

Dariusz Jakubas

Factors affecting the breeding success of the grey heron (*Ardea cinerea*) in northern Poland

Received: 5 April 2004 / Revised: 9 July 2004 / Accepted: 13 July 2004 / Published online: 9 September 2004
© Dt. Ornithologen-Gesellschaft e.V. 2004

Abstract The aim of this study was to estimate the importance of factors affecting the breeding success of the grey heron (*Ardea cinerea*) in three colonies in the northern Poland (Mosty, Kiersity and Kąty Rybackie), differentiated in population size, habitat type and feeding areas used by birds. The highest mean number of fledglings (39–51 days old) per nest in 2000–2002 combined was recorded at Kąty Rybackie (3.2 ± 0.91 SD). Lower values were recorded at Kiersity (2.5 ± 1.11) and Mosty (2.8 ± 1.20). Breeding success increased with the size of the heronry ($r_7 = 0.77$, $P < 0.05$) and was the highest in the biggest, at Kąty Rybackie (716–879 nests). In the studied colonies, the number of feeding visits was the most important factor affecting breeding success. At Kąty Rybackie and Kiersity, chick mortality significantly decreased with increasing numbers of feeding visits per nest. The highest breeding success was recorded in the colonies with feeding areas situated nearby (Kąty Rybackie and Mosty). Siblicide was also a very important reason of chick mortality in those colonies (54% and 32% chicks died in nests where sibling aggression was observed). Other factors, independent of the level of feeding, like predation, human disturbance, weather condition and experience of parent birds, seem to be of negligible importance.

Keywords Breeding success · Chick mortality · Colony size · Number of feeding visits · Siblicide

Introduction

The breeding biology of the grey heron *Ardea cinerea* is well documented in Europe (e.g. Lowe 1954; Owen 1960; Milstein et al. 1970; Creutz 1981; Utschick 1982; Stotskaja 1983, 1984; van Vessem and Draulans 1987; Czapulak and Adamski 2003). However, few data have been published about factors influencing the breeding success and the importance of the individual factors (Owen 1960; van Vessem and Draulans 1986 a, 1986b, 1986c; Marion 1989).

Evidence that food is a limiting factor during the breeding season exists for a number of altricial birds (Drent and Draan 1980; Martin 1987). However, there are some other external environmental factors (natural enemies, such as predators and parasites, atmospheric conditions, illness and human disturbance) and intrinsic factors (clutch size, age structure of local population) independent of food abundance which affect the breeding success. Particular populations may be affected by more than one, perhaps all, of the different factors, but often one factor emerges as of overriding importance at any one time. Different factors can sometimes act together. One factor might enhance or reduce the effect of another, so that their combined impact on population levels is greater or less than the sum of their individual effects (Newton 1998).

The aim of this study was to estimate the importance of factors affecting the breeding success of the grey heron in colonies differentiated in size, habitat type and feeding areas used by birds.

Methods

All three studied heronries are situated in the northern Poland (Fig. 1). The colony at Mosty (54°37'N, 18°29'E) is situated in the Reda Valley, 10 km north off Gdynia, 1.7 km from the Gulf of Puck coast (the Baltic Sea). There were 279–412 nests in 2000–2002 in common alder (*Alnus glutinosa*) in a small wood. The heronry is

Communicated by F. Bairlein

D. Jakubas
Department of Vertebrate Ecology and Zoology,
University of Gdańsk, al. Legionów 9, 80–441 Gdańsk,
Poland
E-mail: biodj@univ.gda.pl
Tel.: +48-58-3410360
Fax: +48-58-3412016

