Selective Foraging of Grey Heron (*Ardea cinerea*) in Relation to Density and Composition of the Littoral Fish Community in a Submontane Dam Reservoir

ROBERT GWIAZDA[1,2] AND ANTONI AMIROWICZ[1]

[1]Karol Starmach Department of Freshwater Biology, Institute of Nature Conservation
Polish Academy of Sciences, Mickiewicza 33, 31-120 Kraków, Poland

[2]Internet: gwiazda@iop.krakow.pl

Abstract.—Grey Herons foraged in a high number only in one of three preferred foraging areas in the Dobczyce Reservoir, S. Poland: (1) the backwater area at the main tributary inlet (MTI), (2) the shore of the near-dam pool (NDP), and (3) shallow lateral bay (SLB). Median value of the fraction of herons foraging in MTI was 64% of all counted in the reservoir in 2001-2002 despite the smallest fish density there (2 times smaller than in NDP, and by one order of magnitude than in SLB). Roach (*Rutilus rutilus*) was the most abundant both in the heron diet (13 species) and in littoral fish communities (8 species). Total length of prey ranged within 4.2-26.5 cm. The individual size range of littoral fish was similar (4.6-31.5 cm). However, the size distributions in three foraging areas and in heron diet were different. Fish longer than the median total length of heron prey, i.e. ≥8 cm in total length constituted 51.9% of heron diet, 34.7% of the fish community in MTI, 8.5% in the psammolittoral of NDP, and only 5.2% in the phytolittoral of SLB. The strategy of selective choice of longer fish from those occurring at foraging sites allowed greater reward with roughly unchanged foraging cost. This may explain why Grey Heron foraged mainly in the habitat with the lowest fish abundance and highest water turbidity but with the largest prey size. *Received 25 July 2005. accepted 23 December 2005.*

Key words.—feeding strategy, food composition, foraging habitat, prey size.

Waterbirds 29(2): 226-232, 2006

Food supply is commonly regarded as an ecological factor ultimately controlling the size of bird colonies (Baxter and Fairweather 1998) and affecting individual foraging. Availability and richness of food of appropriate quality is also important and colonial birds often forage far from nesting or roosting sites (e.g., Hamilton *et al.* 1967). As the abundance of aquatic organisms is strongly determined by hydrological conditions in their habitats, such factors as water level fluctuation may be important for water birds (Ham 1975; Briggs *et al.* 1997; Dimalexis and Pyrovetsi 1997). Both the composition of the prey base and hydrological conditions are relatively diverse, unstable, and often unpredictable in dam reservoirs owing to the effects of dam operations. However, despite possible deviations from natural conditions, these artificial lakes, especially the lowland ones, are usually populated by rich bird communities (Feriancová-Masárová 1962; Stawarczyk and Karnaś 1992). Every species occurring there must cope with the challenge of artificially created and managed environments and flexible foraging strategies are needed. Herons may adopt different tactics and achieve variable foraging efficiencies in response to a particular lake, habitat conditions and prey characteristics (Dimalexis *et al.* 1997). Studies on such changes will help management of colonial waterbird species and to better understand elements of their life-history strategies.

Among bird species successfully colonizing Central European dam reservoirs are herons, the most common being the Grey Heron (*Ardea cinerea* L., 1758). This species occurs in shallow standing and flowing waters (Cramp and Simmons 1977; Voisin 1991; Del Hoyo *et al.* 1992) and its foraging habitats and prey vary widely among regions (Fasola 1994) as well as with season (Cramp and Simmons 1977; Voisin 1991; Del Hoyo *et al.* 1992). The composition of food of the Grey Heron has been studied in very different freshwater habitats such as rivers, deltas, and lakes (Owen 1955; Cook 1978; Fasola 1986; Moser 1986; Marquiss and Leitch 1990; Feunteun and Marion 1994). In contrast, diet of Grey Heron in colonies at dam reservoirs and the relations between diet composition and the available food base are poorly known (Gwiazda 2005). Some data concerning changes in the diet of this species, compared with changes in the composition of its food base following introductions of new fish species or extinction of some of the previously occurring ones have been presented (Peris *et al.* 1994; Adams and Mitchell 1995).

