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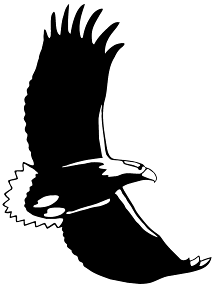

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Productivity of the Great Egret (*Ardea alba*) and Grey Heron (*A. cinerea*) in mixed heronries in Poland and behavioral response of fledglings to a drone

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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

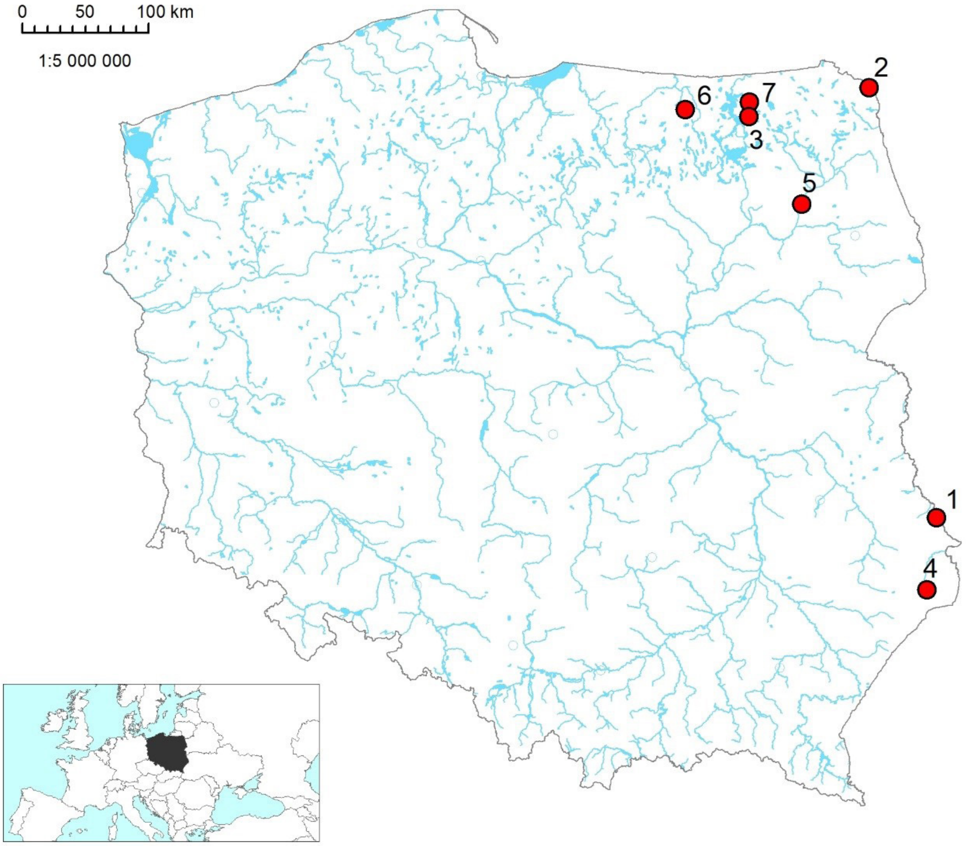

Fig. 1. Location of studied colonies. The numbers on the map correspond to numbering and colony names in Table 1.

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 georeferencing 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.*

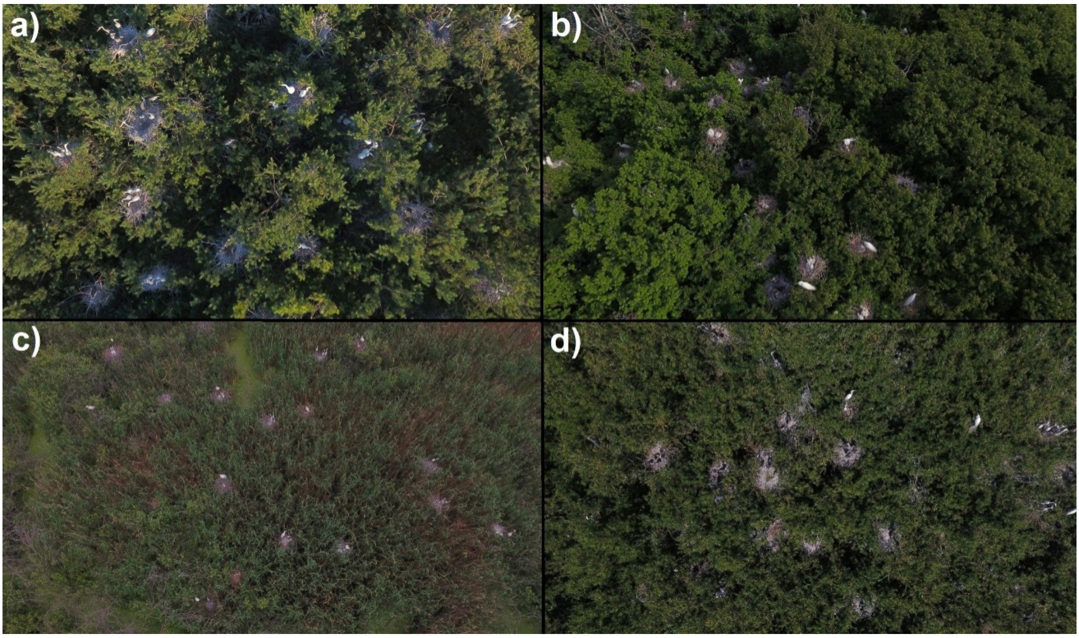

Fig. 2. Drone views from colonies with different vegeation types: a) Kruklin Lake, nests in coniferous trees, b) Gaładuś Lake, nests on trees and bushes, c) Dubienka, nests on willows and in reeds, d) Biebrza National Park, nests on willows. Colour figure is available in the online version of the article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

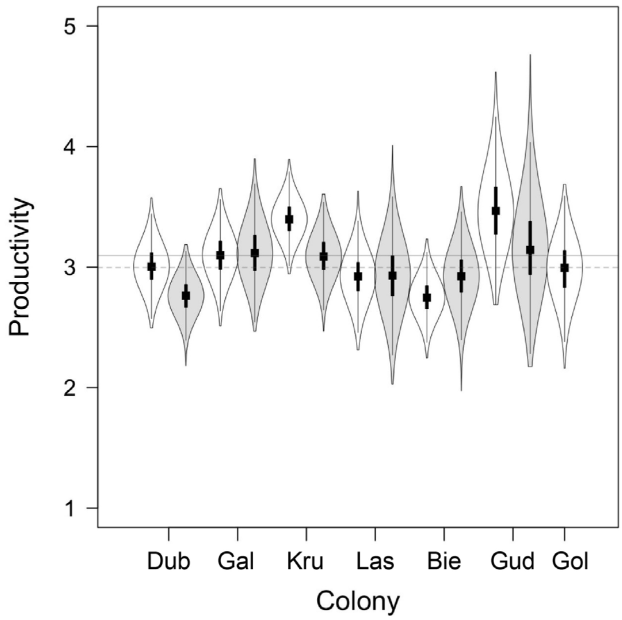

Fig. 4. Productivity estimates of the Great Egret and Grey Heron in Poland in 2018 shown as posterior density kernels. White – Great Egret, grey – Grey Heron. Points inside the violins show medians, thin vertical lines – 95% BCI. Grey horizontal lines show species-specific means: solid – Great Egret,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

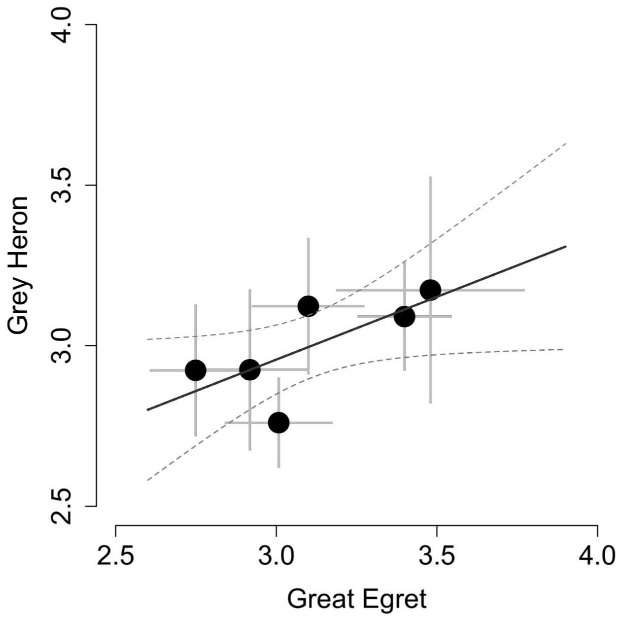

Fig. 5. Relationships between productivity in Great Egret and Grey Heron. Points show means of the posterior distributions, whiskers their SD. Solid line shows estimated relationship, dashed lines its 95% CI.

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.