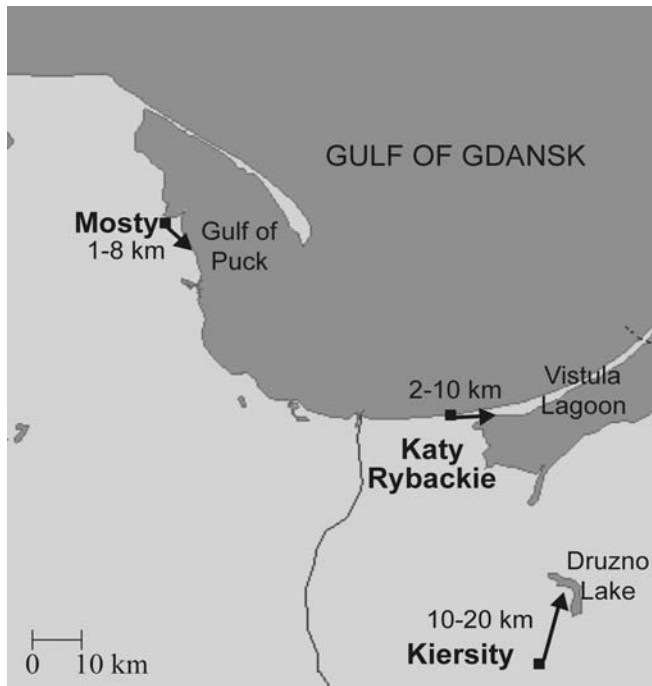


Fig. 1 Localities of studied heronries and main directions and distances of the foraging flights of grey herons (*Ardea cinerea*)

periodically exposed to strong winds. The colony adjoined buildings in Mosty village.

The colony at Kiersity (53°57'N, 19°28'E) is situated in the Iawa Lake District, 10 km south off Druzno Lake. This is an inland colony, situated away from the sea coast. There were 215–277 nests in 2000–2002 in 140-year-old pedunculate oak (*Quercus robur*) in a small wood on the shore of the Korsuń Lake (22.5 ha). Human activity in the colony is low.

The colony at Kały Rybackie is situated in the Kały Rybackie reserve in the Vistula Spit (54°21'N, 19°14'E), 100 m from the Gulf of Gdansk (the Baltic Sea) shore and 2 km from the Vistula Lagoon. This colony is mixed with the cormorants (*Phalacrocorax carbo*) and is the biggest of the three studied. There were 716–879 nests in 2000–2002 in Scot's pine (*Pinus sylvestris*) in the coastal pine forest. Because of the coastal locality, the colony is periodically exposed to strong winds.

In 2000–2002, all occupied nests in the studied colonies were noted. Trees with nests were individually marked with a tape. The number of chicks in nests and the frequency of feeding visits of parent birds (number of feedings per nest) were recorded. Each year four to eight all-day observations (from dawn to dusk) of 21–42 nests in the nestling period (from the end of April to the end of June) were performed (Table 1). The nests were observed from the distance of 10–50 m by one or two people in blinds situated on mounds.

The number of chicks and the number of feedings per nest were analysed in three age categories: medium-aged chicks (21–27 days old), large chicks (28–38 days) and fledgling stage (39–51 days). Counting chicks at each age

Table 1 Number of observations and nests in all studied colonies of grey heron (*Ardea cinerea*) in 2000–2002

Number	Season	Colony		
		Mosty	Kiersity	Kały Rybackie
Daylong observations	2000	5	4	4
	2001	7	7	7
	2002	8	8	8
	Total	20	19	19
Observed nests	2000	21	24	29
	2001	24	35	33
	2002	25	33	42
	Total	70	92	104

stage was performed in all visible nests (sample sizes were dependent on the visibility related mainly to stage of leaves development). Data for younger chicks (up to 21 days) were not considered because of difficulty in counting very small chicks.

The chick mortality was considered as the percentage of chicks which died between two age categories: medium-aged chicks and fledgling stage in the observed nests. Final breeding success was considered as the mean number of fledglings per nest.

Nests in which at least one instance of aggressive behavior or the effects of it (pecking the youngest chick, moving it outside the nest or observations of dead chick in the nest; precise description in Jakubas 2004a) were noted at least once during observations, were considered to be at risk to sibling aggression.