Assuming that the Grey Heron tends to (1) aggregate in habitats rich in food and (2) maximizes energy input in relation to foraging cost, some general assumptions concerning its foraging strategy may be made. Two possible elements of Grey Heron foraging strategy seem to be most important: selecting (1) the best of available foraging sites and (2) better prey items among those available at a foraging site. But, what makes a foraging site the best one? And which individual fish of those available is the best to select? The main aim of this study was to answer these questions taking into consideration the density, species composition, and size distribution in fish community in shallows of a medium-sized reservoir with a stable, slowly growing Grey Heron nesting colony.

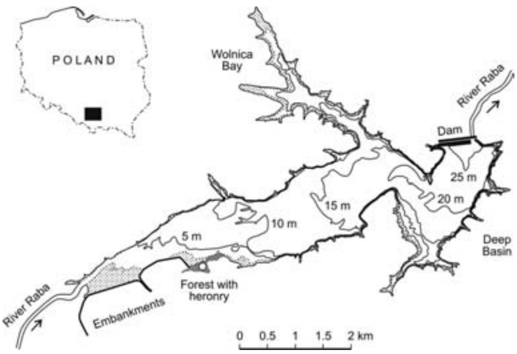

Figure 1. Grey Heron foraging areas in the Dobczyce Reservoir in 2001-2002. The breeding colony is marked with the open circle. Dotted area remained not used in 2002.

METHODS

Field work was carried out in 2001 and 2002. Three main foraging areas of Grey Heron in the reservoir were determined: (1) the backwater area at the Raba inlet located c. 1.3 km from heronry, (2) the western shore of the pool at the reservoir dam (the Deep Basin)—c. 3.8 km from heronry, and (3) the end of a shallow lateral bay (the Wolnica Bay)—c. 4.5 km from heronry (Fig. 1). Herons were counted from the shore once or twice a month from March till December (i.e., during the whole period without ice cover). On each counting, the same sectors of the shoreline were visited at each site. Their lengths were roughly equal in the Raba inlet (1.3 km) and the Wolnica Bay (1.4 km), while that in the Deep Basin was shorter (0.5 km).

Regurgitations were collected under nests from late May till early July 2002 when most nestlings were >20 days old. The undigested or partly digested fishes were identified to species. Undigested specimens were measured in the field while the total lengths of the partly digested ones were reconstructed on the basis of other biometric measurements (Amirowicz unpubl. data). In total, 94 fishes were recorded.

Fish community composition was assessed on the basis of catches obtained by using a small beach net (10 m wing length, 5 mm knot-to-knot mesh size) on 3 and 10 June 2002 at three sites selected within the Grey Heron feeding areas. At each site and date two hauls were taken in the shallow littoral (0-1 m). Contents of the net were stored separately and regarded as the catch per unit of effort (CPUE). Collected fish were measured and weighted. In total, 1203 fishes were caught.

Three tests were used in statistical analysis of the obtained results: (1) General Linear Model to compare the differences between numbers of herons observed in particular foraging places (SPSS 11.5.0), (2) the chi-square test to estimate the significance of the differences between fractions of dominant species in the heron diet and in the fish community, and (3) Kolmogorov-Smirnov two-sample test to determine differences in distribution of fish length in the diet of herons and at particular foraging site (Sokal and Rohlf 1987).

STUDY AREA

The study was carried out in the Dobczyce Reservoir (49°52'N, 20°02'E, altitude 270 m) on the Raba river (the Vistula basin, Carpathian Mts.) in southern Poland 30 km south of Cracow. This is a submontane eutrophic reservoir with an area of 985 ha, volume of 108 millions m^3, shoreline of c. 42 km and mean depth of 11 m (max. c. 27 m) (Fig. 1). According to the data of Regional Board of Water Management (RZGW), within the study period the fluctuations of water level were 4.1 and 3.0 m in 2001 and 2002, respectively. Only 4.8-5.7% of the total area in 2001 and 5.1-5.6% in 2002 fell into the shallow water zone (depth <1 m; calculated according to Amirowicz 1998). In general, the littoral zone in the Dobczyce Reservoir is narrow because of steep slopes of the inundated valley. Aquatic macrophytes were scarce.