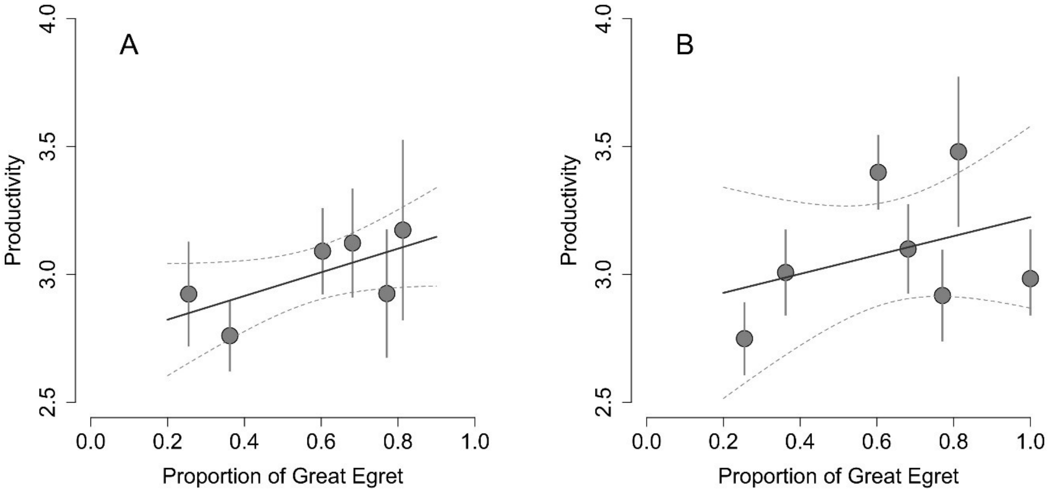

Fig. 6. Relationships between productivity of Grey Heron (A) and Great Egret (B) and the proportion of Great Egret in the colony. Points show means of the posterior distributions (for productivity), whiskers their SD. Estimated relationships are shown with solid lines, their 95% CI with dashed lines.

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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References

Abramchuk, A.V. & Abramchuk, S.V. 2005: Great white egret in Belarus – ecology and distribution. — Berkut 15: 50–55.

Afán, I., Máñez, M. & Díaz-Delgado, R. 2018: Drone Monitoring of Breeding Waterbird Populations: The Case of the Glossy Ibis. — Drones 2: 42. https://doi.org/10.3390/drones2040042

Almasi, B., Jenni, L., JenniI-Eiermann, S. & Roulin, A. 2010: Regulation of stress response is heritable and functionally linked to melanin-based coloration. — Journal of Evolutionary Biology 23(5): 987–996. https://doi.org/10.1111/j.1420-9101.2010.01969.x

Angelier, F., Parenteau, C., Trouvé, C., & Angelier, N. 2018: The behavioural and physiological stress responses are linked to plumage coloration in the rock pigeon (*Columbia livia*). — Physiology & Behavior 184: 261–267. https://doi.org/10.1016/j.physbeh.2017.12.012

Arnott, W.G. 2007: Birds in the ancient world from A to Z. — Taylor & Francis e-Library.

Ashoori, A., Rakhshbhar, Y., Galeotti, P. & Fasola, M. 2020: Effects of protective nesting associations with Whiskered Terns on the breeding success of Great Crested Grebes. — Ardea 107: 328–332. https://doi.org/10.5253/arde.v107i3.a5

Baillie, S.R. 2008: Integrated population monitoring of breeding birds in Britain and Ireland. — Ibis 132: 151–166. https://doi.org/10.1111/j.1474-919X.1990.tb01035.x

Barr, J.R., Green, M.C., DeMaso, S.J. & Hardy, T.B. 2020: Drone surveys do not increase colony-wide flight behaviour at waterbird nesting sites, but sensitivity varies among species. — Scientific Reports 10: 3781. https://doi.org/10.1038/s41598-020-60543-z

Bates, D., Maechler, M., Bolker, B. & Walker, S. 2015: Fitting Linear Mixed-Effects Models Using lme4. — Journal of Statistical Software 67: 1–48. https://doi.org/10.18637/jss.v067.i01

Bennets, R.F., Fasola, M., Hafner, H. & Kayser, Y. 2000: Influence of environmental and density-dependent factors on reproduction of Little Egrets. — Auk 117*:* 634–639. https://doi.org/10.2307/4089589

Brisson-Curadeau, É., Bird, D., Burke, C., Fifield, D.A., Pace, P., Sherley, R.B. & Elliott, K.H. 2017: Seabird species vary in behavioural response to drone census. — Scientific Reports 7: 17884. https://doi.org/10.1038/s41598-017-18202-3

Brown, C.R. & Brown, M.B. 1996: Coloniality in the Cliff Swallow: The Effect of Group Size on Social Behavior.

— The University of Chicago Press, Chicago.

Burger, J. 2018: Productivity of waterbirds in potentially impacted areas of Louisiana in 2011 following the Deepwater Horizon oil spill. — Environmental Monitoring and Assessment 190: 131. https://doi.org/10.1007/s10661-017-6428-y

Cantu de Leija, A., Mirzadi, R.E., Randall, J.M., Portmann, M.D., Mueller, E.J. & Gawlik, D.E. 2023: A meta-analysis of disturbance caused by drones on nesting birds. — Journal of Field Ornithology 94: 3. https://doi.org/10.5751/JFO-00259-940203

Chabot, D., Craik, S.R. & Bird, D.M. 2015: Population census of a large Common Tern colony with a small unmanned aircraft. — PLOS ONE 10: e0122588. https://doi.org/10.1371/journal.pone.0122588

Chodkiewicz, T., Chylarecki, P., Sikora, A., Wardecki, Ł., Bobrek, R., Neubauer, G., Marchowski, D., Dmoch, A., Kuczyński, L. 2019. Raport z wdrażania art. 12 Dyrektywy Ptasiej w Polsce w latach 2013–2018: stan, zmiany, zagrożenia. — Biuletyn Monitoringu Przyrody 20: 1–80. (In Polish)

Chylarecki, P., Chodkiewicz, T., Neubauer, G., Sikora, A., Meissner, W., Woźniak, B., Wylegała, P., Ławicki, Ł., Marchowski, D., Betleja, J., Bzoma, S., Cenian, Z., Górski, A., Korniluk, M., Moczarska, J., Ochocińska, D., Rubacha, S., Wieloch, M., Zielińska, M., Zieliński, P. & Kuczyński, L. 2018: Trendy liczebności ptaków w Polsce. — GIOŚ, Warszawa. (In Polish)

Collins, S.A., Giffin, G.J. & Strong, W.T. 2019: Using flight initiation distance to evaluate responses of colonial-nesting Great Egrets to the approach of an unmanned aerial vehicle. — Journal of Field Ornithology 90: 382–390. https://doi.org/10.1111/jofo.12312

Corregidor-Castro, A., Scarton, F., Panzarin, L., Verza, E. & Valle R.G. 2023: Faster and Better: Comparison between Traditional and Drone Monitoring in a Cryptic Species, the Purple Heron *Ardea purpurea*. — Acta Ornithologica 57: 134–142. https://doi.org/10.3161/00016454AO2022.57.2.002

Cramp, S. & Perrins, C.M. (Eds). 1993: The birds of the Western Palearctic. Vol. VII. — Oxford University Press, Oxford.

Clutton-Brock, T.H. (Ed.). 1988: Reproductive success. — University Chicago Press, Chicago.

Czapulak, A. & Adamski, A. 2002: Reproduction biology of the Grey Heron *Ardea cinerea* nesting in reed rushes. — Notatki Ornitologiczne 43: 207–217. (In Polish with English abstract)

Desante, D.F. & Rosenberg, D.K. 1998: What do we need to monitor in order to manage landbirds? — In Avian Conservation: Research and Management (eds. J.M. Marzluff, R. Sallabanks): 93–106. Island Press, Washington, DC.

Dimalexis, A., Pyrovetsi, M. & Sgardelis, S. 1997: Foraging Ecology of the Grey Heron (*Ardea cinerea*), Great Egret (*Ardea alba*) and Little Egret (*Egretta garzetta*) in Response to Habitat, at 2 Greek Wetlands. — Colonial Waterbirds 20: 261–272. https://doi.org/10.2307/1521692

Dwyer, M.W. 1988: Breeding biology of the Great Egret in Sedgwick Co., Kansas. — Kansas Ornithological Society Bulletin 39: 21–26.

Faber, M., Batleja, J., Gwiazda, R. & Malczyk, P. 2001.:Mixed colonies of large white-headed gulls in southern Poland. — British Birds 94: 529–534.

Fasola, M., Rubolini, D., Merli, E., Boncompagni, E. & Bressan, U. 2009: Long-term trends of heron and egret populations in Italy, and the effects of climate, human-induced mortality, and habitat on population dynamics. — Population Ecology 52: 59–72. https://doi.org/10.1007/s10144-009-0165-1

Fernández-Cruz, M. & Campos, F. 1993. The breeding of Grey Heron (*Ardea cinerea*) in Western Spain: The influence of age. — Colonial Waterbirds 16: 53–58. https://doi.org/10.2307/1521556

Hristo, K., Shurulinkov, P., Ralev, A. & Zafirov, I. 2008: Great white Egret (*Egretta alba*) – a new breeding species of a mixed Heronry at Dragoman marsh, Western Bulgaria. — Acta Zoologica Bulgarica 60: 209–212.

Galarza, A. 2020: Breeding biology of the Little Egret *Egretta garzetta* on the southern coast of the Bay of Biscay. — Bird Study 67: 85–92. https://doi.org/10.1080/00063657.2020.1779653

Gill, F.B. 2007: Ornithology (Third ed.). — New York: W.H. Freeman and Company.

Ivanchev, V.P., Pavlov, D.D., & Kutuzova, O.R. 2019: Dynamics of colonial settlements of Grey Heron (*Ardea cinerea* L.) and Great Egret (*Ardea alba* L.) and stages of Great Egret expansion on the territory of Ryazan and Yaroslavl regions. — Ecosystem Transformation 2: 44–50. https://doi.org/10.23859/estr-180519

Jakubas, D. 2005: Factors affecting the breeding success of the Grey Heron (*Ardea cinerea*) in northern Poland. — Journal of Ornithology 146: 27–33. https://doi.org/10.1007/s10336-004-0051-8

Janiszewski, T. & Glubowski, M. 2002: Breeding of the great white egret *Egretta alba* and night heron *Nycticorax nycticorax* on the Jeziorsko Reservoir in 2002. — Notatki Ornitologiczne 43: 259–262. (In Polish with English abstract)

Kelly, J.P., Fischer, B., Millus, S. & Condeso, T.E. 2015: Heron and egret monitoring results at West Marin Island: 2010 nesting season. Report to the San Pablo Bay National Wildlife Refuge. — Cypress Grove Research Center, Audubon Canyon Ranch.