The collection every 7–10 days of all eggshells (destroyed and successfully hatched) on the ground below the nests during the incubation and hatching periods in all colonies allowed the estimation of the number of eggs destroyed by nest predators (such shells had distinct crevices made by a predator's beak). At Mosty and Kiersity, the eggshells were collected in the whole colony area, at Kały Rybackie in the plot with 170 nests.

The main foraging areas of herons from studied colonies were identified by the observations from a helicopter (two flights in 1999 in the vicinity of heronries at Mosty and Kały Rybackie) and by searching of potentially attractive places (chosen after studying topographic maps) on foot (for all colonies). The distances between the feeding areas and the colony was measured from the topographic maps.

The data were analysed with ANOVA, Student *t*-test, Chi-square test (Yates' correction was used in all 2×2 chi-square tests; Zar 1990) and Pearson's correlation coefficient.

Results

Mean number of chicks per brood

The mean number of nestlings per brood with medium-aged chicks was 3.4–3.7 and with fledglings was 2.5–3.2

Table 2 Mean brood size in three chick age categories in 2000–2002 combined (paired letters *a, b* Newman-Keuls test, $P < 0.05$)

Colony	Chick's age categories								
	Medium-aged, 21–27 days old			Large chicks, 28–38 days old			Fledgling stage, 39–51 days old		
	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>
Mosty	3.4	0.79	47	3.1	1.02	50	2.8 ^a	1.20	36
Kiersity	3.4	0.76	63	3.0	1.07	72	2.5 ^b	1.11	60
Kąty Rybackie	3.7	0.72	81	3.4	0.80	82	3.2 ^{ab}	0.91	78

(Table 2). The analysis also included totally failed pairs. Two-factor ANOVA of brood size versus season and colony revealed significant effect of the colony in case of fledglings ($F_{2,4} = 11.5$, $P < 0.05$). The effect of the year ($F_{2,4} = 1.09$, n.s.) and interaction ($F_{2,165} = 0.76$, n.s.) were not significant. Effects for the other age categories were not significant. The intercolonial comparison showed that the highest mean number of fledglings per nest in 2000–2002 combined was recorded at Kąty Rybackie (Table 2). Lower values were recorded at Kiersity (Newman-Keuls test, $P < 0.005$) and Mosty (Newman-Keuls test, $P < 0.05$).

The mean number of chicks at fledgling stage is shown in Table 3. Each season, the highest brood size

Table 3 Mean brood size at fledgling stage in 2000–2002 (paired letters *a* Duncan test, $P < 0.05$)

Year	Colony	Mean	SD	<i>n</i>
2000	Mosty	3.2	1.64	9
	Kiersity	2.3	1.57	10
	Kąty Rybackie	3.6	0.63	16
2001	Mosty	2.6	1.07	10
	Kiersity	2.6	1.04	23
	Kąty Rybackie	3.1	1.04	25
2002	Mosty	2.6	1.00	17
	Kiersity	2.5 ^a	1.01	27
	Kąty Rybackie	3.2 ^a	0.90	37

was recorded at Kąty Rybackie and the lowest at Kiersity. However, significant differences were noted only in 2002 (ANOVA, $F_{2,78} = 3.95$, $P < 0.05$; Duncan test, $P < 0.05$).

Factors affecting the breeding success

Brood size

Mean brood size decreased significantly during the nestling period in the nests with 3–4 chicks in all studied colonies in 2000–2002 combined (Table 4). In rare small broods (1–2 chicks) the breeding losses were not recorded. The few nests with five chicks were not analysed because of too small sample size.

The intercolonial differences in the mean number of fledglings per nest were not noted in nests with 3 chicks (ANOVA, $F_{2,60} = 2.56$, n.s.). In broods of four chicks at Kiersity the number of fledglings was significantly lower than at Kąty Rybackie (ANOVA, $F_{2,75} = 4.85$, $P < 0.05$; Newman-Keuls test, $P < 0.05$).

