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Productivity of the Great Egret (*Ardea alba*) and Grey Heron (*A. cinerea*) in mixed heronries in Poland and behavioral response of fledglings to a drone

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Productivity of avian populations provides important demographic information helpful in understanding population dynamics and processes involved during species expansions**.** We tested the hypothesis that the productivity of the two species of ecologically similar herons that breed together in mixed heronries is related to their expansion status. We expected the expansive species, colonizing the new area and increasing in numbers, to outperform the native species, whose abundance is stable. We studied the breeding success of two herons in mixed colonies in eastern Poland in 2018: Great Egret (*Ardea alba*) (an expansive species, increasing breeding range and population size), and the Grey Heron (*Ardea cinerea*) (a native species, stable breeding population). Mean productivity (number of young per nest) was similar for Great Egret and Grey Heron and appeared correlated to each other in mixed heronries. Productivity of both species was unrelated to the colony size, but Grey Heron tended to have higher productivity as the proportion of Great Egret nests in the colony increased. Similar productivity of both species can be explained by the sufficient food resources coupled with the low level of competition. The two species differed significantly in their response of young to the approaching drone: the mean probability of a young Great Egret adopting an upright display was 0.47 compared to only 0.18 in a young Grey Heron ($p=0.025$). This was unlikely an age-related difference as the fledglings of both species were at a similar stage of development, but may represent some kind of a species-specific trait. Our research once again shows that UAVs allow a quick and non-invasive study of the size of the breeding populations and reproductive performance of herons, egrets and other wading birds.

1. Introduction

Productivity of bird populations is an important component of population dynamics, along with survival rates, abundance and dispersal (Clutton-Brock 1988, Newton 1998). Combining available data (*e.g.* abundance and productivity from monitoring schemes, survival rates from ringing) allows for a simultaneous study of the two demographic rates influencing population size changes over time (Kéry & Schaub 2011). The obvious benefits of such joint analyses led to the development of integrated population modeling (IPM) which represents the modern-day framework for a full understanding of population dynamics (Schaub & Kéry 2021). In consequence, IPM is a perfect tool for identifying actions and measures needed for more effective protection and management of populations (Baillie 1990, Desante & Rosenberg 1998). The level of productivity allows assessment of the condition of the population and co-shapes its dynamics (Stephens *et al.* 2019, Plard *et al.* 2020). In the case of an expanding, rapidly spreading species, a high level of reproduction would be expected (Sakai *et al.* 2001, Whitney & Gabler 2008, Keller *et al.* 2011).

However, in some species, it remains a challenge to obtain productivity estimates from ground surveys. This is true for several tree-nesting waterbirds, such as herons, ibises, cormorants, spoonbills, whose nests are frequently located high on trees or alternatively at low level in vast marshy areas (Cramp & Perrins 1993). Furthermore, ground surveys involve much greater disturbance of the birds: the presence of observers walking within a colony can lead to breeding failures due to nest abandonment or greater exposure to predation (Burger 1981, Nisbet 2000, Zbyryt & Menderski 2017). In recent years, less invasive methods to study reproductive success of birds have become available with the use of unmanned aerial vehicles (UAVs), commonly called drones (Chabot *et al.* 2015, Barr *et al.* 2020, Zbyryt 2018). UAVs are used for surveying wildlife because of their fast operation, low costs, researcher safety, transportability and fine spatial resolution (Linchant *et al.* 2015, Weissensteiner *et al.* 2015, Valle 2022). They have been used to study colonial waterbirds such as terns, gulls and herons (Chabot *et al.* 2015, Brisson-Curadeau *et al.* 2017, Valle & Scarton 2018, Zbyryt 2019). Despite the rapidly developing technology, or perhaps mainly because of it, data on the behavioral response of many species of birds to the approach of drones is still sparse, including herons (Zbyryt & Menderski 2017). The increasingly common use of drones for ecology research represents a dramatic advance, but at the same time, it requires the urgent acquisition of data on its harm for birds (especially in the breeding season) on as many species as possible, since tolerance to drone intrusion is highly species-specific (Barr *et al.* 2020).

About 13% of bird species breed in colonies (Lack 1968, Wittenberger & Hunt 1985, Brown & Brown 1996, Gill 2007). The benefits of colonial nesting have been suggested to include lower levels of predation, and information exchange (Ward & Zahavi 1973), but the disadvantages include increased exposure to infections, and competition (*e.g.* for food, nesting material and nesting sites) (Wittenberger & Hunt 1985, Brown & Brown 1996). The phenomenon of breeding in mixed-species colonies occurs in various bird species (Nuechterlein 1981, Faber *et al.* 2001, Valera *et al.* 2003, Ashoori *et al.* 2020). Mixed heronries have been known since ancient times (Arnott 2007). However, data on reproductive success of Great Egret and Grey Heron in mixed colonies is missing.