Kéry, M. & Schaub, M. 2012: Bayesian population analysis using WinBUGS: a hierarchical perspective. — Academic Press, Boston. https://doi.org/10.1016/C2010-0-68368-4

Koshelev, A.I. & Koshelev, V.A. 1999: Breeding of herons in the reed beds of the Northern Priazovie wetlands. — Branta 2: 39–49.

Kuramoto, T., Nishihara, H., Watanabe, M., & Okada, N. 2015: Determining the Position of Storks on the Phylogenetic Tree of Waterbirds by Retroposon Insertion Analysis. — Genome Biology and Evolution 7: 3180–3189. https://doi.org/10.1093/gbe/evv213

Linchant, J., Lisein, J., Semeki, J., Lejeune, P. & Vermeulen, C. 2015: Are unmanned aircraft systems (UASs) the future of wildlife monitoring? A review of accomplishments and challenges. — Mammal Review 45: 239–252. https://doi.org/10.1111/mam.12046

Maddock, M. & Baxter, G.S. 1991: Breeding Success of Egrets Related to Rainfall: A Six-Year Australian Study. — Colonial Waterbirds 14: 133–139. https://doi.org/10.2307/1521502

Marion, L. 1979: La croissance corporelle du heron cendre (*Ardea cinerea*) du Bretagne. Approche de la signification ecologique. — Oiseau R.T.F 49: 1–30. (In French)

McVaugh, W. Jr. 1972: The development of four North American Herons. — Living Bird 11: 155–173.

Manikowska-Ślepowrońska, B., Ślepowroński, K. & Jakubas, D. 2016: Grey Heron *Ardea cinerea* productivity in relation to habitat features and different spatial scales. — Polish Journal of Ecology 64: 384–398. https://doi.org/10.3161/15052249PJE2016.64.3.008

Müllner, A., Eduard Linsenmair, K. & Wikelski, M. 2004: Exposure to ecotourism reduces survival and affects stress response in hoatzin chicks (*Opisthocomus hoazin*). — Biological Conservation 118: 549–558. https://doi.org/10.1016/j.biocon.2003.10.003

Newton, I. 1998: Population limitation in birds. Academic Press, London.

Nisbet, I.C.T. 2000: Disturbance, habituation, and management of waterbird colonies. — Waterbirds 23: 312–332.

Nuechterlein, G.L. 1981: “Information parasitism” in mixed colonies of western grebes and Forster's terns. — Animal Behavior 29: 985–989.

Parejo, D., Sánchez, J.M. & Avilés, J.M. 2001: Breeding biology of the Little Egret (*Egretta garzetta*) in southwestern Spain. — Ornis Fennica 78: 31–38.

Plard, F., Bruns, H.A., Cimiotti, D.V., Helmecke, A., Hötker, H., Jeromin, H., Roodbergen, M., Schekkerman, H., Teunissen, W., van der Jeugd, H. & Schaub, M. 2020: Low productivity and unsuitable management drive the decline of central European lapwing populations. — Animal Conservation 23: 286–296. https://doi.org/10.1111/acv.12540

Petrova, O.R. & Pavlov, D.D. 2016: First finding of Great Egret *Casmerodius albus* nesting in Yaroslavl oblast. — Russian Journal of Biological Invasions 7: 290–293. https://doi.org/10.1134/S2075111716030103

Pugacewicz, E. & Kowalski, J. 1997: First breeding case of Great Egret *Egretta alba* in Poland in XX century. — Notatki Ornitologiczne 38: 323–325 (in Polish with English summary).

R Core Team 2019. R: A Language and Environment for Statistical Computing. — R Foundation for Statistical Computing, Vienna, Austria.

Rohatgi, A. 2020: WebPlotDigitizer (version 4.4), computer software. Retrieved from http://arohatgi.info/WebPlotDigitizer

Rubolini, D, & Fasola, M. 2008: Geographic patterns in reproductive parameters among Nearctic herons (Ardeidae). — Auk 125: 374–383. https://doi.org/10.1525/auk.2008.07018

Sakai, A.K., Allendorf, F.W., Hol, J.S., Lodge, D.M., Molofsky, J., With, K.A., Baughman, S., Cabin, R.J., Cohen, J.E., Ellstrand, N.C., Mccauley, D.E., O'neil, P., Parker, I.M., Thompson, J.N. & Weller, S.G. 2001: The Population Biology of Invasive Species. — Annual Review of Ecology, Evolution, and Systematics 32: 305–332. https://doi.org/10.1146/annurev.ecolsys.32.081501.114037

Schaub, M. & Kéry, M. 2021: Integrated Population Models. Theory and Ecological Applications with R and JAGS. — Academic Press.

Soler, M. & Soler, J.J. 1992: Latitudinal trends in clutch size in single brooded hole nesting bird species – a new hypothesis. — Ardea 80: 293–300.

Stephens, P.A., Vieira, M.V., Willis, S.G. & Carbone, C. 2019. The limits to population density in birds and mammals. — Ecology Letters 22: 654–663. https://doi.org/10.1111/ele.13227

Stolbunov, I.A., Kutuzova, O.R., Krylov, A.V. & Pavlov, D.D. 2017: Northward range expansion by Great Egret *Ardea alba* and the impact of a mixed heron-egret colony on fish species in the adjacent waters. — Vogelwelt 137: 124–128.

Świętochowski, P., Korniluk, M., Tumiel, T. & Wereszczuk, M. 2010. Liczebność i rozród czapli białej *Egretta alba* na Bagnach Biebrzańskich w roku 2010: — Dubelt 2: 97–99. (In Polish with English abstract)

Valera, F., Casas-Crivillé, A. & Hoi, H. 2003: Interspecific parasite exchange in a mixed colony of birds. — Journal of Parasitology 89: 245–250.

Weissensteiner, M.H., Poelstra, J.W. & Wolf, J.B.W. 2015: Low-budget ready-to-fly unmanned aerial vehicles: An effective tool for evaluating the nesting status of canopy-breeding bird species. — Journal of Avian Biology 46: 425–430. https://doi.org/10.1111/jav.00619

Ward, P. & Zahavi, A.1973: The importance of certain assemblages of birds as “information-centres” for food-finding. — Ibis 115: 517–534.

West-Eberhard, M. 2003: Developmental Plasticity and Evolution. — New York: Oxford University Press.

Whitney, K.D. & Gabler, C.A. 2008: Rapid evolution in introduced species, ‘invasive traits’ and recipient communities: challenges for predicting invasive potential. — Diversity and Distributions 14: 569–580. https://doi.org/10.1111/j.1472-4642.2008.00473.x

Wittenberger, J.F. & Hunt, G.L. 1985: *The adaptive significance of coloniality in birds*. — In Avian biology, vol. 8. (eds. D.S. Farner, J.R. King & K.C. Parkes): 1–78. Academic Press, Orlando.

Valle, R.G. 2022: Rapid drone semi-automated counts of wintering Greater Flamingos (*Phoenicopterus roseus*) as a tool for amateur researchers. — Ibis 164: 320–328.

https://doi.org/10.1111/ibi.12993

Valle, R. & Scarton, F. 2018: Use of drones in surveys of breeding waterbirds along the north-western Adriatic Sea coasts (NE Italy). — Bollettino del Museo di Storia Naturale di Venezia 69: 69–75. (In Italian with English abstract)

Valle, R.G., Scarton, F. & Verza, E. 2021a: *Ardea alba* (Linnaeus, 1758): recent increase of breeding in the Po Delta. — Bollettino del Museo di Storia Naturale di Venezia 72: 103–104.

Valle, R.G., Verza, E., Sattin, L. & Scarton, F. 2021b: Data on the breeding biology of Eurasian Spoonbill *Platalea leucorodia* in the northern Adriatic wetlands. — Bollettino del Museo di Storia Naturale di Venezia 72: 73–82.

Valle, R.G. & Scarton, F. 2022: Rapid assessment of productivity of Purple Heron (*Ardea purpurea*) by drone conducted monitoring. — Ardeola 69: 231–248. https://doi.org/10.13157/arla.69.2.2022.ra4

Valle, R.G., Corregidor-Castro, A., Verza, E. & Scarton, F. 2022: Drone monitoring improves nest detection of Squacco Herons *Ardeola ralloides*, but fails to assess its productivity. — Ornis Hungarica 30: 176–187. https://doi.org/10.2478/orhu-2022-0028

Zbyryt, A. & Menderski, S. 2017: Methodological recommendations for nest counts of the Grey Heron *Ardea cinerea* and Great Egret *A. alba* in breeding colonies. — Ornis Polonica 58: 197–202. (In Polish with English abstract)

Zbyryt, A. 2018: The impact of drones on birds and their application in ornithological research and conservation. — Ornis Polonica 59: 56–70. (In Polish with English abstract)

Zbyryt, A. 2019: Numbers and distribution of breeding population of the Great Egret *Ardea alba* in Poland. — Ornis Polonica 60: 235–244.