Heronry size

The mean number of medium-aged and large chicks per nest were not correlated with the colony size (number of occupied nests) in 2000–2002 ($r_7 = 0.28$, n.s. for medium-

Table 4 Mean number of fledglings (39–51 days old) in the nests with different brood size at the stage of medium-aged chicks (21–27 days old). Difference one-tailed Student *t*-test for dependent variables

Number of medium-aged chicks		Mosty		Kiersity		Kąty Rybackie	
		Fledglings	Difference	Fledglings	Difference	Fledglings	Difference
1	Mean	1.0	-	1.0	-	1.0	-
	<i>n</i>	2	-	1	-	1	-
2	Mean	2.0	-	2.0	-	2.0	-
	<i>n</i>	1	-	3	-	2	-
3	Mean	2.4	$t_{15} = 2.76$	2.1	$t_{23} = 4.83$	2.6	$t_{22} = 2.86$
	SD	0.81	$P < 0.01$	0.93	$P < 0.001$	0.66	$P < 0.01$
	<i>n</i>	16		24		23	
4	Mean	3.3	$t_{12} = 1.90$	2.8	$t_{19} = 5.33$	3.6	$t_{44} = 4.30$
	SD	1.32	$P < 0.05$	1.01	$P < 0.001$	0.69	$P < 0.001$
	<i>n</i>	13		20		45	
5	Mean	5.0	-	4.7	-	4.0	-
	SD	0.00	-	0.58	-	0.89	-
	<i>n</i>	1	-	3	-	6	-

aged chicks and $r_7=0.43$, n.s. for large chicks). In case of fledgling stage, breeding success increased with the heronry size ($r_7=0.77$, $P<0.05$; Fig. 2).

Age of breeding birds

In 19 breeding pairs (5% of total studied in all colonies and seasons), one of the mates was a first time breeder in its second calendar year (usually female, sexed during copulation). These individuals were mostly recorded at Mosty (1–5 nests in 2000–2002) and once at Kiersity (1 nest in 2002). In all colonies combined, the number of smaller broods (1–3 medium-aged chicks, 77%) was higher in nests with a 2-year-old bird than in other nests (45%; $\chi^2_1=7.31$, $P<0.01$).

Distance between the colony and feeding areas

At Mosty, the feeding areas were situated close to the colony (up to 8 km; Fig. 1) and high quality and easy to catch prey were very abundant (round goby *Neogobius melanostomus*). Flight distance for the herons from Kiersity was the longest within the studied colonies. The main feeding area (Druzno Lake) was 10–20 km from the colony (Fig. 1). Herons only occasionally foraged at Korsuń Lake, adjoining the colony and in small ponds 2 km from the colony. Those feeding areas were insufficient for maintenance of all birds from the colony, especially during the nestling period. At Kąty Rybackie, the main feeding areas were situated in the coastal

waters of the Vistula Lagoon, 2–8 km from the colony (Fig. 1). Additionally, some birds foraged in the colony, on fish regurgitated by cormorants, especially during the nestling period (Wojczulanis 2003).

Number of feeding visits per nest

At Kiersity and Kąty Rybackie, chick mortality significantly decreased with the increasing in the number of feedings of large chicks and fledglings per nest. In all studied colonies the number of feedings of medium-aged nestlings per nest per day was not correlated with the chick mortality (Table 5, Fig. 3).

Siblicide

Sibling aggression was recorded in a quarter of nests observed at Kiersity and Kąty Rybackie (2000–2002 combined). At Mosty, sibling aggression did not occur at all. At Kąty Rybackie, 54% of dead chicks in all observed nests died in the nests with recorded sibling aggression (Table 6). The value at Kiersity (32%) was lower than at Kąty Rybackie ($\chi^2_1=9.2$, $P<0.005$). However, in 2000, breeding losses at Kiersity were noted only in the nests where aggressive behavior had been observed.