In the present study, we investigated the productivity of the two species of herons in eastern Poland with aerial surveys using a UAV. Our study species were the Great Egret (*Ardea alba*), which has rapidly colonized vast areas of central Europe since the 1980s (Ławicki 2014) and has nested consistently in Poland since 1997 (Pugacewicz & Kowalski 1997), and the Grey Heron (*Ardea cinerea*), which is a native species to the study area and has been stable in numbers over the last decade (Chylarecki *et al.* 2018). These two wading birds were rarely recorded breeding together in the same colonies in Central, South and Western Europe (Hristo *et al.* 2008, Zbyryt 2019), possibly because the Great Egret was extremely rare across Europe and confined to its southern parts, so that their breeding ranges did not overlap until recently (Ławicki 2014). Mixed colonies of both species are much more common in Eastern than in Central and Western Europe (Abramchuk & Abramchuk 2005, Petrova & Pavlov 2016, Stolbunov *et al.*

2017, Ivanchev *et al*. 2019). We also attempted to assess the behavioral response of adult herons and egrets and their fledglings to the drone's approach. Earlier studies in our studied colonies showed that at the stage of laying and incubation of eggs, drones caused disturbance to a limited number of adult birds in the colony (Zbyryt & Menderski 2017). Other research throughout the breeding season showed the flush responses and flight initiation distances (FIDs) of nesting adults of Great Egret to the direct vertical approach of a drone changed during the breeding season (Collins *et al.* 2019), but the authors do not explain whether it may be related to habituation, which could also be the case. However, we had no knowledge so far of how young birds reacted to the drone. From studies on the White Stork (*Ciconia ciconia*), another wading bird, it is known that the behavioral reaction of young to the drone's approach may change throughout the breeding season (Zbyryt *et al.* 2020).

The main aim of our study was to estimate, for the first time, the productivity of Great Egret and Grey Heron in mixed colonies, since there are no such assessments published so far. We tested the hypothesis that the productivity of both species of herons would improve with increasing colony size as was previously found for Grey Heron (Jakubas 2005). We also collated the scarce, published productivity estimates for the Great Egret to compare with our results. Finally, we investigated behavioural responses of adults and chicks of both species to the drone flights to complete still insufficient data on harm drone surveys can cause to breeding birds.

2. Methods

2.1. Fieldwork

The research was conducted in eastern Poland in six mixed-species (Great Egret and Grey Heron) and one single-species (Great Egret only) breeding colonies (Fig. 1), which included all but one of the Great Egret heronries known in Poland in 2018 (Zbyryt 2019). One of the authors (AZ), trained for UAV use, flew a small quadrocopter to take photographs of nests with young in all of the colonies. In the study area, both heron species in mixed colonies begin nesting at about the same time (Zbyryt, unpubl. data). Flights over the colonies were conducted from June 10 to June 26 in 2018, at the late phase of the chick-rearing period. This choice was motivated by the will to not disturb adult birds during the critical period of egg laying and incubation, and, at the same time, it restricts the interpretation of productivity reported here as referring to successful breeders only (*i.e.*, pairs with chicks successfully hatched and survived up to the day drone flights were performed). The age of the Grey Heron chicks was estimated based on Marion's (1979) criteria. The same pattern of development of the young was assumed for the Great Egret because it is very similar in terms of both the length of parental care and the growth of nestlings (Dwyer 1988, McVaugh 1972). To estimate productivity, we counted the number of 21–38 d old chicks per nest (see Ślepowrońska *et al.* 2016). We excluded from analysis small chicks (<21 d) which can be easily predated (4 nests; 0.9% of all nests), nest in which an adult bird was sitting, which made it impossible to see its contents (5 nests; 1.1%), and nests with eggs that did not hatch (2 nests; 0.5%). After 34 d of age the young may move away from the nest for considerable periods; when adults return the young come back to the nest to feed (Dwyer 1988). The presence of young outside the nest can make it difficult to assign them to a particular nest. However, during the study, only three such cases were recorded, and in each of them the young were in the crown of a tree with a single nest. Therefore, they were assigned to the nearest single nest.

The drone took off from ground level at a distance of at least 100 m from the colony. The flight was not programmed; each time take-off, flight and landing was carried out by the operator manually. At a distance of about 50 m from the colony, the drone flew at a speed of 1–2 m per second. At a similar speed, the drone flew over the colony while inspecting the nests, avoiding sharp ascents and descents. The minimum height of the drone flying above the nests was 50 m or more. Photographic documentation of all nests with young was collected except for one colony (see below). At least five images of each nest from different heights and angles were taken to collect sufficient material for assessing the number of chicks. In most cases, one photograph included