Zbyryt, A., Dylewski, Ł., Morelli, F., Sparks, T.H. & Tryjanowski, P. 2020: Behavioural responses of breeding white storks *Ciconia ciconia* to an Unmanned Aerial Vehicle. — Acta Ornithologica 55: 243–251. https://doi.org/10.3161/00016454AO2020.55.2.009

Ornis Fennica 100: 159–169. 2023

Consistent delay in recent timing of passerine autumn migration

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Climate change affects important biological processes, bird migration phenology being a particular well-documented one. While spring migration have been found to advance by numerous studies, autumn migration is less studied and show more variable change in timing. Few studies of autumn migration are based on data from after 2000, leaving the last two decades to be relatively less studied. Here, we investigate recent change in autumn migration phenology of European passerines. The most recent available bird ringing data from Denmark is used to analyse phenological change of median and late migration of 14 passerine migrants between 2003–2021. We find an overall delay of autumn migration, mainly driven by short-distance migrants. All short-distance migrants, one out of five medium-distance and three out of five long-distance migrants delay autumn migration. None of the included species advance autumn migration significantly. As climate change has continuously resulted in milder conditions in north-western Europe, we expect this to cause further effects on migration phenology also in recent decades. Our results provide novel insight into recent migration phenology trends, and the observed delay in long-distance migrants may illustrate a changed response to climate change.

1. Introduction

Climate change has profound and well documented effects on important ecological processes (Walther *et al.* 2002, Parmesan *et al.* 2013). One such process is the biannual bird migration of the northern hemisphere (Sparks *et al.* 2005). The effects of climate change on spring migration phenology have been thoroughly investigated (Thorup *et al.* 2007, Lehikoinen *et al.* 2019, Horton *et al.* 2020, Neate-Clegg & Tingley 2022) and studies of spring migration timing have found migratory birds to adjust migration speed en route (Tøttrup *et al.* 2008), allowing an earlier onset of breeding and potentially an increase in breeding area residence time (Cotton 2003, Tøttrup *et al.* 2006b, Rubolini *et al.* 2007, van Buskirk *et al.* 2009). How these changes in spring migration phenology will affect population dynamics is highly dependent on the scale and direction of change of subsequent autumn migration phenology (Thorup *et al.* 2007). Unfortunately, less is known about the effects of climate change on autumn migration (Gallinat *et al.* 2015).

Earlier studies report both advancements and delays in migration timing, with results varying greatly between species (Jenni & Kéry 2003, Tøttrup *et al.* 2006a, van Buskirk *et al.* 2009, Neate-Clegg & Tingley 2022).

Most studies on autumn migration phenology are based on data prior to the 2000s while fewer studies based on recent data are available (Horton *et al.* 2020, Neate-Clegg & Tingley 2022). One of the recent studies found no over-all trend in timing of autumn migration of long-distance neotropical migrants in the period 1960–2019 because trends differed widely between species (Neate-Clegg & Tingley 2022) but the long time period of the study could mask recent trends. Another recent study generally found advancement of peak autumn migration of nocturnal migrants using remote-sensing data (Horton *et al.* 2020). The lack of studies of recent change is problematic because the rate of global temperature increase is accelerating and has never been higher (Smith *et al.* 2015). Studies based on the newest available data can therefore provide important and novel insight into the rate and direction of migration change, as temperature can be expected to have a larger impact on phenology in recent years than in the 1900s.

The aim of this study is to investigate most recent changes in bird migration phenology with specific focus on autumn, as a limited number of studies have investigated this season. For our purpose, we use the most recent available bird ringing data from Denmark to analyse change in autumn migration phenology for 14 passerine bird species over 19 consecutive years.

2. Method

Standardized ringing was conducted in Blåvand, the westernmost point in Denmark (55°33'25.2"N 8°05'06.0"E) (Fig. 1). Here, all catches from the standardised autumn ringing season (from August 1st until November 15th) of the years 2003 to 2021 are included in the study. Standardized ringing is conducted from 30 minutes before sunrise and for the subsequent five hours. Ringing is conducted with fixed-position mist-nets, deploying a mean of 225 net meters per day in the period. Catch effort increased in the period (slope: 9.3 net-meter-hours per day per year, $p<0.001$). However, there was no significant change in the number of birds trapped (N) (slope: –27 N per year, $p=0.465$) or the number of birds trapped corrected for catch effort (N’) (slope: –37 N’ per year, $p=0.242$). There was a slight negative relationship between N’ and catch effort (net-meter-hours) (slope: –0.06 N’ per net-meter-hour, $p<0.001$). This could be caused by closing of nets when birds where too numerous to handle responsibly.

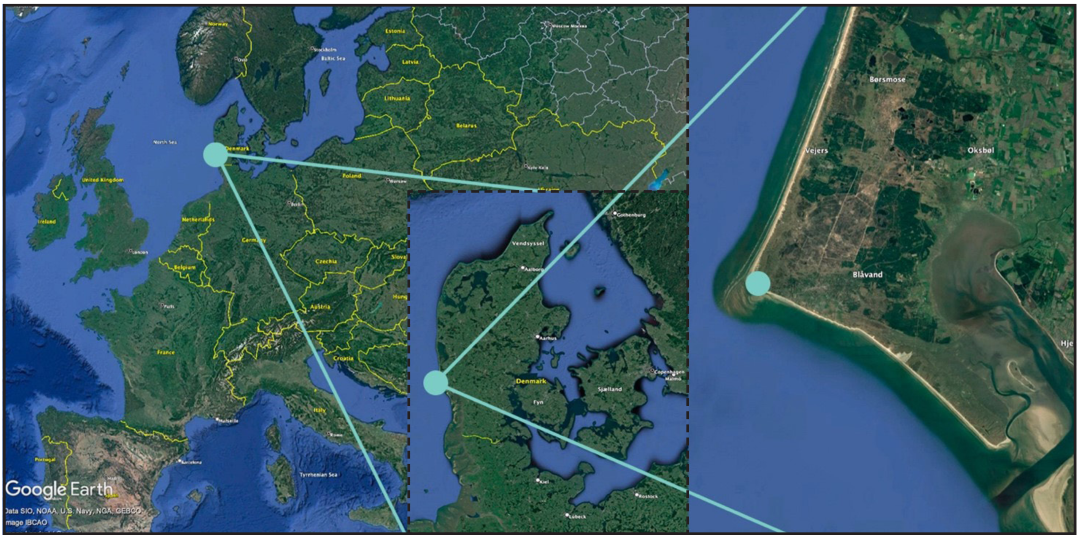

Fig.1. Location of Blåvand Ringing Station. The station is situated on the tip of an angled stretch of coastline. Colour figure is available in the online version of the article at https://doi.org/10.51812/of.128225.

Conditions are kept constant by keeping nets in fixed positions and vegetation in constant height and thickness. A Helgoland trap was installed in 2017 in close proximity to a number of the nets. To test whether the trap affected the number of birds caught, the number of birds caught per day as a function of catch effort (net-meter-hours) were modelled as a generalized linear model. Results show a small but significant negative effect of the trap on the number of birds caught (approx. 7 birds per season). Therefore, we do not consider the effects of the trap large enough to influence results of this study.

2.2. Data material

A total of 52,939 individual birds of 112 species have been ringed in the autumn seasons of the period. We included all migrant species exceeding a minimum of 10 individuals ringed in a season, for a minimum of 18 out of 19 years (after correcting for catch effort). A few species with migration periods ending after the ringing season was also excluded after visual inspection of the dataset. The final dataset consists of 34,134 individuals distributed on 14 species, with the mean number of individuals per species being 2438, ranging from 510 (Redwing, *Turdus iliacus*) to 6,937 (Goldcrest, *Regulus regulus*). Of the 14 species included, four of these are short-distance migrants, five are medium-distance and five are long-distance (following Tøttrup *et al.* 2006a). Migration distance was defined by location of wintering grounds, with short-distance migrants wintering mainly in northern and central Europe, medium-distance wintering in southern Europe and North Africa, and long-distance wintering in sub-Saharan Africa. The Danish bird migration atlas was used for data on wintering grounds (Bønløkke *et al.* 2006). The majority of birds ringed in Blåvand have breeding territories on the Scandinavian Peninsula or in Finland (Bønløkke *et al.* 2006).

2.3. Statistical analyses

Analytical approach broadly follows a study of autumn migration phenology in Denmark from 1976 to 1997 (Tøttrup *et al.* 2006a) to allow direct comparison of the time periods. Analyses of phenology was performed on two measures of migration timing: median and late migration departure. Median and late migration departure is defined as the Julian date when 50% and 5% of the total catch remains to be caught, respectively, calculated for each autumn season. Early migration departure (95% remaining to be caught) was initially included in analyses (in accordance with Tøttrup *et al.* 2006a), but showed on visual inspection to be greatly influenced by local breeding birds. This was evident in a large number of catches and re-catches of resident individuals, which far outnumbered migrating individuals of the same species during the onset of the migration period. The measure for early departure was therefore excluded.

Two types of statistical analysis were performed: mixed-effect linear models (MELM) and quantile regression (QR). MELM was used to analyze departure of the whole group and migration groups, while QR was used to analyze departure of single species.

MELM allows species to be included as a random effect, taking into consideration the different migration timing of each species, and is therefore used to analyze groups of several species. For MELM, the total daily catch (N) of each species was corrected for catch effort by standardizing to 900 net-meter-hours (N’) per day. N’ was used to calculate the date when 50% and 5% of the total yearly catch remained to be caught, corresponding to the date for the median and late passage of the migration. Figure 2 illustrates how the dates for median and late migration passage are calculated from the dataset. Regression was then performed as the Julian date when 50% and 5% remained to be trapped as a function of year, using slope as the phenological change (days per year change in departure). MELM results are presented in table 1.