Predation and human disturbance

The main reason of breeding losses in the incubation period and at the beginning of nestling period was predation of corvids, such as raven (*Corvus corax*), carrion crow (*Corvus cornix*) and magpie (*Pica pica*). At Mosty, 0.6–0.7% ($n=570$ –574 eggshells), at Kiersity 1.5–3.1% ($n=310$ –496 eggshells), at Kąty Rybackie 1.1–2.7% ($n=309$ –310 eggshells) of all found eggshells (destroyed and hatched) in 2001–2002 were eggshells with crevices made by the nest predator's beak. Losses were underestimated because nest predators often flew away with eggs and small chicks.

During 58 day-long observations in all colonies and seasons, no attacks by a predator on nestlings or adult birds was observed. However, during one short visit at Kąty Rybackie, one attack (probably unsuccessful) by a white-tailed eagle (*Haliaeetus albicilla*) on nestlings was observed. At Mosty, just one successful attack by a

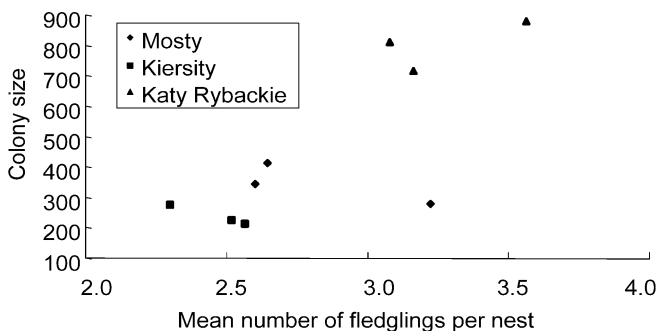


Fig. 2 Relationship between the mean number of fledglings per nest and the colony size in 2000–2002

Table 5 Correlation between the number of feeding visits per nest per day and chick mortality in the particular nests in the studied colonies in 2000–2002 combined

Colony	Chick's age categories								
	Medium-aged chicks			Large chicks			Fledgling stage		
	<i>r</i>	<i>P</i>	<i>n</i>	<i>r</i>	<i>P</i>	<i>n</i>	<i>r</i>	<i>P</i>	<i>n</i>
Mosty	0.11	0.47	47	-0.08	0.60	45	-0.05	0.80	33
Kiersity	-0.22	0.08	63	-0.37	0.003	62	-0.35	0.01	52
Kąty Rybackie	-0.06	0.62	81	-0.27	0.02	80	-0.36	0.001	77

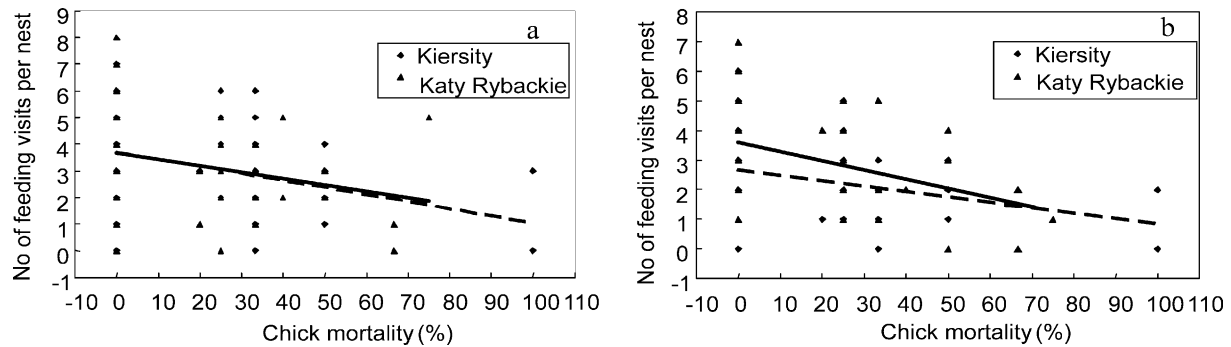


Fig. 3 Relationship between the number of feeds of large chicks (a) and fledglings (b) per nest per day and chick mortality (%) in the heronries at Kiersity and Katy Rybackie