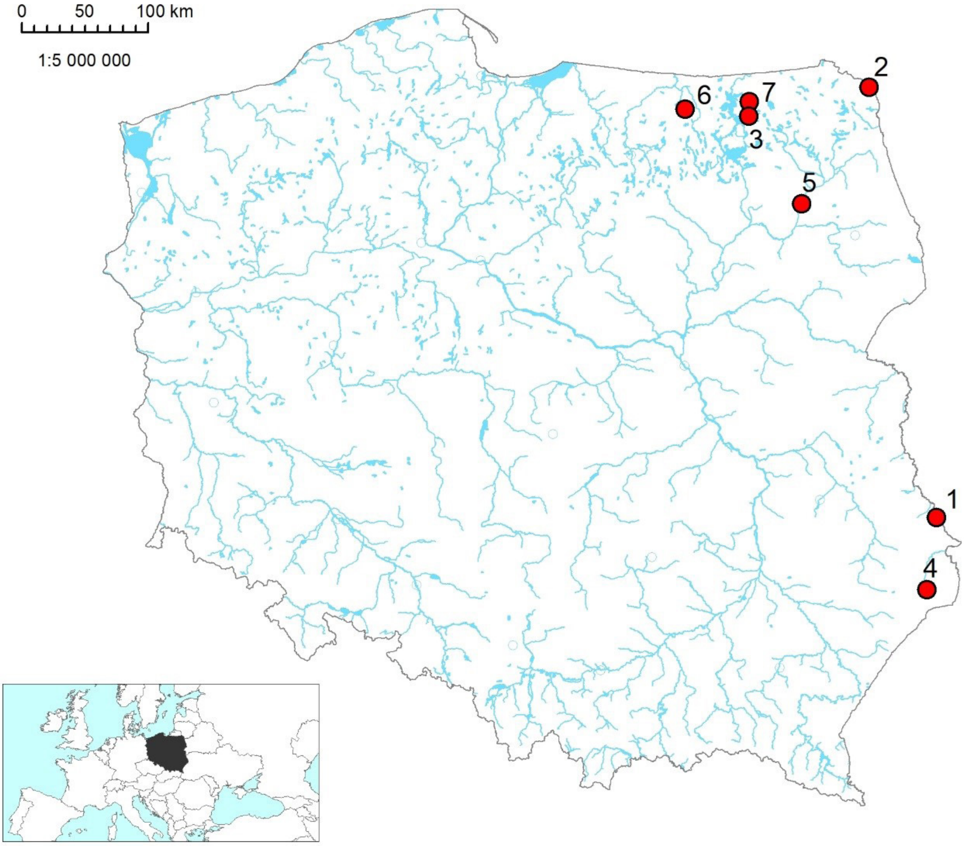

Fig. 1. Location of studied colonies. The numbers on the map correspond to numbering and colony names in Table 1.

more than one nest with fledglings. During drone flights we recorded whether fledglings and adults stayed on the nest or flushed. To avoid problems with overexposure of the photos caused by bright sunlight, the pictures were taken on cloudy days, in the early morning or late afternoon.

In the case of one heronry located on an island in Gaładuś Lake (site-centre location: 54.189229°N, 23.415260°E) pictures of nests were taken exclusively in the northern part of the colony. Productivity for this colony could only be determined for 38 out of 248 breeding pairs (~15%) of Great Egret and for 24 out of 116 breeding pairs (~21%) of Grey Heron due to operational safety reasons. There was great difficulty in collecting photographic material for all nests, because the actual operating time of the Phantom 4 battery is about 20 minutes (see below). The total number of nests for each heron species was assessed from the ground, but most nests could not be viewed sufficiently well to ensure an exact count of the number of young.

2.2. Specification of UAV

A Phantom 4 (DJI, Shenzhen, China) drone was used with an in-built 12 Mp camera (20 mm lens), coloured white. The camera used had an internal global positioning system (GPS) that enabled geo-referencing of each image. This is one of the most popular drones in private use in the world (http://www.dronesbuy.net/drones-forsale-amazon). The basic parameters of this drone are a maximum length of 590 mm including propellers, a mass of 1380 g, a maximum speed of 20 m/s, a maximum ascent and descent speed of 6 and 4 m/s, a vertical and horizontal positioning accuracy of 0.5 and 1.5 m with GPS positioning, respectively. The Phantom 4 utilizes the automatic Collision Avoidance System with an effective sensor range of 0.20–20.0 m (www.dji.com/phantom-4/info). It has 5 directions of obstacle sensing and 4 directions of obstacle avoidance (no sensors at the back). The volume of this device without propellers is 16 370 cm^3 and the noise level is 82 dBA. The drone was equipped with LiPo (Lithium Polymer) batteries with a capacity of 5350 mAh. One battery allows up to 28 minutes of flight.

2.3. Analysis of photographs

The number of fledglings was determined manually by analyzing the aerial photographs of different individual nests in Picasa 3.9 (Google). We assessed the behavior of fledglings for the presence of a drone in 100 randomly selected nests (55 Grey Heron and 45 Great Egret). Two categories were used: 1) no visible reaction and 2) upright display. In addition, we checked at how many nests adult birds stayed or got flushed on the drone's approach. As the photos were taken in series in suitable lighting conditions, we had no problems with identifying the species, the individual chicks in the nests and their behavior, irrespective of vegetation type (Fig. 2 and 3).