MELM for median migration:
Julian date at 50% ~ year + (1|species)

MELM for late migration:
Julian date at 5% ~ year + (1|species)

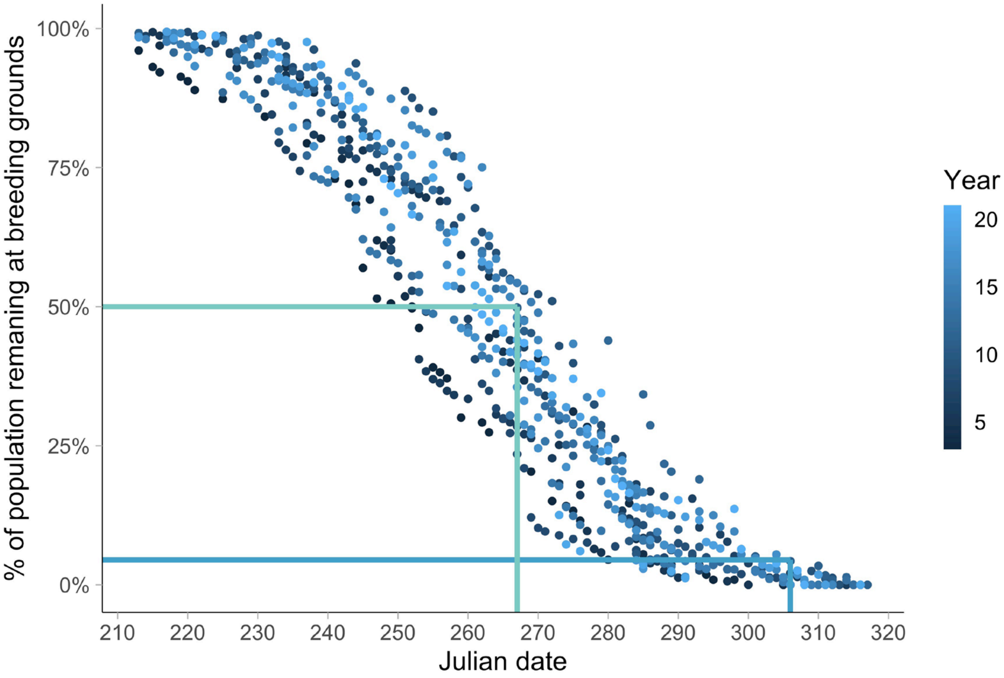

Fig. 2. Percentage of dunnock population remaining at breeding grounds for the years 2003–2021. Lines represents the dates when 50% of the population (light blue) and 5% (dark blue) remained in 2011 representing median and late migration, respectively. Colour figure is available in the online version of the article at https://doi.org/10.51812/of.128225.

QR does not incorporate species as random effects but can utilize a bigger dataset (date of all individual catches instead of dates for median and late migration). QR was performed on the actual Julian dates of all individual catches for each species as a function of year, on 50% and 5% quantiles. Slope of QR describe phenological change in days per year. QR is illustrated for dunnock in figure 4. As QR is based on more datapoints, it is statistically stronger than MELM when analyzing responses of single species instead of multiple-species groups. QR results can be found in table 2.

QR for median migration:
Julian date of catch ~ year of catch, tau=0.5

QR for late migration:
Julian date of catch ~ year of catch, tau=0.05

Testing across all species and quantiles introduces repetitions of tests. To control for family-wise error rate, p-values are Holm-Bonferroni corrected (Rice 1989). Reported p-values are non-corrected, while significance codes for results in table 1 and 2 are marked with parentheses when results are non-significant after correction.

All data work and statistical tests were performed with R, version 4.2.1 (R Core Team, 2022), using the packages “tidyverse” (Wickham *et al.*, 2019), “Quantreg” (Koenker 2022) and “Stats” (R Core Team 2022).

3. Results

3.1. Whole group and migration group analyses

Overall, migrants delayed median autumn departure with 0.19 days per year (95% CI of slope=0.05–0.33, p=0.008) and 0.30 days per year for late population departure (95% CI= 0.14–0.46, p<0.001).

This change in migration timing is mostly driven by short-distance migrants which are found to delay the most. See table 1 for details.

Short-distance migrants show the greatest change in departure, with 0.28 days per year (95% CI=0.05–0.51, p=0.017) and 0.39 days per year (95% CI=0.16–0.62, p<0.001) for mean and late population parts, respectively (Fig. 3).

Medium-distance migrants show no over-all significant change in departure timing, though one medium-distance migrant have the longest delay of all species.

Long-distance migrants showed no significant change in departure for mean population parts but a tendency for delayed departure of late population parts (0.33 days per year, p=0.032, nonsignificant after correction) (Table 1).

Table 1. Change in timing of autumn migration for all species combined and by migration strategy over 19 years (2003–2021) as results of mixed effects models. Slope represents days pr. year change for median (50% of population remaining to be caught) and late (5% of the population remaining) population departure. Positive values correspond to delayed departure. Significance level: 0.05 *; 0.01 **; 0.001 ***; 0. (*) indicates non-significant results after Holm-Bonferroni correction of p-values.

Group	Median migration (50%)		Late migration (5%)	
	Slope	Conditional R^2	Slope	Conditional R^2
All species	0.19**	0.93	0.30***	0.90
Short-distance migrants	0.28*	0.74	0.39***	0.39
Medium-distance migrants	0.20	0.74	0.19	0.53
Long-distance migrants	0.10	0.88	0.33(*)	0.86

Table 2. Change in timing of autumn migration in 15 species of passerine birds over 19 years (2003–2021) as results of quantile regression (QR). Slope represents days pr. year change for median (50% of population remaining to be caught) and late (5% of the population remaining) population departure. Positive values correspond to delayed departure. Significance level: 0.05 *; 0.01 **; 0.001 ***; 0. (*) indicates non-significant results after Holm-Bonferroni correction of p-values.

Common name	Scientific name	Migration distance	Median migration (50%)	Late migration (5%)
			QR slope	QR slope
Blackbird	*Turdus merula*	Short	0.32***	0.24***
Common Chaffinch	*Fringilla coelebs*	Short	0.25(**)	0.54***
Eurasian Wren	*Troglodytes troglodytes*	Short	0.25***	0.29(*)
Goldcrest	*Regulus regulus*	Short	0.27***	0.61***
Common Chiffchaff	*Phylloscopus collybita*	Medium	–0.01	–0.01
Dunnock	*Prunella modularis*	Medium	0.47***	0.69***
European Robin	*Erithacus rubecula*	Medium	0.05	–0.06
Redwing	*Turdus iliacus*	Medium	0.08	0.20
Song Thrush	*Turdus philomelos*	Medium	–0.13	0.33(*)
Eurasian blackcap	*Sylvia atricapilla*	Long	0.42***	0.42***
Common Whitethroat	*Curruca communis*	Long	0.28(*)	0.51(*)
Garden Warbler	*Sylvia borin*	Long	0.07	0
Pied Flycatcher	*Ficedula hypoleuca*	Long	0.32***	–0.28
Willow Warbler	*Phylloscopus trochilus*	Long	0.26***	0.21

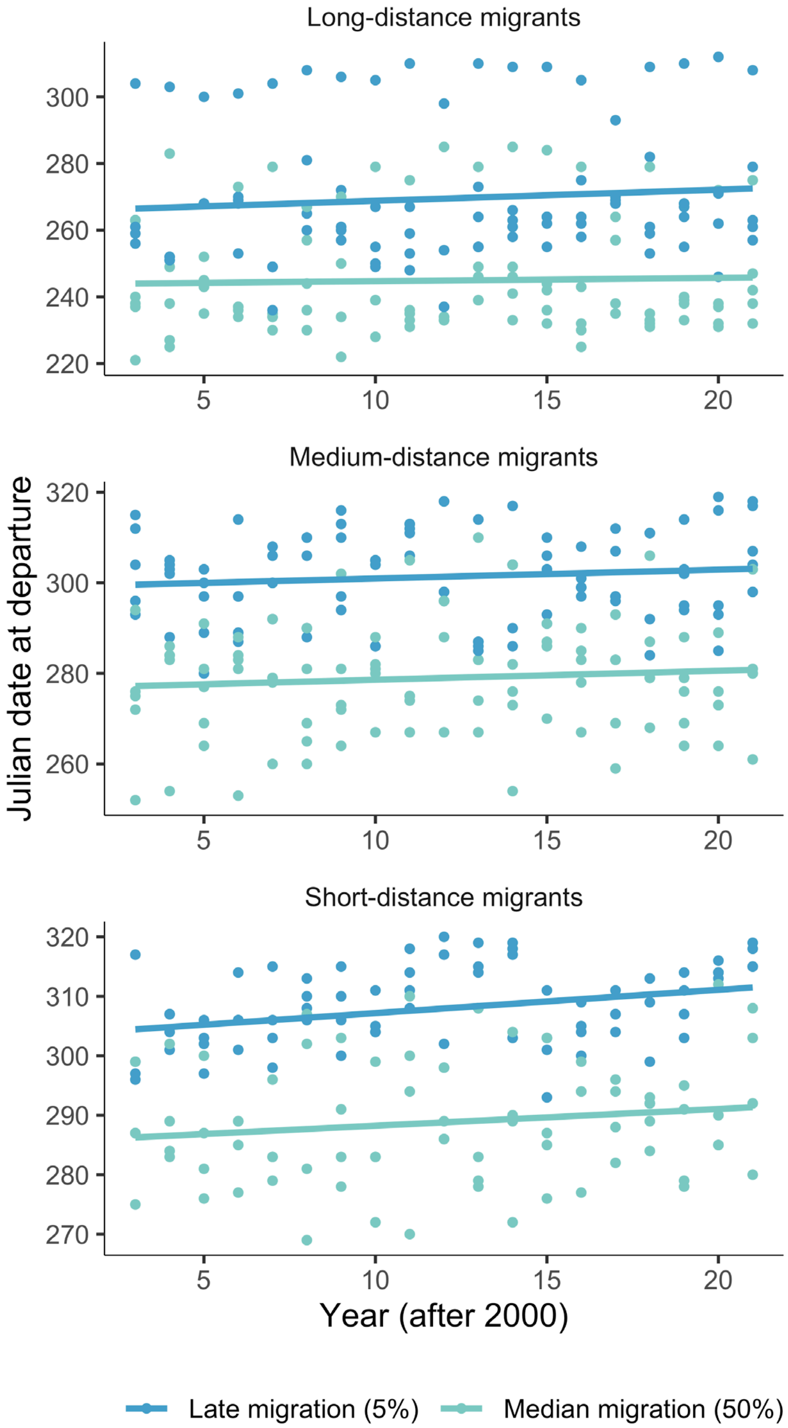

Fig. 3. Change in autumn migration for migration groups. Dark blue points represent dates when 5% of the population remains at breeding grounds (median population departure), light blue points represent dates when 50% remains (late population departure). Trends are illustrated by linear regression lines. Colour figure is available in the online version of the article at https://doi.org/10.51812/of.128225.