Table 6 Percentage of chicks which died in the nests with sibling aggression in relation to all dead chicks in all observed nests at Kiersity and Katy Rybackie in 2000–2002 combined

Number of chicks which died	Kiersity	Katy Rybackie
In all nests	60	39
In nests with observed aggressive behavior	19	21
% of total	32	54

goshawk (*Accipiter gentilis*) on a flying fledgling was seen (Jakubas 2004a).

Only the colony at Mosty, near to buildings, was permanently exposed to human disturbance. The area of the heronry was not easily accessible because of canals and mud. However, during 20 day-long observations, two 1-h intrusions of a group of children scaring adult herons and fledglings were observed. Working by machines and people in the orchard adjoining the colony and relatively frequent flights of planes and helicopters from a nearby airfield did not disturb herons.

Adverse weather condition

Strong wind, occurring especially in the coastal zone, caused losses of eggs, small chicks and whole nests. At Katy Rybackie, after strong winds in April 2000, 15 fallen nests, 61 broken eggs and 3 dead adult herons were found. In May 2001, during the all-day observation, two nests with 3 and 4 chicks fell to the ground. A few nestlings survived the fall, but were too small to survive.

Discussion

Mean clutch size and mean number of medium-aged chicks per nest were similar in all colonies (Jakubas 2003), so intercolonial differences in the final breeding success was not caused by differences in the clutch size.

In the present study, predation (nests on trees, sporadic visits of big birds of prey), adverse weather (strong winds occurred occasionally in colonies situated close to the sea) and human disturbance (more important only at Mosty) were a negligible reason of chick mortality. In other heronries, in Belgium, England, and in the islands of the Japan Sea (van Vessem and Draulans 1986a; van Vessem 1991; Milstein et al. 1970; Stotskaja 1983), predation also had marginal importance. Human disturbance (especially human foot traffic) locally can negatively affect the breeding success, e.g. in great blue herons (*Ardea herodias*) in Ohio and Pennsylvania, (Carlson and McLean 1996). Herons nested at Mosty, in an area adjoining pasture and houses, responded to human activities by abandonment of their nests and the building of new nests in the more distant, unoccupied, wet part of the wood, where human traffic was lower (Jakubas 2003).

It seems that in the present study, the number of feeding visits (amount of food available to the nestlings) was the most important factor affecting the breeding success of the grey heron. The relationship between the number of feeding visits per nest and chick mortality was significant in the case of large chicks and fledglings. At that stage, food demands of the total brood were high and not all parent birds were able to bring sufficient amounts of food. This resulted in an increase in chick mortality because of starvation and/or siblicide (Mock et al. 1987). Siblicide was a reason of death for 54% of chicks at Katy Rybackie, 32% at Kiersity and as much as 88% in the heronry on the island in the Japan Sea (Stotskaja 1984). In all studied colonies, the percentage of nests with sibling aggression was not correlated with the number of feeds per chick (Jakubas 2004a). However, the lack of siblicidal behaviour at Mosty was probably an effect of foraging by parent birds in feeding areas close to the colony, with an abundance of high quality and easily caught prey. Chicks were satiated and, in contrast to the other studied colonies, did not attempt to join feeding bouts at neighbouring nests. In consequence, the chick mortality rate was low (Jakubas 2004a, 2004b) and the number of feeds per nest was not correlated with the chick mortality. Too large a distance between the heronry and the feeding area has a negative influence on the number of feeding visits and, in consequence, on the breeding success (Simpson et al. 1987; Frederick and Spalding 1994). It occurred at Kiersity,

where the feeding areas were situated far from the colony and the lowest breeding success and the highest chick mortality rate were recorded (Jakubas 2004a).