2.4. Statistical analysis

We applied a binomial for bounded counts-type model to estimate species- and colony-specific mean productivity. These models are an appropriate choice when counts are bounded by an upper limit (such as the number of nestlings in a brood), in contrast to standard Poisson models for unbounded data (Kéry 2010). In our case, the number of young in the nest could not exceed the maximum number of eggs that a female lays (six in both species). We fitted a single model, including a species fixed effect (two levels) and a colony-species combination random effect (13 levels, separate intercepts for all colony-species combinations). We carried out a Bayesian analysis in WinBUGS software (Spiegelhalter *et al.*

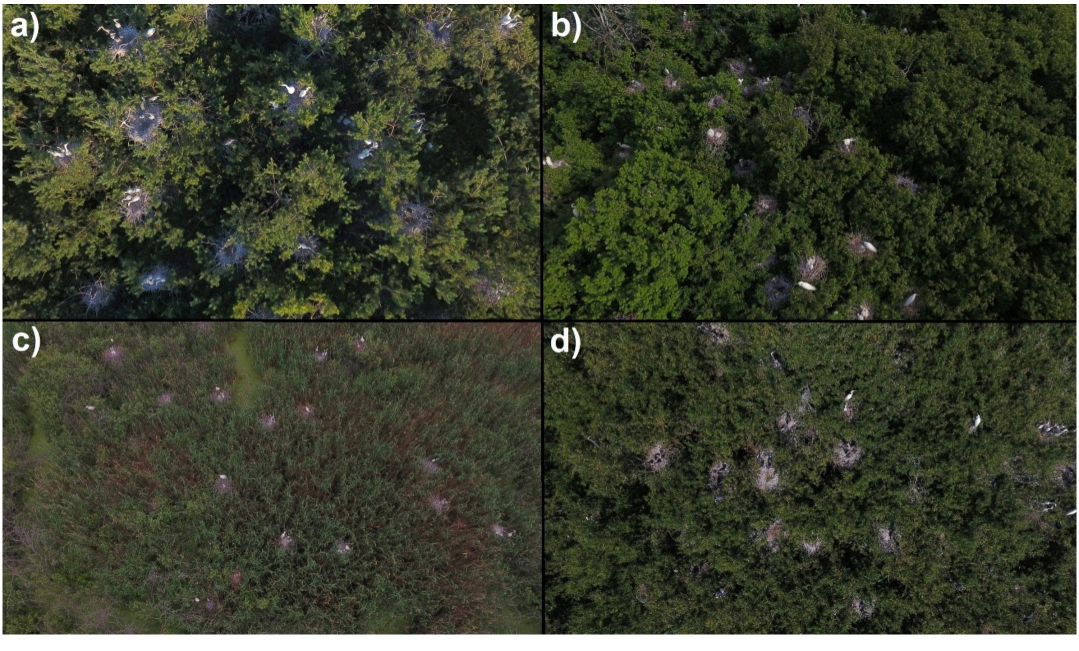

Fig. 2. Drone views from colonies with different vegeation types: a) Kruklin Lake, nests in coniferous trees, b) Gaładuś Lake, nests on trees and bushes, c) Dubienka, nests on willows and in reeds, d) Biebrza National Park, nests on willows. Colour figure is available in the online version of the article at https://doi.org/10.51812/of.119429.

Fig. 3. Examples of fledglings' responses to the drone: 1) no visible reaction (left) and 2) upright display (right). Colour figure is available in the online version of the article at https://doi.org/10.51812/of.119429.

2003) to account for small sample sizes in some colony-species groups, run from within R 3.6.1 (R Core Team 2019) via the R2WinBUGS package (Sturtz *et al.* 2005). The quantity estimated with our models represents the expected proportion of maximum clutch size for both species of herons and all colonies, which, multiplied by maximum clutch size (6) gives productivity. We used uninformative priors and ran three Markov chain Monte Carlo (MCMC) simulations with conservative settings: 1.5 million iterations (the first 0.5 million discarded as 'burn-in') and a thinning rate of 1,000. Chains converged quite slowly after the default BUGS logit function in the model likelihood was replaced by the manual transformation. This suggests the former could have caused problems with convergence as has already been reported (see Appendix in Kéry 2010, page 281). Convergence was monitored visually by assessing chain behaviour and by Gelman-Rubin-Brooks statistics ($\hat{R}$, Gelman & Hill 2007). Under a final run, $\hat{R}$ values were ≤ 1.02 and chains mixed well in all cases, indicating successful convergence. Parameters were summarized with means and SD of posterior distributions along with 95% confidence intervals presented as 2.5% and 97.5% percentiles of posterior distributions (Bayesian credible intervals, BCI). Personalized tests quantifying differences between species and among colonies (Kéry 2010) were performed manually, by comparing posterior distributions. For six mixed colonies, Pearson correlations were used to compare the patterns of performance (posterior productivity estimates) of the two species, after checking for normality (Shapiro-Wilk's test: Grey Heron, W=0.924, p=0.535, Great Egret: W=0.944, p=0.692). To verify, if colony-specific productivity was related to (1) the size of the colony and (2) proportion of Great Egret nests in the colony, we used linear models with species productivity estimates formed the (normally distributed) response, and where size (the total number of nests) or the proportion of Great Egret nests among all were treated as predictors.

Between species differences in behavioural responses of young herons to the drone were assessed with a generalized linear mixed model. Responses were categorized as 1 (upright display) or 0 (no reaction) and treated as a binary response in the model. Species was included as a fixed effect, and nest id was added as a random effect to account for non-independence of individual responses within single nests. Due to relatively large sample sizes and a balanced dataset, model fitting was done with frequentist approach in lme4 library (Bates *et al.* 2015) in R (R Core Team 2019).