3.2. Single species analysis

Results show that all short-distance migrants have significantly delayed departure (Table 2). Goldcrests (*Regulus regulus*) show the largest overall change for the group, delaying median population departure with 0.27 days per year ($p<0.001$) and 0.61 days per year for late population departure ($p<0.001$).

Blackbirds (*Turdus merula*) delayed departure with 0.32 days per year ($p<0.001$) and 0.24 days per year ($p<0.001$) for median and late population departure, respectively. Common Chaffinch (*Fringilla coelebs*) shows a tendency for delayed departure for median population (0.25 days per year, $p=0.008$, non-significant after correction), while late population departure is significantly delayed by 0.54 days per year ($p<0.001$).

Eurasian Wren (*Troglodytes troglodytes*) show significantly later departure of 0.25 days per year ($p<0.001$) for median population parts, and a tendency for delayed departure of late population parts (0.29 days per year, $p=0.015$, non-significant after correction).

The Dunnock (*Prunella modularis*) is the only medium distance migrant to show significant change in autumn migration timing with the largest departure delay of all species in the study. Median population departure is found to delay with 0.47 days per year ($p<0.001$) and with 0.69 days per year ($p<0.001$) for late population departure (Fig. 4).

We found significant delay in departure for three long-distance migrants: Eurasian Blackcap (*Sylvia atricapilla*), Pied Flycatcher (*Ficedula hypoleuca*) and Willow Warbler (*Phylloscopus trochilus*). Departure of Eurasian Blackcap is significantly delayed with 0.42 days per year ($p<0.001$) for both median and late population departure. Pied Flycatcher departure has been

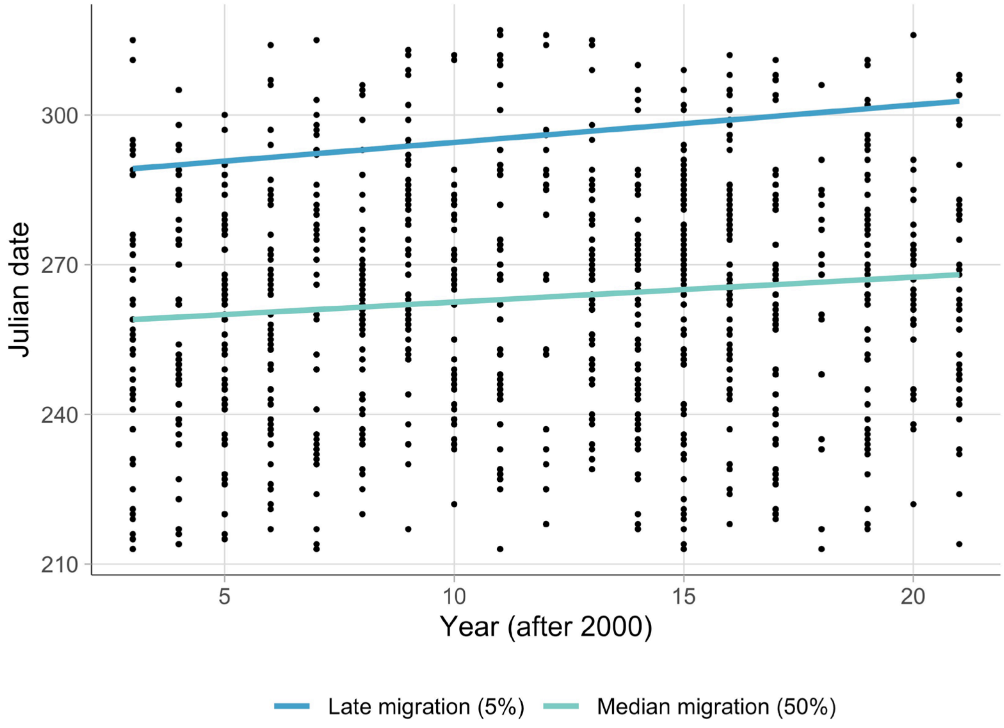

Fig. 4. Change in migration phenology of dunnock. Points represent individual captures. Lines represent quantile regression of 5% and 50% quantiles. Colour figure is available in the online version of the article at https://doi.org/10.51812/of.128225.

significantly delayed by 0.32 days per year ($p<0.001$) for median population departure. Willow Warbler show a significant delay in median population departure of 0.26 days per year ($p<0.001$).

Common Whitethroat (*Curruca communis*) show tendencies for delayed median and late population departure (0.28 days per year, $p=0.036$, and 0.51 days per year, $p=0.023$, respectively (both are non-significant after correction).

4. Discussion

Other studies have shown widely different direction and magnitude of change in migration timing between species (Tøttrup *et al.* 2006a, Thorup *et al.* 2007, van Buskirk *et al.* 2009, Neate-Clegg & Tingley 2022). Here, we report an overall delay of autumn migration. Short-distance migrants delay migration most evidently, which is in accordance with studies looking at earlier time periods (Jenni & Kéry 2003, van Buskirk *et al.* 2009, Lehikoinen 2011, Haest *et al.* 2019). We also find delayed migration of three long-distance migrants, a group that have previously been found to advance autumn migration (Jenni & Kéry 2003, Tøttrup *et al.* 2006a, Haest *et al.* 2019). None of the included species advanced autumn migration significantly.

In this study, data from the most recent 19 years have been analysed to gain insight in current phenological change. Our result suggests that long distance migrants may react differently to climate change in the last two decades than in the previous century. This could be the result of the accelerating rate of temperature rise, which is especially high in Europe (Smith *et al.* 2015). The acceleration has tripled since 1981 and Europe has experienced the ten warmest years during the last two decades (NOAA 2022). The effect of climate change on migration timing can therefore be expected to be most prominent during the 21st century, compared to other influencing factors. A recent study found that short-distance migrants have responded more to climate change in recent years, as observed species overwintered at breeding grounds more frequently during the latter half of the study (Bókony *et al.* 2019). It has also been shown that migration timing can shift quickly in response to climate. A relationship has been observed between the North Atlantic Oscillation and the timing of spring migration timing (Forchhammer *et al.* 2002), demonstrating the short-term adaptive capabilities of migrant birds. We propose that long-distance migrants may have shifted from primarily advancing autumn migration during the 20th century to delaying autumn migration in recent decades due to the increasing effects of climate change. Our results support previous observed delay in autumn migration of short-distance migrants (Jenni & Kéry 2003, van Buskirk *et al.* 2009, Lehikoinen 2011, Haest *et al.* 2019).

Direct comparison of such phenological studies should be made with caution as ringing stations and observatories are recording birds from different geographical areas where regional climatic conditions may vary and potentially impact the results. Birds migrating over Christiansø and Blåvand are originating from the Scandinavian Peninsula and Finland, although Christiansø most likely receives more birds from Finland and Russia, and Blåvand receives more from Norway (Bønløkke *et al.* 2006). How comparable the populations of Blåvand and Christiansø are will most likely also differ between species. Some species show clear migration divides through Denmark, like White Wagtail (*Motacilla alba*) and Common Whitethroat, while the populations of south-west migrants can be expected to be more similar (Bønløkke *et al.* 2006).

We find stronger evidence for delayed autumn migration in short-distance compared to long-distance migrants. This difference could be the result of the controlling factors of migration timing (*e.g.*, Newton 2007). Short-distance migrants are more often facultative migrants, with timing and extent of autumn migration being controlled mostly by breeding ground conditions such as climate and food availability (Newton 2007). Long-distance migrants are considered obligate migrants, with migration timing being controlled in part by day length (Newton 2007). The timing of autumn migration could be expected to change as a product of micro-evolution, altering the endogenous control of migration timing. An evolutionary change such as this is expected to be a slower response than phenotypic plasticity. Thus, the difference in migration delay between short- and long-distance migrants could be an expression of difference in the underlying mechanisms.