The fish community consists of 19 species (Amirowicz 2000). The dominants are cyprinid, Roach (*Rutilus rutilus*), Bream (*Abramis brama*), Bleak (*Alburnus alburnus*), and percid species, Perch (*Perca fluviatilis*), and Pikeperch (*Stizostedion lucioperca*). Subdominants are White Bream (*Blicca bjoerkna*)), Rudd (*Scardinius erythrophthalmus*), and Chub (*Leuciscus cephalus*). Remaining eleven species were relatively rare.

Grey Herons were present since the reservoir was created in 1986 (Gwiazda 1989) but breeding was not recorded until 1999 (Gwiazda 2000). In 2001 and 2002, 44 and 53 nests were occupied in the small forest of about 8 ha (Fig. 1). Human access in the shore zone is strictly limited (the reservoir stores water for municipal purposes) and the waterfowl is not disturbed.

RESULTS

Number of Herons and Fish Abundance in Foraging Areas

The number of Grey Herons counted changed during the period of study, however, in both years it followed a similar annual pattern with peaks in June (70 individuals in 2001, and 76 in 2002) (Fig. 2). Herons foraged in the highest number in the Raba inlet (Fig. 1). The other two foraging areas were visited by smaller numbers of birds. The differences between the number of herons using the sites are significant (ANOVA: $F_{2,63} = 8.644$, $p = 0.017$). No interactions between the number of herons and time were found. Median value of the fraction of herons foraging in the Raba inlet in 2001-2002 was equal to 64% of all counted herons in the reservoir (first quartile—53%, third quartile—84%, N = 18). This pattern remained the same (the Raba inlet: median values—20 and 20.5; Deep Basin: 3 and 0.5; Wolnica Bay: 1 and 5.5 in 2001 (N = 7) and 2002 (N = 8), respectively) and the difference was even more significant (ANOVA: $F_{2,43} = 69.479$, $p = 0.0031$) after excluding from the data set the counts done in June-August when juvenile herons left nests and probably foraged close to the colony.

The density of fish available to herons taken as the CPUE was the greatest in the Wolnica Bay (mean = 250, SD = 271, N = 4), smaller by one order of magnitude in the shore zone of the Deep Basin (mean = 32, SD = 55, N = 4), and the smallest in the Raba inlet area (mean = 18, SD = 10, N = 4). In that last foraging area, the coefficient of variation (i.e., the mean value to SD ratio) was also the smallest being about two times smaller than in the Wolnica Bay, and three times less than in the Deep Basin.

Fish Species Composition

The diet of Grey Heron included 13 fish species, but we caught only eight of those in the littoral. Roach was the most abundant making up 38% by number in the diet of Grey Heron and 76-93% in the sampled communities (Fig. 3). Pikeperch and Perch constituted 20% and 16% of the diet, respectively and ranked as the species of high importance. In the littoral, Perch constituted 1-10% of the fish community while Pikeperch was less abundant (3%; collected only in the Raba inlet). A high fraction of Pikeperch in heron diet was caused by the relatively abundant presence of juveniles of this species (5-7 cm total length) in early July in the shallow littoral. Probably earlier this fish was too small to catch and later it occurred in other sites.

In general, Roach and Perch constituted the overwhelming majority (86-94%) of fish collected in all foraging areas and therefore the fish community composition may be regarded as quite similar everywhere. Rheophilous fishes, i.e. Chub, and especially Spotted Barbel (*Barbus petenyi* Heckel) and Gud-

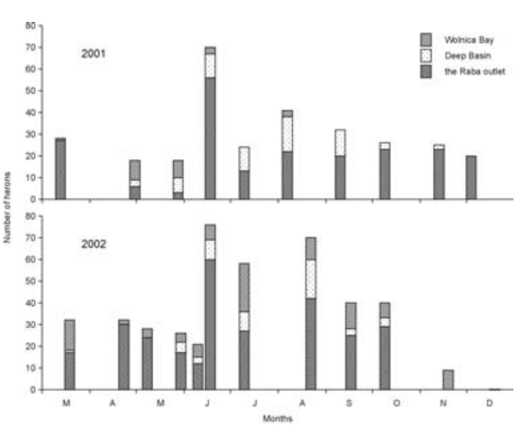

Figure 2. The annual pattern of the numbers of Grey Heron in the foraging areas at the Dobczyce Reservoir.

