L'Oiseau 32: 265–268.
- Schulz, H. 1998: Ciconia ciconia White Stork. BWP Update 2: 69–105.
- Skov, H. 2003: Storken en kultur og natur historie. Og G.E.C. Gads Forlag, Křbenhavn.
- Skovgaard, P. 1920: Storkens Fřde. Danske Fugle 1: 2–9.
- Struwe, B. & Thomsen, K.M. 1991: Studies on the feeding ecology of white storks (*Ciconia ciconia*, L. 1758) at

- Berenhausen (Schleswig-Holstein, Germany). Corax 14: 210–238.
- Szijj, J. & Szijj, L. 1955: Contributions to the food-biology of the white stork (*Ciconia c. ciconia* L.). — Aquila 59: 83–94.
- Thomsen, K.M. & Struwe-Juhl, B. 1994: Vergleichende nahrungsökologische Untersuchungen an Weißstorch-Brutpaaren (*Ciconia ciconia*) in Stapelholm und im Kreis Herzogtum Lauenburg. — Corax 15: 293–308.
- Tornberg, R. & Reif, V. 2007: Assessing the diet of birds of prey: a comparison of prey items found in nest and images. Ornis Fennica 84: 21–31.
- Tryjanowski, P. & Kuźniak, S. 2002: Population size and productivity of the white stork *Ciconia ciconia* in relation to common vole *Microtus arvalis* density. — Ardea 90: 213–217.

- Tryjanowski, P., Karg, M.K., Karg, J. 2003: Food of the red-backed shrike *Lanius collurio*: a comparison of three methods of diet analysis. — Acta ornithologica 38: 59–64.
- Tryjanowski, P., Sparks, T.H., Profus, P. 2005: Uphill shifts in the distribution of the white stork *Ciconia ciconia* in southern Poland: the importance of nest quality. — Diversity and Distributions 11: 219–223.
- Tsachalidis, E.P. & Goutner, V. 2002: Diet of white stork in Greece in relation to habitat. Waterbirds 25: 417–423.
- Walsberg, G.E. 1983: Avian ecological energetics. In Avian Biology. (ed. Farner, D.S. & King, J.R.): 161– 220. Academic Press, New York.
- Zar, J.H. 1999: Biostatistical analysis. 4th ed. Prentice Hall, New Jersey.

Appendix. P = pellet analysis; nD = "non-digestion" methods (" – direct observations, " – food remain analysis, " – analysis of food vomited by chicks), N = number of pellets in pellet analyses, or number of observations in "non-digestion" methods; No. prey shows the number of prey items per study. Percent values are shown separately for invertebrates (invert.) and vertebrates (vert.).

Reference	Method	N	No. prey	% prey items		% biomass	
				Invert.	Vert.	Invert.	Vert.
Antczak et al. 2002	Р	163	5,958	97.2	2.8	34.5	65.5
Barbaud & Barbaud 1997	Р	11	305	80.7	19.3		
Barbaud et al. 2002	Р	676		100.0	0		
Baudoin 1973	Р	24	243	92.6	7.4		
Boehning-Gaese 1992	${\sf nD}^{\sf a}$		4,298	85.2	14.8		
Boukhamza et al. 1995	P	100		99.8	0.2	93.6	6.4
Dolderer 1956	P_ a	66	2,649	97.8	2.2		
Dziewiaty 1992	nD ^a	3,200	3,482	93.6	6.4	16.8	83.2
Haverschmidt 1949	Р	10	91	100.0	0		
Kosicki et al. 2006	nD⁵		23	43.5	56.5		
16 1 1057	nD°		278	79.9	20.1		
Krapivny 1957	nD ^a		261	87.0	13.0		
	nD ^a		439	74.0	26.0		
14 4 1 1 1001	nD ^a		2,895	97.0	3.0		
Kuźniak 1994	nD⁵	0.400	229	87.3	12.7		
Lakeberg 1995	nD ^a	2,166				96.7	3.3
	nD ^a	1,727				91.9	8.1
	nD ^a	2,325				43.6	56.4
	nDª	559	100.010			81.7	18.3
Lázaro et al. 1986	Р	1,064	103,042	99.3	0.7		
Pinowska & Pinowski 1989		669	3,135	84.2	15.8		
	nD ^a			75.3	24.7		
Profus 2006	nD⁵	_	302	69.5	30.5	9.6	90.4
Rékási 1975	Р	5	182	98.4	1.6		
Sackl 1987	Р	108	5,413	97.3	2.7	44.5	55.5
Samusenko 2000	P	69	1,413	96.2	3.8		
	Р	163	4,240	99.6	0.4		
	Р	140	1,758	97.7	2.3		
0.1: 4000	Р	76	523	90.6	9.4		
Schierer 1962	Р	125	1,350	93.6	6.4		
Skov 2003	Р	38	354	96.6	3.4		
Skovgaard 1920	Р	46	1,267	98.7	1.3	0.0	00.0
Struwe & Thomsen 1991	Р	448		67.0	33.0	2.0	98.0
	Р					51.5	48.5
	Р					85.0	15.0
	Р					90.8	8.2
	Р					5.0	95.0
	Р					63.9	36.1
	Р					25.0	75.0
	Р					29.7	70.3
	Р					25.0	75.0
	nD ^a					85.0	15.0
	nD ^a					50.0	50.0
	nD ^a					5.0	95.0
C-!!! 9 C-!!! 4050	nD ^a	0.7	4.000	00.4	0.0	25.0	75.0
Szijj & Szijj 1959	P ~Da	87	1,086	93.1	6.9	20.5	co =
Thomsen & Struwe 1994	nD ^a		8,572	94.9	5.1	39.5	60.5
Tanahalidia 9 Ossatza 2000	nD ^a		9,428	96.9	3.1	38.8	61.2
Tsachalidis & Goutner 2002			4,104	98.9	1.1		
	Р		7,656	97.8	2.2		
	Р		2,237	99.3	0.7		
	Р		6,746	99.3	0.7		