In the present study, in contrast to data from the heronries in Belgium (van Vessem and Draulans 1986b; van Vessem 1991) and colonies of great blue heron in Canada (Butler et al. 1995), the final breeding success was positively correlated with the colony size. Distant feeding areas in the case of the smallest colony at Kiersity and close areas in other bigger studied heronries seem to confirm that distance to the feeding area and its quality (and in consequence breeding success) are a function of colony size (Hafner 1997). Different situations in other heronries could be caused by the fact that some small colonies were newly established at suitable places and hence a high overall breeding success was reached there (van Vessem 1991).

In the studied heronries, final breeding success was a compromise between advantages and disadvantages of breeding in each colony. At Mosty, human disturbance and high participation of second-year birds in breeding were recompensed by a close and attractive feeding area and the lack of siblicide. During the studied seasons, only at Mosty did the number of occupied nests increase (Jakubas 2004b). At Kąty Rybackie, where the highest breeding success was recorded, siblicide and strong winds were balanced by extra food in the colony (fish regurgitated by cormorants). However, the colony size has been decreasing since 2000 (Jakubas 2004b). This has probably been caused by the increasing competition for nesting places with the cormorant (7,197 breeding pairs in 1999 and 9,191 pairs in 2002). At Kiersity, disadvantages (distant feeding area and occurrence of siblicide) predominated and resulted in the lowest breeding success among the studied colonies and a decrease of the colony size (Jakubas 2004b).

Zusammenfassung

Zum Bruterfolg des Graureihers (*Ardea cinerea*) in Nord-Polen

In drei Kolonien in Nord-Polen (Mosty, Kiersity und Kąty Rybackie) wurde untersucht, welche Faktoren den Bruterfolg des Graureihers bestimmen. Die Kolonien unterschieden sich in ihrer Größe, dem Lebensraum und dem Nahrungsraum. Die durchschnittlich größte Anzahl an flüggen Jungen (im Alter von 39-51 Tagen) je Nest wurde in der Kolonie Kąty Rybackie gefunden; in Kiersity und Mosty waren die Zahlen niedriger. Der Bruterfolg war vor allem bestimmt von der Verfügbarkeit von Futter für die Nestlinge. Auch die Tötung von Nestgeschwistern spielte eine wichtige Rolle. Predation, Störungen, Wetter und die Erfahrung der Altvögel waren dagegen unbedeutend. Allerdings ist die Erfassung der relativen Bedeutung einzelner Faktoren in natürlichen Kolonien schwierig, da sie nicht einzeln zu sehen sind, sondern oft zusammen wirken.

Acknowledgments I would like to thank Prof. L. Stempniewicz for critical comments on the first version of the manuscript. This project was supported by grants of the State Committee for Scientific Researches (6 PO4G 030 18) and University of Gdańsk (BW 1140-5-005-0).