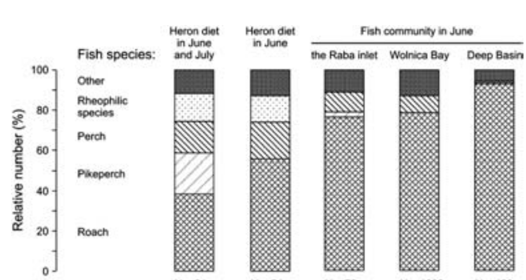

Figure 3. Fish species composition in the diet of Grey Heron and in fish communities at its three main foraging areas of the Dobczyce Reservoir in 2002. The category of other species includes common bream, giebel, common carp, crucian carp, silver bream, bleak, and ruffe in the Heron diet, and ruffe, bleak, common bream, and silver bream in the fish community.

geon (*Gobio gobio* (L.)) which were taken by Grey Heron from the Raba channel out of reservoir constituted slightly less than 14% of all fish in its diet. The remaining seven species were recorded in the diet in single or few specimens.

Comparing fish species composition in the littoral fish samples and in the diet of Grey Heron in the same period (i.e., in June 2002 only), some similarities and differences were found (Fig. 3). The dominant species in littoral and in heron diet was Roach (up to 56%). Also, Perch abundance was high both in littoral samples and in heron diet (18%). However, the difference between the proportions of these two species in the fish samples and diet was statistically significant in the Wolnica Bay ($\chi^2 = 9.582$, df = 1, $P < 0.01$). In the Raba inlet this difference was not significant ($\chi^2 = 3.290$, df = 1, n.s.) but the chi-square test proved that there was a significant difference between the composition patterns consisting of three categories, i.e., Roach, Perch, and other species including the rheophilous fishes and Pikeperch ($\chi^2 = 6.102$, df = 2, $P < 0.05$). In the Deep Basin, difference between proportions of Roach and all remaining species was significant ($\chi^2 = 36.153$, df = 1, $P < 0.001$). Thus, the composition of Grey Heron diet differs to some extent from the species composition of fish communities of its foraging areas.

Fish Length in Grey Heron Diet and in the Fish Community

Fish eaten by Grey Heron ranged 4.2-26.5 cm (median 7.5 cm, first quartile 6.2 cm, third quartile 12.0 cm, N = 92). Although size range in the collected samples of littoral fish communities was similar to heron diet (e.g., 4.6-31.5 cm), the size distribution differed (Fig. 4). In the period when adult herons fed young, fish ≥8 cm (i.e., longer than the median total length of heron prey) constituted 51.9% of heron diet. At the same time this fish length category constituted 34.7% in the Raba inlet area, 8.5% in the littoral of the Deep Basin, and only 5.2% in the Wolnica Bay. The differences between fish length distribution in the heron diet and

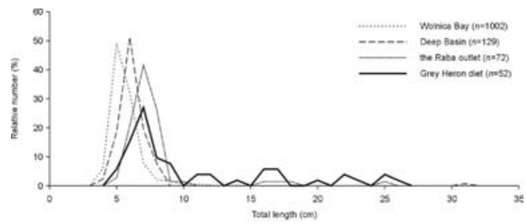

Figure 4. Distribution of fish total length in the diet of Grey Heron and in the littoral fish communities at its three main foraging areas of the Dobczyce Reservoir in June 2002.

in the littoral fish communities were significant ($\chi^2 = 18,98$, $P < 0.001$, and $\chi^2 = 36.96$, $P < 0.001$, respectively) in the Deep Basin and the Wolnica Bay but not in the Raba inlet where the fraction of large fish was greater. This suggests selection by herons of the larger individuals of available fish.

DISCUSSION

Site Selection

The Raba inlet was a site favored by the majority of foraging Grey Herons, undoubtedly, due to open flat areas with shallows in backwaters of the reservoir. Morphological features ensured the permanent existence of water pools, extensive shallow areas of submerged bottom and muddy islands or sandbanks despite the changes in reservoir damming activities. Of note is the fact that the colony of Grey Heron was initiated in the Dobczyce Reservoir after few years with especially good habitat conditions (Gwiazda 2003).