3. Results

3.1. Productivity

The average productivity for all Great Egret colonies was 3.1 fledglings per pair (95% BCI: 2.7–3.5) and that of Grey Heron 3.0 (95% BCI: 2.6–3.4). The highest average productivity of both Great Egret and Grey Heron was in the Gudniki colony (Masuria region, north Poland). The lowest Great Egret productivity was in the

Łaszczów colony (fish ponds, southeastern Poland) and that of Grey Heron at Dubienka (eastern Poland) (Table 1). However, among-colony differences were relatively small: posterior distributions overlapped in all cases and there were no significant colony differences (Table 1, Fig. 4). Similarly, between-species differences within colonies were small and nonsignificant, with a maximum difference of only 0.3 young per pair (Kruklin lake, Masuria region) and widely overlapping zero.

Productivity estimates between species were positively, but not significantly correlated (r=0.71, p=0.12, df=4; Fig. 5) and unrelated to colony size (linear regression slopes, Grey Heron: β=0.0003 ± 0.0006 SE, p=0.70, df=4, Great Egret: β=–0.0001 ± 0.0001 SE, p=0.91, df=5). However, productivity of the Grey Heron tended

Table 1. Summary statistics of the mixed heronries investigated in this work. N nests – number of nests surveyed (equals colony size for all localities except the Gaładuś Lake), Productivity – mean number of young per nest (model estimates: posterior means ± SD). For the Gaładuś Lake, the total colony size is given in parentheses. Numbers in the first column match those on the map in Fig. 1.

No.	Colony name	Great Egret (*Ardea alba*)		Grey Heron (*Ardea cinerea*)	
		N nests	Productivity	N nests	Productivity
1	Dubienka	42	3.01 ± 0.16	74	2.76 ± 0.14
2	Gaładuś	38 (248)	3.01 ± 0.17	24 (116)	3.12 ± 0.21
3	Kruklin	70	3.40 ± 0.14	46	3.09 ± 0.17
4	Łaszczów	37	2.92 ± 0.18	11	2.93 ± 0.25
5	Biebrza National Park	26	2.75 ± 0.14	76	2.92 ± 0.20
6	Gudniki	13	3.48 ± 0.29	3	3.17 ± 0.35
7	Gołdopiwo	17	2.98 ± 0.23	0	–
	Total	243 (453)	3.10 ± 0.16	234 (326)	3.00 ± 0.18

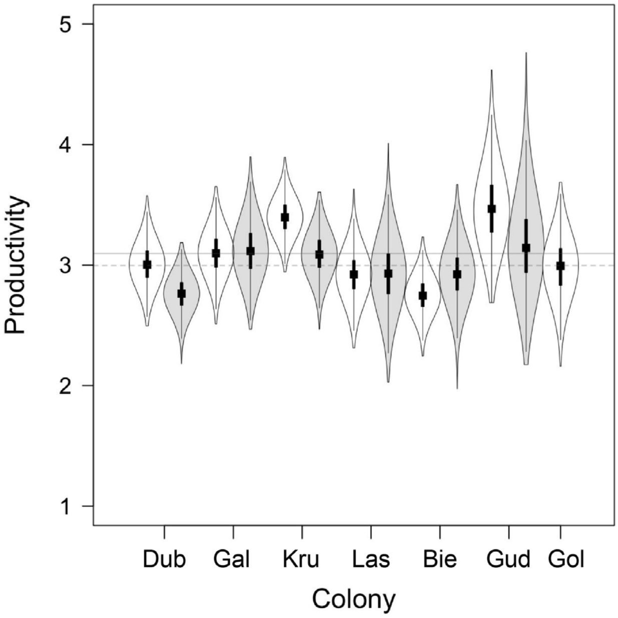

Fig. 4. Productivity estimates of the Great Egret and Grey Heron in Poland in 2018 shown as posterior density kernels. White – Great Egret, grey – Grey Heron. Points inside the violins show medians, thin vertical lines – 95% BCI. Grey horizontal lines show species-specific means: solid – Great Egret, dashed – Grey Heron. The sequence of colonies matches that in Table 1.

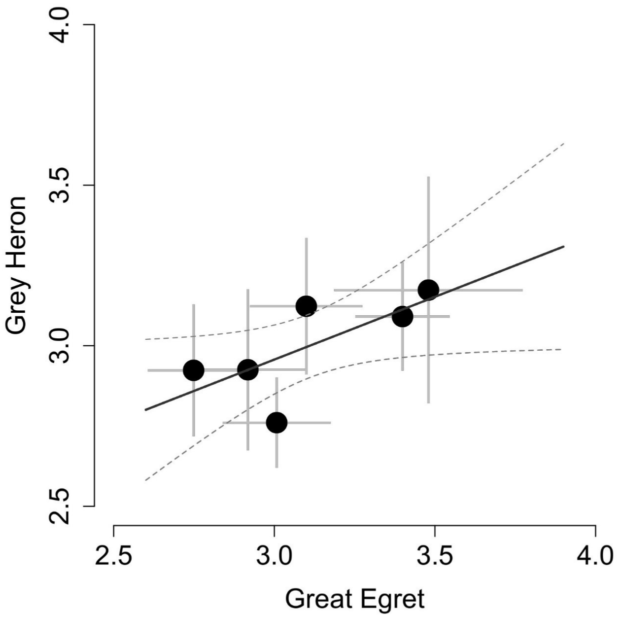

Fig. 5. Relationships between productivity in Great Egret and Grey Heron. Points show means of the posterior distributions, whiskers their SD. Solid line shows estimated relationship, dashed lines its 95% CI.

to depend on the proportion of Great Egret nests in the colony (linear regression slope: β=0.463 ± 0.258 SE, p=0.15, df=4; Fig. 6A), more so than in Great Egret (β=0.370 ± 0.420 SE, p=0.42, df=5; Fig. 6B).