References

- Butler RW, Whitehead PE, Breault AM, Moul IE (1995) Colony effects on fledging success of great blue herons (*Ardea herodias*) in British Columbia. *Colon Waterbirds* 18:159–165
- Carlson BA, McLean BE (1996) Buffer zones and disturbance types as predictors of fledging success in great blue herons, *Ardea herodias*. *Colon Waterbirds* 19:124–127
- Creutz G (1981) Der Graureiher. Ziemsens, Wittenberg-Lutherstadt
- Czapulak A, Adamski A (2002) Biologia rozrodu czapli siwej *Ardea cinerea* gniazdującej w szuwarze trzcinowym. *Not Ornithol* 43:207–217
- Drent RH, Draan S (1980) The prudent parent: energetic adjustments in avian breeding. *Ardea* 68:225–252
- Frederick PC, Spalding MG (1994) Factors affecting reproductive success by wading birds (Ciconiiformes) in the Everglades. In: Davis SM, Odgen JC (eds) Everglades: the ecosystem and its restoration. St. Lucie Press, Delray Beach, Fla.
- Hafner H (1997) Ecology of wading birds. *Colon Waterbirds* 20:115–120
- Jakubas D (2003) Czynniki wpływające na ekologię rozrodu czapli siwej *Ardea cinerea* L. – porównanie 4 kolonii lęgowych w północnej Polsce. PhD Thesis, University of Gdańsk, Poland
- Jakubas D (2004a) Sibling aggression and breeding success in the grey heron. *Waterbirds* 27:297–303
- Jakubas D (2004b) The response of grey heron to rapid increase of the round goby. *Waterbirds* 27:304–307
- Lowe FA (1954) The heron. Collins, London
- Marion L (1989) Territorial feeding and colonial breeding are not mutually exclusive: the case of the grey heron (*Ardea cinerea*). *J Anim Ecol* 58:693–710
- Martin TE (1987) Food as a limit on breeding birds: a life history perspective. *Annu Rev Ecol Syst* 18:453–487
- Milstein PL, Prestt I, Bell AA (1970) The breeding cycle of the grey heron. *Ardea* 58:171–257
- Mock DW, Lamey TC, Ploger BJ (1987) Proximate and ultimate roles of food amount in regulating egret sibling aggression. *Ecology* 68:1760–1772
- Newton I (1998) Population limitation in birds. Academic Press, London
- Owen DF (1960) The nesting success of the heron *Ardea cinerea* in relationship to the availability of food. *Proc Zool Soc Lond* 133:597–617
- Simpson K, Smith JNM, Kelsall JP (1987) Correlates and consequences of coloniality in great blue herons. *Can J Zool* 65:572–577
- Stotskaja EE (1983) [The waders (*Ciconiiformes*) coloniality study with special reference to Gray Heron (*Ardea cinerea* L.)] in: Coloniality in birds, function, evolution. Collection of papers, University of Kuibyshev, Oblastnaya Tipografia, Kuibyshev (in Russian)
- Stotskaja EE (1984) [Parental behaviour and some peculiarities of the gray heron (*Ardea cinerea*) nesting on the Furugelm Island, Japan Sea]. *Ornitologija* 19:128–134 (in Russian)
- Utschick, H. (1982) Nahrungsgrundlagen und Aktivitätsmuster des Graureihers (*Ardea cinerea*) in Bayern. *Garmisch Vogelkd Bericht* 10:52–72
- Vessem J van (1991) Timing of egg-laying, clutch size and breeding success of the Grey Heron, *Ardea cinerea*, in the north of Belgium. *Gerfaut* 81:177–193
- Vessem J van, Draulans D (1986a) Factors affecting the length of the breeding cycle and the frequency of nest attendance by grey herons *Ardea cinerea*. *Bird Study* 33:98–104

- Vessem J van, Draulans D (1986b) On the adaptive significance of colonial breeding in the grey heron *Ardea cinerea*: inter- and intracolony variability in breeding success. *Ornis Scand* 17:356–362
- Vessem J van, Draulans D (1986c) Nest attendance by male and female Grey Heron. *J Field Ornithol* 57:34–41
- Vessem J van, Draulans D (1987) Spatial distribution and time budget of radio-tagged grey herons, *Ardea cinerea*, during the breeding season. *J Zool* 213:507–534
- Wojczulanis K (2003) Rola pokarmu wykrztuszonego przez kormorany *Phalacrocorax carbo* w diecie czapli siwej *Ardea cinerea* w kolonii mieszanej w Kątach Rybackich. MSc Thesis, University of Gdańsk, Poland
- Zar JH (1996) *Biostatistical analysis*. Prentice-Hall, Upper Saddle River, N.J.