The additional advantage of the Raba inlet area was its proximity to the heronry. Maximum numbers of Grey Herons recorded at the Dobczyce Reservoir in early summer, mainly in the Raba inlet may be explained by the presence of newly fledged birds. However, they were observed in considerable numbers as early as in the end of June not only in the Raba inlet but in both other foraging sites as well. The increased numbers of herons in autumn were associated with the arrival of migrating birds.

In the rocky littoral zone of a Scottish sea loch, adult Grey Herons showed a preference for foraging in an area of high fish species richness and abundance (Carss and Elston 2003). However, we found herons were the most numerous in backwaters at the Raba inlet, with relatively low fish density. In general, high fish numbers in the shallows of the Dobczyce Reservoir is characteristic of Wolnica Bay. Also the results of Jelonek and Godlewska (2000) showed that fish density was four to ten times greater in the Wolnica Bay than in other parts of reservoir. Those differences and these in the CPUE in our study may be explained by different habitat conditions in particular foraging areas. The shallow and relatively well vegetated littoral in the Wolnica Bay offers the best nursery habitat to fish fry and juveniles. The bare psammolittoral and the most oligotrophic conditions in the Deep Basin are considerably less advantageous to fish. In the Raba inlet the water is rich in nutrients but turbid owing to the suspended mineral particles, and therefore poor in plankton, an important fish food. Therefore, heron foraging efficiency may be the lowest (but most predictable, *vide* lower coefficient of variation) in the Raba inlet.

It seems evident that the density of fish in shallow water was not the main factor determining the choice of foraging location by Grey Heron. Possibly, fish species or length was a key factor in this case. At two different types of rice fields, despite different density and biomass of prey organisms, no differences in the number of Grey Herons were recorded (Lane and Fujioka 1998). Small numbers of fish greater than 10 cm in length in both systems resulted in neither rice fields type as good foraging habitats for herons.

Prey Selection

In the foraging areas of Grey Heron, eight fish species were caught, or less than half of the total of 19 species recorded in the reservoir (Amirowicz 2000). This result reflects the differences in relative abundance of particular species in the littoral zone. Four hauls per site gave us the possibility to collect the most abundant fishes, while more repetitions seem to be necessary for the rare ones. Herons were more effective in sampling rare species. They are Giebel *Carassius auratus gibelio* (Bloch), Common Carp *Cyprinus carpio* L., and Crucian Carp *Carassius carassius* (L.), which were recorded in the reservoir since its origin both in research and commercial catches, however, in very low numbers. The remaining eight species of the reservoir fish community were recorded neither in littoral, nor in heron diet in this study. It should also be stressed that almost all of the 13 species present in the Grey Heron diet occur in the littoral fish community of the reservoir. The only exceptions were Spotted Barbel and Gudgeon which occurred only in lotic habitats in the Raba channel above its inlet into the reservoir.

Grey Heron usually eat fish 10-25 cm long, although fish up to 40 cm (Del Hoyo *et al.* 1992) and eels to 60 cm may be taken (Owen 1955, Cramp and Simmons 1977). Fasola (1994) found that Grey Heron diet was characterized by specific prey weights within the range of 0.01-82 (126) g DW in southern Europe. Similarly Owen (1955) found at three heronries in Great Britain, the size range of the same fish species caught at the Dobczyce Reservoir was wide (5-25 cm and 4.2-26.5 cm, respectively) but most of them were of small or medium size (interquartile range 6.2-12.0 cm in our study). In Wytham colony, fish were caught selectively too and those between 10-16 cm were most frequently taken (Owen 1955). Also in the Arcachon Bay (southwest France) relatively small (12-18 cm) and medium (19-25 cm) sized fishes (mainly eels) were caught more frequently by breeding Grey Herons in May-June (Lekuona 1999).