3.2. Behavioural response to the drone

A total of 32 adult birds (22 Great Egrets and 10 Grey Herons) were recorded in all colonies, of which only 4 birds were flushed during the drone flight – three Grey Herons (9% of all adult birds) and one Great Egret (3%). In the Kruklin colony, adult Grey Herons flew to two nests and began to feed the young. After they regurgitated food both birds flew away.

None of the fledglings left the nest during drone's flights. Responses of 318 young birds were assessed (149 Great Egrets and 169 Grey Herons). The probability that a young will take an upright display, differed significantly between species (p=0.025). The mean probability of taking an upright display was 0.470 (95% CI: 0.282–0.668) for Great Egret, while only 0.184 (0.086–0.351) for Grey Heron.

4. Discussion

Our study documents, for the first time, the productivity of the Great Egret from several mixed heronries in Central Europe. Most data on Great Egret's productivity come from North America, while there is little information from Europe (Table 2). Data on productivity of both studied herons are rather scarce and derive mainly from single-species heronries (for the Grey Heron see the review in Manikowska-Ślepowrońska *et al.* 2016). This may be due to the fact that the Great Egret has only recently increased its European range and population size. In the 21st century, breeding of the Great Egret was recorded for the first time in 13 European countries (Ławicki 2014). The greatest development of Great Egret breeding colonies began in the last decade (Zbyryt 2019). It is known that birds that colonize novel habitats face many problems, such as the lack of knowledge of local food resources and the threats posed by predators and humans (West-Eberhard 2003). Therefore, nesting in the proximity of native, ecologically similar species (here: Grey Heron) or more experienced individuals and relying on their experience can be beneficial. This may explain why only one Great Egret colony occurs in the absence of Grey Heron.

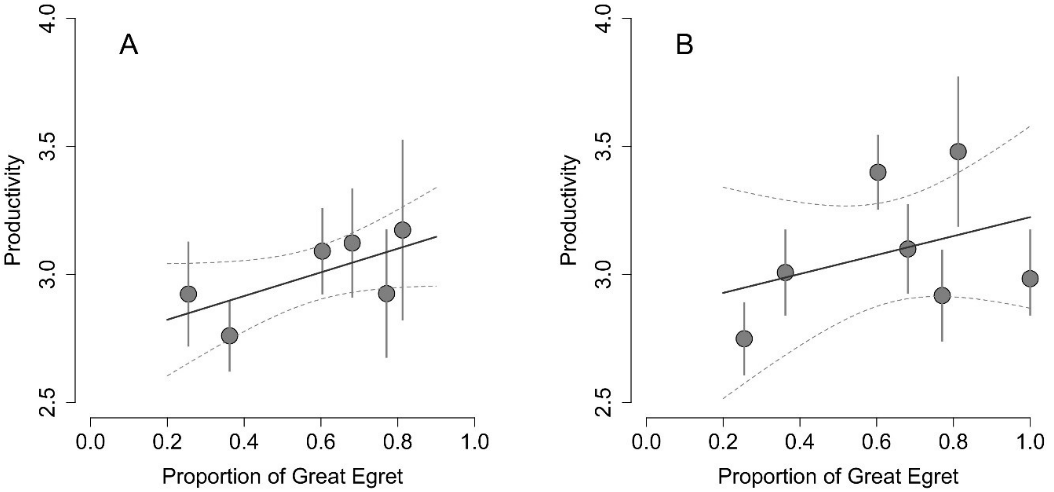

Fig. 6. Relationships between productivity of Grey Heron (A) and Great Egret (B) and the proportion of Great Egret in the colony. Points show means of the posterior distributions (for productivity), whiskers their SD. Estimated relationships are shown with solid lines, their 95% CI with dashed lines.

The productivity (mean number of chicks per nest) of Grey Heron in individual European colonies was variable, ranging from 2.2 in western Spain (Fernández-Cruz & Campos 1993) to 3.9 in SW Poland (Czapulak & Adamski 2002). Average productivity in mixed colonies reported in the current paper (3.0) is similar to single-species colonies of Grey Heron breeding in Europe (Manikowska-Ślepowrońska *et al.* 2016). Published productivity estimates of the Great Egret in Europe, North America and Australia varied from 2.05 in the Audubon Canyon Ranch, California to 3.7 in the Azov Sea wetlands, Ukraine, so our results fall well within this range (Table 2). It is interesting that the productivity of European (*A. a. alba*) is slightly higher than that of the American (*A. a. egretta*) and the Australian (*A. a. modesta*). This result is consistent with the widely recognized phenomenon that avian clutch size tends to increase with latitude, and large clutches are the most productive ones (Soler & Soler 1992, Rubolini & Fasola 2008).