The increased temperature at breeding grounds in northern Europe leads to a longer growing season (Liu *et al.* 2016), and thereby prolonged resource availability. Delay in autumn migration of short-distance migrants could simply be driven by the benefit of exploiting these recourses. It has been suggested by Jenni & Kéry (2003) that an evolutionary pressure to migrate before the dry season of the Sahel has driven phenological advancement of long-distance migrants in autumn (Jenni & Kéry 2003). Earlier onset of spring migration and breeding allowed autumn migration to advance, and thereby migrants to pass the Sahel when conditions where more favorable. This is supported by the results of Thorup *et al.* (2007) as they observe only a small increase in breeding-area residence time of long-distance migrants during the same period, suggesting that autumn migration had been advancing in the same magnitude as in spring. The delayed migration of long-distance migrants observed in this study, suggests that the benefit of migrating before the Sahel dry season has become less important compared to the benefits of delaying migration. Examples of these benefits are the possibility for migrants to exploit the extended resource availability on breeding grounds to achieve better physical conditions prior to autumn migration (Tøttrup *et al.* 2006a) and a longer post-breeding moult period for species that moult flight feathers allowing for better plumage quality. Both of these benefits could be expected to increase survival of long-distance migrants. It has also been proposed that delayed autumn migration could be due to an extended breeding period, allowing migrants to produce more offspring (Tøttrup *et al.* 2006a). It is likely that this is true for spring migration, as it has been found that multi-brooded species advance first arrival date of spring migration more than single-brooded species (Végvári *et al.* 2010). Whether delayed autumn migration is also the result of an extended breeding season, and thereby increased reproductive output, is less certain. A study of Reed Warbler (*Acrocephalus scipaceus*) showed significantly earlier onset of the breeding season in the period 1970–2006, while the end of the breeding season did not shift (Halupka *et al.* 2008).

Whether delay in autumn migration has the potential to affect population dynamics, depends on the factors that drive this change. While delay of autumn migration may not necessarily influence reproductive output of migratory birds directly, it is very likely to affect survival. Understanding how survival is changing in different species and the dynamics that control autumn migration timing will shed light on future change and conservation issues.

Varpuslintujen syysmuuton ajoittumisen viivästyminen

Ilmastonmuutos vaikuttaa tärkeisiin biologisiin prosesseihin, joista lintujen muuttuva muuttofenologia on erityisen hyvin dokumentoitu. Vaikka lukuisat tutkimukset ovat osoittaneet kevätmuuton aikaistuvan, syysmuuttoa on tutkittu vähemmän. Sen ajoituksessa näkyy myös enemmän vaihtelua. Harvat syysmuuton tutkimukset perustuvat tuoreimpiin, vuoden 2000 jälkeisiin tietoihin, minkä vuoksi viimeisintä kahta vuosikymmentä on tutkittu suhteellisen vähän. Tässä tutkimuksessa selvitämmekin varpuslintujen syysmuutossa viime aikoina tapahtuneita muutoksia Euroopassa. Aineistomme koostuu Tanskan uusimmista saatavilla olevista rengastustiedoista. Niiden avulla analysoimme 14 varpuslinnun syysmuuttoon liittyviä muutoksia vuosina 2003–2021. Tutkimuksessa havaitsimme, että syysmuutto on yleisesti viivästynyt, mikä johtuu pääasiassa lyhyen matkan muuttolinnuista. Kaikki lyhyen matkan muuttajat, yksi viidestä keskimatkan muuttajasta ja kolme viidestä pitkän matkan muuttajasta viivyttivät syysmuuttoa. Yksikään tutkimuksessa mukana olleista lajeista ei aikaistanut syysmuuttoa merkittävästi. Koska leudommat olosuhteet ovat yhä yleisempiä luoteis-Euroopassa ilmastonmuutoksen seurauksena, odotamme muuttuvien olosuhteiden vaikuttavan muuttofenologiaan myös tulevina vuosikymmeninä. Tuloksemme tarjoavat uutta tietoa lintujen viimeaikaisista syysmuuton trendeistä ja osoittavat, että havaittu viive pitkän matkan muuttajissa voi kuvastaa muuttunutta reagointia ilmastonmuutokseen.

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References

Bókony, V., Barta, Z. and Végvári, Z. 2019: Changing migratory behaviors and climatic responsiveness in birds. — Frontiers in Ecology and Evolution 7: 89. https://doi.org/10.3389/FEVO.2019.00089

Bønløkke, J., Madsen, J. J., Thorup, K., Pedersen, K. T., Bjerrum, M., & Rahbek, C. 2006: Dansk Trækfugleatlas. — Rhodos A/S & University of Copenhagen.

Cotton, P.A. 2003: Avian migration phenology and global climate change. — Proceedings of the National Academy of Sciences 100: 12219–12222. https://doi.org/10.1073/PNAS.1930548100

Forchhammer, M.C., Post, E. & Stenseth, N.C. 2002: North Atlantic Oscillation timing of long- and short-distance migration. — Journal of Animal Ecology 71: 1002–1014. https://doi.org/10.1046/j.1365-2656.2002.00664.x

Gallinat, A.S., Primack, R.B. & Wagner, D.L. 2015: Autumn, the neglected season in climate change research. — Trends in Ecology and Evolution 30: 169–176. https://doi.org/10.1016/j.tree.2015.01.004

Haest, B. Hüppop, O., van de Pol, M. & Bairlein, F. 2019: Autumn bird migration phenology: A potpourri of wind, precipitation and temperature effects — Global Change Biology 25: 4064–4080. https://doi.org/10.1111/gcb.14746

Halupka, L., Dyrcz, A. & Borowiec M. 2008: Climate change affects breeding of reed warblers *Acrocephalus scirpaceus*. — Journal of Avian Biology 39: 95–100. https://doi.org/10.1111/J.0908-8857.2008.04047.X

Horton, K.G., La Sorte, F.A., Sheldon, D., Lin T-Y, Winner, K., Bernstein, G., Maji, S., Hochachka, W.M. & Farnsworth, A. 2020: Phenology of nocturnal avian migration has shifted at the continental scale. — Nature Climate Change 10: 63–68. https://doi.org/10.1038/s41558-019-0648-9

Jenni, L. & Kéry, M. 2003: Timing of autumn bird migration under climate change: Advances in long-distance migrants, delays in short-distance migrants. — Proceedings of the Royal Society B: Biological Sciences 270: 1467–1471. https://doi.org/10.1098/rspb.2003.2394

Koenker, R. 2022: Quantreg: Quantile Regression'. https://CRAN.R-project.org/package=quantreg.

Lehikoinen, A. 2011: Advanced autumn migration of sparrowhawk has increased the predation risk of long-distance migrants in Finland. — PLoS One 6: e20001. https://doi.org/10.1371/JOURNAL.PONE.0020001

Lehikoinen, A., Lindén, A., Karlsson, M., Andersson, A., Crewe, T.L., Dunn, E.H., Gregory, G., Karlsson, L., Kristiansen, V., Mackenzie, S., Newman, S., *Røer*, J.E., Sharpe, C., Sokolov, L.V., Steinholtz, Å., Stervander, M., Tirri, I.S. & Tjørnløv, R.S. 2019: Phenology of the avian spring migratory passage in Europe and North America: Asymmetric advancement in time and increase in duration. — Ecological Indicators 101: 985–991. https://doi.org/10.1016/J.ECOLIND.2019.01.083

Liu, Q., Fu, Y.H., Zhu, Z., Liu, Y., Liu, Z., Huang, M., Janssens, I.A. & Piaoal, S. 2016: Delayed autumn phenology in the Northern Hemisphere is related to change in both climate and spring phenology. — Global Change Biology 22(11): 3702–3711. https://doi.org/10.1111/GCB.13311

Neate-Clegg, M.H.C. & Tingley, M.W. 2022: Adult male birds advance spring migratory phenology faster than females and juveniles across North America. — Global Change Biology 29: 341–354. https://doi.org/10.1111/gcb.16492

Newton, I. 2007: The Migration Ecology of Birds. — Academic Press, Cambridge. https://doi.org/10.1016/B978-0-12-517367-4.X5000-1

NOAA (2022) Monthly Global Climate Report for Annual 2021. — NOAA National Centers for Environmental Information.

Parmesan, C.,Burrows, M.T., Duarte, C.M., Poloczanska, E.S., Richardson, A.J., Schoeman, D.S. & Singer, M.C. 2013) Beyond climate change attribution in conservation and ecological research. Ecology Letters 16: 58–71. https://doi.org/10.1111/ELE.12098.

R Core Team 2022: R: A Language and Environment for Statistical Computing. Vienna, Austria. https://www.R-project.org/

Rice, W.R. 1989: Analyzing tables of statistical tests. — Evolution 43: 223–225.

Rubolini, D., Møller,A.P., Rainio, K. & Lehikoinen, E. 2007: Intraspecific consistency and geographic variability in temporal trends of spring migration phenology among European bird species. — Climate Research 35: 135–146. https://doi.org/10.3354/CR00720

Smith, S.J., Edmonds, J., Hartin, C.A., Mundra, A. & Calvin, K. 2015: Near-term acceleration in the rate of temperature change. — Nature Climate Change 5: 333–336. https://doi.org/10.1038/nclimate2552

Sparks, T.H., Bairlein, F., Bojarinova, J.G., *Hüppop, O.*, Lehikoinen, E.A., Rainio, K., Sokolov, L.V. & Walker, D. 2005: Examining the total arrival distribution of migratory birds — Global Change Biology 11: 22–30. https://doi.org/10.1111/J.1365-2486.2004.00887.X

Thorup, K., Tøttrup, A.P. & Rahbek, C. 2007: Patterns of phenological changes in migratory birds. — Oecologia 151: 697–703. https://doi.org/10.1007/s00442-006-0608-8

Tøttrup, A.P., Thorup, K. & Rahbek, C. 2006a: Changes in timing of autumn migration in North European songbird populations. — Ardea 94: 527–536.

Tøttrup, A.P., Thorup, K. & Rahbek, C. 2006b: Patterns of change in timing of spring migration in North European songbird populations. — Journal of Avian Biology 37: 84–92.