The fact that larger fish were more often found in the food of Grey Heron than in the littoral fish community in the Dobczyce Reservoir may be explained simply by the preference by herons of larger prey. Even in the situations of high abundance of small fish and relatively small costs of hunting (Voisin 1991), herons probably did not attack every small fish but waited for larger prey. According to Feunteun and Marion (1994) size could play an important role in the choice of prey. In their study of Grey Herons at Grand-Lieu's Lake (France) preference for largest sizes of Catfish (*Ictalurus melas* (Raf.)) (18-34 cm) and the neglect of smaller ones was recorded. In contrast, small species such as Three-spined Stickleback (*Gasterosteus aculeatus* L.) were not found in the diet, whereas they were very numerous in habitats. Under experimental conditions, captive Grey Herons selected larger individuals of Mosquito Fish (*Gambusia affinis)* (Britton and Moser 1982). Herons consumed almost exclusively *Gambusia* females which are much larger than males, even when offered in ratios where they were outnumbered by males.

It may be concluded that for Grey Heron it is more profitable to forage on large fish. Relative costs of hunting of larger fish are probably similar or only a little higher while the benefit of prey body mass is much greater because it rises with the third power of linear dimension. Spatial distribution of foraging Grey Herons during the breeding season is probably determined by a trade-off between costs and benefits of foraging area versus site fidelity (Van Vessem and Draulans 1987). Therefore, the strategy of the selective choice of longer fish from those occurring in a foraging place makes it possible to obtain more energy with roughly comparable costs. Thus, the best foraging site is perhaps that where larger fish can be encountered. Probably this may explain why Grey Herons foraged mainly in the "worst" habitat (i.e., with low fish abundance and high water turbidity) in the Dobczyce Reservoir.

LITERATURE CITED

Adams, C. E and J. Mitchell. 1995. The response of a Grey Heron *Ardea cinerea* breeding colony to rapid change in prey species. Bird Study, 42: 44-49.

Amirowicz, A. 1998. Consequences of the basin morphology for fish community in a deep-storage submontane reservoir. Acta Hydrobiologia 39 (1997), Suppl. 1: 35-56.

Amirowicz, A. 2000. Pozycja ryb w sieci troficznej litoralu [Participation of fish species in food web of the littoral zone]. Pages 215-221 *in* Zbiornik Dobczycki: Ekologia-Eutrofizacja-Ochrona [The Dobczyce Reservoir: Ecology-Eutrophication-Restoration] (J. Starmach and G. Mazurkiewicz-Boroń, Eds.). Kraków, Karol Starmach Institute of Freshwater Biology [in Polish].

Baxter, G. S. and P. G. Fairweather. 1998. Does available foraging area, location or colony character control the size of multispecies egret colonies? Wildlife Research 25: 23-32.

Briggs, S. V., S. A. Thornton and W. G. Lawler. 1997. Relationships between hydrological control of River Red Gum wetlands and waterbird breeding. Emu 97: 31-42.

Britton, R. H. and M. E. Moser. 1982. Size specific predation by Herons and its effect on the sex-ratio of natural populations of the mosquito fish *Gambusia affinis* Baird and Girard. Oecologia 53: 146-151.

Carss, D. N. and D. A. Elston. 2003. Pattern of association between algae, fishes and grey herons *Ardea cinerea* in the rocky littoral zone of a Scottish sea loch. Estuarine Coastal and Shelf Science 58: 265-277.

Cramp, S. and K. E. L. Simmons (Eds). 1977. The Birds of the Western Palearctic, Vol. 1. Oxford University Press, Oxford.

Cook, D. C. 1978. Foraging behaviour and Food of Grey Herons *Ardea cinerea* on the Ythan Estuary. Bird Study 25: 17-22.

Del Hoyo, J., A. Elliott and J. Sargata. 1992. Handbook of the Birds of the World (Vol. 1). Lynx Edicions, Barcelona.

Dimalexis, A. and M. Pyrovetsi. 1997. Effect of water level fluctuations on wading bird foraging habitat use at an irrigation reservoir, Lake Kerkini, Greece. Colonial Waterbirds 20: 244-252.

Dimalexis, A., M. Pyrovetsi and S. Sgardelis. 1997. Foraging ecology of the Grey Heron *(Ardea cinerea*), Great Egret (*Ardea alba*) and Little Egret (*Egretta garzetta*) in response to habitat, at two Greek wetlands. Colonial Waterbirds 20: 261-272.

Fasola, M. 1986. Resource use of foraging herons in agricultural and nonagricultural habitats in Italy. Colonial Waterbirds 9: 139-148.

Fasola, M. 1994. Opportunistic use of foraging resources by heron communities in southern Europe. Ecography 17: 113-123.