For our studied colonies in eastern Poland, the productivity of herons does not appear to be related to colony size, contrary to earlier studies of Grey Heron colonies in northern Poland, where productivity improved with increasing colony size (Jakubas 2005). This indicates the absence of density-dependent processes on reproductive performance of these two species, which has also been shown in others herons, for example Little Egret *Egretta garzetta* in southwestern Spain (Parejo *et al.* 2001). Although there is evidence that this effect may occur in Little Egret (Bennets *et al.* 2000, Galarza 2020), it seems to be site-dependent. It is also surprising that the increase in Grey Heron productivity appears to be linked to the proportion of Great Egret nests in the colony. Various factors may be responsible for this phenomenon, for example Grey heron might benefit from better antipredator response in Great Egret (new expanding species, unhabituated, more vigilant, as shown by higher responses of young birds to the drone in this study) or its ability to find prey more efficiently by ‘identifying’ good foraging places (Dimalexis *et al.* 1997) following “information centre” hypothesis (Ward & Zahavi 1973).

We found very similar, high productivity in both species of herons. This indicates that the food resources were plentiful, which can translate into low between species competition despite some overlap in foraging niches (Fasola *et al.* 2009). However, we do not know to what extent the niches of our studied herons overlap. One would expect that the Great Egret, as an

Table 2. Summary of Great Egret productivity in various colonies worldwide (for the Grey Heron see the review in Manikowska-Ślepowrońska *et al.* 2016)

No.	Locality	Years	Main foraging habitats	Nest location	Productivity: Mean number of fledglings in colony (± SD)	No. of nests (fledglings)	References
1	7 colonies in eastern Poland pooled	2018	lakes, wetlands, fish ponds	on trees and shrubs, in reeds	3.10 (± 0.16)	289 (883)	this study
2	High Island, Texas, USA	2009–2010	estuarine habitats, coastal	on shrubs	2.61 (± 0.11)	–	Mcinnes 2011
3	Atchafalaya Basin, USA	2011	estuarine habitats, wetlands	on tress and shrubs	2.68 (± 0.27)	–	Burger 2018
4	West Marin Island, USA	1993–2011	estuarine habitats, coastal	on tress and shrubs	1.31 (± 0.33)[†]	–	Kelly *et al.* 2015
5	Audubon Canyon Ranch, California, USA	1967–1979	coastal	on trees	2.05	319 (653)	Pratt & Winkler 1985
6	Riomar Island, Florida, USA	1973	coastal	on shrubs	2.18	11 (24)	Maxwell & Kale 1977
7	Waitangiroto Nature Reserve, New Zealand	1949–1999	estuarine habitats, coastal	on trees and shrubs	0.96 (± 0.51)[‡]	1360 (1307)	Miller 2001
8	Wetlands Centre at Shortland, Australia	1982–1988	estuarine habitats, coastal	on trees	2.14 (± 0.25)	–	Maddock & Baxter 1991
9	Azov Sea, Ukraine	1992–1997	coastal	no data	3.7 (± 0.36)	–	Koshelev & Koshelev 1998
10	Biebrza National Park, Poland	2009	wetlands	on shrubs	3.56 (± 0.58)	–	Świętochowski *et al.* 2010
11	Jeziorsko Reservoir, Poland	2001	reservoir, wetlands	on shrubs	2.82 (± 0.73)	–	Janiszewski & Glubowski 2002

[†] Productivity expressed as the number of young fledged per nest attempt (including brood losses), incomparable with the remaining ones in the table. Data read from the graph using the WebPlotDigitizer software (Rohatgi 2020).

[‡] Productivity calculated for each active nest

expanding species, should have lower productivity due to less experienced individuals. But due to the common nesting of both herons, Great Egret breeding pairs can benefit from the experience of the more experienced individuals of native Grey Heron.

The productivity in both species appeared to be correlated across colonies (Fig. 4), however this relationship was not significant and is best interpreted as indicative only, which suggests that common factors, for example food availability or predation pressure, may be responsible for observed (small) between-colony differences. Besides, there is a close phylogenetic relationship between species (Kuramoto *et al.* 2015) and they occupy a similar ecological niche (Fasola *et al.* 2009).

Since our results derive from only one year, it would be desirable to continue productivity research under the Monitoring of Birds of Poland programme (Chylarecki *et al.* 2018, Chodkiewicz *et al.* 2019) to enable tracking of the population dynamics of both heron species.

Our research once again shows that UAVs allow a quick and non-invasive study of the size of the breeding populations and reproductive performance of herons, egrets and other wading birds (Zbyryt & Menderski 2017, Corregidor-Castro *et al.* 2023, Tobółka *et al.* 2023). Similarly to Valle *et al.* (2021a, 2021b) and Valle and Scarton (2022), who monitored Spoonbills (*Platalea leucorodia*) and Purple Herons (*Ardea purpurea*) in reedbeds, we did not noticed any issues related to finding nests or young herons in shrubby or forested habitats as was reported in some other studies (*e.g.*, Afàn *et al.* 2018 for Glossy Ibises *Plegadis falcinellus*, Valle *et al.* 2022 for Squacco Herons *Ardeola ralloides*). The nearly non-invasive nature of this method was confirmed by the behavior of both young and adult birds at the nests as the drone approached. Only single adult birds were flushed during the drone flights and we even recorded instances of feeding the young during the inspection of the colony using a drone. In contrast, ground surveys scare all birds in the colony (Zbyryt & Menderski 2017, Corregidor-Castro *et al.* 2023).

A meta-analysis of disturbance caused by drones on nesting birds showed that the use of drones has an overall small disturbance effect on nesting birds. Disturbance effects were strongest for ground solitary and non-ground solitary nesters at altitudes of ≤50 m, whereas colonial nesters showed no evidence of disturbance effect regardless of the drone altitude (Cantu de Leija *et al.* 2023). Studies on the flight initiation distance of the Great Egret in Florida showed significant differences in the response of adults depending on the stage of the brood. Almost twice as many birds flew out of the nest in the incubation stage than in the nestling stage (Collins *et al.* 2019). However, during this second stage, significantly more adult birds escaped from nests with chicks over two weeks old than from nests with younger chicks. During this study, we flew over colonies at altitudes of 50 meters and above. This likely contributed to the observed small number of adult birds that flew away, especially considering that this occurred during the breeding stage when they are more susceptible to disturbances.

Juveniles react with greater stress to threats than adults (Müllner *et al.* 2004). In the study of the White Stork, adult birds often did not fly away from the nest when approached by the drone, even when it was within 1 m of the tested bird. On the other hand, young storks reacted differently depending on the stage of development. The younger ones usually showed a passive attitude, and the older ones tried to scare the approaching drone (Zbyryt *et al.* 2020). In our research, adult birds also showed different reactions to the drone than juveniles. They reacted behaviorally to the presence of the drone less frequently. In addition, we showed different responses to approaching drones between fledglings depending on the species. The mean probability of Great Egrets adopting an upright display was two and a half times that of Grey Herons. This was probably not due to a difference in age as the fledglings of both species were at a similar stage of development. Thus, this may be some kind of species-specific trait.

Clear differences in the amount of melanin in the plumage of both heron species may be one of the explanations for the differences in behavioral response to a stress factor. It is known that sensitivity to corticosterone is linked to melanin-based coloration in wild birds (Angelier *et al.* 2018). Usually, individuals with darker plumage caused by eumelanin have a better ability to cope in stressful situations (Almasi *et al.* 2010). Therefore, it would be interesting to investigate the differences in stress response between young Grey Herons and Great Egrets by examining corticosterone concentration.

Jalohaikaran (*Ardea alba*) ja harmaahaikaran (*A. cinerea*) tuottavuus sekakoloniassa Puolassa ja poikasten reaktiot drone-lennokkeihin

Lintukantojen tuottavuus tarjoaa tärkeää demografista tietoa, joka auttaa ymmärtämään lintujen populaatiodynamiikkaa ja laajenemisprosesseja. Tässä tutkimuksessa testasimme hypoteesia, että kahden samassa sekakoloniassa lisääntyvän ekologialtaan samankaltaisen haikaralajin tuottavuus liittyy niiden laajenemisen vaiheeseen: oletimme uudelle alueelle pesiytyvän lajin menestyvän paremmin verrattuna alkuperäiseen lajiin, jonka runsaus on jo vakiintunut. Haikaralajit, joiden pesintämenestystä tutkimme, olivat jalohaikara (*Ardea alba*, laajeneva laji, jonka pesimisalue ja populaation koko ovat kasvussa) ja harmaahaikara (*Ardea cinerea*, alkuperäinen laji, jolla on vakaa lisääntymispopulaatio). Tutkimus tehtiin lintujen sekakoloniassa Itä-Puolassa vuonna 2018.

Keskimääräinen tuottavuus (eli poikasten määrä pesää kohden) oli samankaltainen jalohaikaralla ja harmaahaikaralla. Kummankaan lajin tuottavuus ei ollut merkittävästi sidoksissa pesimäkolonian kokoon, mutta harmaahaikaralla oli taipumus korkeampaan tuottavuuteen, kun jalohaikaran pesien osuus koloniassa kasvoi. Lajien samankaltaista tuottavuutta voidaan selittää riittävillä ruokaresursseilla yhdistettynä vähäiseen kilpailuun.

Kahden lajin poikasten reaktiot lähestyviin kauko-ohjattaviin lennokkeihin (eli droneihin) olivat erilaisia. Jalohaikaroiden todennäköisyys ottaa pystyasento oli merkitsevästi suurempi kuin harmaahaikaroiden. Tämä ei todennäköisesti johtunut ikäeroista, koska molempien lajien poikaset olivat saman kehitysvaiheen tasolla. Tämä voi siis olla jonkinlainen lajispesifinen piirre. Dronet kuitenkin mahdollistavat nopean ja vähän häiriötä aiheuttavan tavan tutkia haikaroiden, koskeloiden ja muiden rantalintujen pesimäpopulaatioiden kokoa ja lisääntymismenestystä.

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