Feriancová-Masárová, Z. 1962. Bedeutung der Stausperre Oravská Priehrada für den Zug und das Nisten der Wasservogel. Biologia (Bratislava) 17: 340-354 [in Czech with German summary].

Feunteun, E. and L. Marion. 1994. Assessment of Grey Heron predation on fish communities: the case of the largest European colony. Hydrobiologia 279/280: 327-344.

Gwiazda, R. 1989. Initial stage of bird settlement on the Dobczyce dam reservoir (Vistula basin, southern Poland). Acta Hydrobiologia 31: 373-384.

Gwiazda, R. 2000. Awifauna i inne kręgowce [Avifauna and other vertebrates]. Pages 149-162 *in* Zbiornik Dobczycki: Ekologia-Eutrofizacja-Ochrona [The Dobczyce Reservoir: Ecology-Eutrophication-Restoration] (J. Starmach and G. Mazurkiewicz-Boroń, Eds.). Karol Starmach Institute of Freshwater Biology, Kraków [in Polish].

Gwiazda, R. 2003. Changes in the piscivorous bird community at Polish submontane reservoir between 1990 and 2000 in relation to water level. Pages 211-220 *in* Interaction Between Fish and Birds: Implication for Management (J. Cowx, Ed.). Blackwell Science Ltd., Oxford.

Gwiazda, R. 2005. Diet composition and changes in numbers and foraging areas of grey heron Areda cinerea population in a submontane reservoir: an effect of dam operation. Acta Zoologica Sinica 51: 215-221.

Ham, I. 1975. Fluctuations in numbers of heron couples (Ardeidae) in the inundation area of the Begej river (Carska bara) during the period 1950-1976. Arhiv bioloskih nauka, Beograd 27: 61-68 [in Serbian with English summary].

Hamilton, W. J. III, W. M. Gilbert, F. H. Heppner and R. J. Planck. 1967. Starling roost dispersal and hypothetical mechanism regulating rhythmical animal movement to and from dispersal centers. Ecology 48: 825-833.

Jelonek, M. and M. Godlewska. 2000. Ichtiofauna [Ichthyofauna]. Pages 149-162 *in* Zbiornik Dobczycki: Ekologia-Eutrofizacja-Ochrona [The Dobczyce Reservoir: Ecology-Eutrophication-Restoration (J. Starmach J. and G. Mazurkiewicz-Boroń, Eds.). Karol Starmach Institute of Freshwater Biology, Kraków [in Polish].

Lane, S. J. and M. Fujioka, M. 1998. The impact of changes in irrigation practices on the distribution of foraging egrets and herons (Ardeidae) in the rice fields of Central Japan. Biological Conservation 83: 221-230.

Lekuona, J. M. 1999. Food and foraging activity of grey herons, *Ardea cinerea*, in a coastal area during the breeding season. Folia Zoologica 48: 123-130.

Marquiss, M. and A. F. Leitch. 1990. The diet of Grey Herons *Ardea cinerea* breeding at Loch Leven, Scotland, and the importance of their predation on ducklings. Ibis 132: 535-549.

Moser, M. E. 1986. Prey profitability for adult Grey Herons *Ardea cinerea* and the constrains on prey size when feeding young nestlings. Ibis 128: 392-405.

Owen, D. F. 1955. The food of the Heron (*Ardea cinera*) in the breeding season. Ibis 97: 276-295.

Peris, S. J., F. J. Briz and F. Campos. 1994. Recent changes in the food of the Grey Heron *Ardea cinerea* in central-west Spain. Ibis 136: 488-489.

Sokal, R. R. and J. Rohlf. 1987. Introduction to biostatistics. W. H. Freeman and Company, New York.

Stawarczyk, T. and A. Karnaś. 1992. Succession of breeding waterfowl in 1977-1991 on Turawski Reservoir. Birds of Silesia 9: 1-15 [in Polish with English summary].

Van Vessem, J. and D. Draulans. 1987. Spatial distribution and time budget of radio-tagged grey herons, *Ardea cinerea*, during the breeding season. Journal of Zoology (London) 213: 507-534.

Voisin, C. 1991. The herons of Europe. T & AD Poyser, London.