Tøttrup, A.P., Thorup, K., Rainio, K., Yosef, R., Lehikoinen, E. & Rahbek C. 2008: Avian migrants adjust migration in response to environmental conditions en route. — Biology Letters 4(6): 685–688. https://doi.org/10.1098/rsbl.2008.0290

van Buskirk, J., Mulvihill, R.S. & Leberman, R.C. 2009: Variable shifts in spring and autumn migration phenology in North American songbirds associated with climate change. — Global Change Biology 15: 760–771. https://doi.org/10.1111/J.1365-2486.2008.01751.X

Végvári, Z., Bókony, V., Barta, Z. & Kovacs G. 2010: Life history predicts advancement of avian spring migration in response to climate change. Global Change Biology 16: 1–11. https://doi.org/10.1111/J.1365-2486.2009.01876.X

Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O. & Bairlein, F. 2002: Ecological responses to recent climate change. — Nature 416: 389–395. https://doi.org/10.1038/416389a

Wickham, H., Averick, M., Bryan, J., ..., Yutani, H. 2019: Welcome to the tidyverse. — Journal of Open Source Software 4: 1686. https://doi.org/10.21105/joss.01686

Ornis Fennica 100: 170–187. 2023

Conspecific density drives sex-specific spatial wintertime distribution and hoarding behaviour of an avian predator

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Most studies on intraspecific competition, *i.e.*, competition among individuals of the same species, have been conducted during the breeding season. Yet, at northern latitudes, intraspecific competition is expected to be particularly strong under the harsh weather conditions of the non-breeding season with limited number of resources available per individual. We studied the food-hoarding behaviour of wintering Eurasian Pygmy Owls (*Glaucidium passerinum*) along with sex- and age-specific spatial distribution in relation to fluctuating main prey abundance (voles) and conspecific density using a 15-year dataset. In low vole abundance years, increasing conspecific density reduced the total prey number stored by an owl, suggesting high costs of exploitative competition. The distance between the stores of nearest neighbours was greater when both were females, suggesting that the spatial avoidance is driven by sex-specific competition. However, food stores of females had a larger amount of prey items, especially when the nearest neighbour was of the same sex. The number of stores hoarded by an owl increased with increasing conspecific densities. Distributing the prey items to multiple store-sites instead of one (shifting from larder-hoarding towards scatter-hoarding) can help to reduce the overall loss to potential pilfering when conspecific density is high. These results combined suggest that high conspecific density inflames sex-specific interference competition, rather than solely exploitative competition, and in turn drives the observed sex-specific spatial distribution. Adopting a sex-specific spatial distribution according to hoarding and aggressive behaviour can be a way to reduce the severity of intraspecific competition locally and could have cascading effects on the prey community.

1. Introduction

Competition, together with food abundance and predation risk, is one of the central drivers of animal behaviour, spatial distribution, and population dynamics (Sih *et al.* 1985, Gurevitch *et al.* 2000). High densities of competitors may lead to demographic or individual density-dependent effects, *i.e.*, causing a decrease in fitness components such as survival (Armstrong *et al.* 2002) or fecundity (Korpimäki 1987, Ferrer & Donazar 1996, Both 1998). Competition occurs among individuals exploiting the same resources belonging either to the same or different species (intraspecific or interspecific competition, respectively). Individuals within a species usually occupy highly similar niches, and thus competition is expected to be intense (Schoener 1974). Intraspecific competition is consequently often found to have a higher impact on fitness than interspecific competition (Carrete *et al.* 2006, Svanbäck *et al.* 2008, Morosinotto *et al.* 2017a).

When resources become a limiting factor, either due to a decrease in their availability or to a higher number of competing individuals, intraspecific competition gets more intense and may affect reproductive success (Morosinotto *et al.* 2017a), food consumption and somatic growth rate (Amundsen *et al.* 2007). In general, competition may involve indirect interactions through *resource depletion*, where some individuals are more effective at exploiting a certain resource, reducing the amount available to others (*exploitative competition*; Miller 1967, Charnov *et al.* 1976, Schoener 1983, review in Dhondt 2012). It may also involve direct interactions, such as fighting, theft or ritualised combat, where some individuals aggressively interfere with the use of resources by other competitors (*interference competition*; Miller 1967, Schoener 1983, review in Dhondt 2012). Negative effects of competition may further arise via *resource depression* (sensu Charnov *et al.* 1976), a process that does not require the actual capture of any prey by the predator. The presence of a predator may in fact bring about a decrease in the capture rate of the prey in its vicinity, due to the detrimental effects of its foraging activity on the behaviour and micro-distribution of prey.

As competition is costly (*e.g.*, Abramsky *et al.* 2001, review in Dhondt 2012), animals have evolved ways to reduce the costs of competition and to minimize the risk of aggressive interactions (*e.g.*, Valeix *et al.* 2007, review in Dhondt 2012). Among these strategies, there is the selection of the habitat or territory where to live, trying to avoid areas with a high density of competitors (Avgar *et al.* 2020) or with scarce resources, and the niche separation between age classes or sexes (*e.g.*, Svanbäck & Bolnick 2007). The difference in competitive abilities among individuals can affect their spatial distribution (ideal despotic distribution; Fretwell 1972), where highly territorial dominant individuals will first occupy the best unoccupied sites (ideal pre-emptive distribution; Pulliam & Danielson 1991), while inferior competitors will have to settle for less favourable habitats (*e.g.*, Ziv *et al.* 1993, Calsbeek & Sinervo 2002). Niche separation can rise from difference between age and sex classes in their respective competitive ability, as they often exhibit differences in foraging due to experience, skills, or life history strategy (Marchetti & Price 1989, Smith & Metcalfe 1994, Coulson *et al.* 2001, Ishikawa & Watanuki 2002, Field *et al.* 2007, Faegre *et al.* 2020, Masoero *et al.* 2020). This marked difference in experience and size leads to separation in prey selection. For example, many birds of prey show pronounced reversed sex-specific size dimorphism (*i.e.*, females are the larger sex; Massemin *et al.* 2000, Krüger 2005, Korpimäki & Hakkarainen 2012). Larger females are capable of hunting for larger-sized prey, whereas smaller males can be more efficient hunters in catching agile prey, like birds (Mills *et al.* 2019), especially in structurally complex environments such as forests (Hakkarainen & Korpimäki 1991, Pérez-Camacho *et al.* 2015, 2018).

A vast majority of studies on intraspecific competition in birds have been conducted during the breeding season, as direct effects on reproductive success are often of primary interest (*e.g.*, Dann & Norman 2006, Denac 2006, Garabedian *et al.* 2022). Yet, at northern latitudes, intraspecific competition is expected to be particularly strong under the harsh climatic conditions of the non-breeding season, which can lead to food limitation, significant source of mortality during wintertime (Taylor 1994, Hakkarainen *et al.* 2002, Reigert & Fuchs 2011), and to skewing of the adult sex ratio by sex-biased mortality (Chang & Wiebe 2016). Here, we investigate the wintertime sex- and age-specific spatial distribution of a small avian predator, the Eurasian Pygmy Owl (*Glaucidium passerinum;* hereafter "Pygmy Owl"), and its impact on the food hoarding of individuals (terms "storing" and "caching" are also used hereafter) using 15 years of data on food-store composition and captured individuals collected in Finland. The main prey of Pygmy Owls are voles of the genera *Myodes* and *Microtus* (Kellomäki 1977, Halonen *et al.* 2007, Masoero *et al.* 2020), which in North Europe exhibit three-year high-amplitude population cycles (Korpimäki *et al.* 2005), resulting in pronounced among-year fluctuations in the abundance of main food for Pygmy Owls.

During the breeding season, Pygmy Owls were found to avoid breeding close to conspecifics, but this avoidance decreased when voles were abundant (Morosinotto *et al.* 2017a). In autumn and early winter, Pygmy Owls store prey in natural cavities and nest boxes (Solheim 1984a, Terraube *et al.* 2017, Masoero *et al.* 2018, 2020). This behaviour has probably evolved to reduce starvation risk during winter, when resources are scarce (Vander Wall 1990). Like many species of birds of prey, also Pygmy Owls present reversed sexual size dimorphism, with females being larger than males, and show both age- and sex-specific differences in prey use (Masoero *et al.* 2018, 2020). When comparing the food-storing behaviour between the sexes and age classes, females and yearlings hoarded stores with a greater number of prey items than males and adults respectively (Masoero *et al.* 2018), stored more small mammals and tended to store fewer birds under low food availability (Masoero *et al.* 2020).

Based on the previous knowledge on the density-dependent effects during the breeding season as well as the age- and sex-specific differences in hoarding behaviour, we expected that: 1) spatial distribution of Pygmy Owls will depend on age- and sex-specific hoarding strategies, as avoiding neighbours with similar hunting strategies reduces exploitative intraspecific competition, 2) owls will have more stores when conspecific density is high to decentralize stored prey items to avoid potential pilfering and interference competition, and 3) overall, high conspecific density, as well as the age and sex spatial distribution, will modify hoarding success (number of stored prey), especially when voles are scarce.

2. Material and methods

2.1. The study system

The study area consists of *ca.* 1,000 km^2 of forests and agricultural lands in the Kauhava region, western Finland (63°N, 23°E), where *ca.* 300 sites with two nest boxes per forest site were provided for Pygmy Owls (a landscape map of the study area with nest-box sites in Fig. S1 of Morosinotto *et al.* 2017a). The proportion of coniferous forests is 66% and that of agricultural land 25% of the study area. The management of the forest lands has created a mosaic of clear-cut and sapling areas as well as different-aged forests where the main tree species are scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*) and in smaller proportions some deciduous trees (Hakkarainen *et al.* 2003, Morosinotto *et al.* 2017a, Korpimäki *et al.* 2020). For more details on the habitat structure and vegetation age classes please see Morosinotto *et al.* (2017a) and Baroni *et al.* (2021). The data for this study were collected from 2003 to 2017.

Pygmy Owls inhabit mature and old coniferous forests of Europe and Asia (Schönn 1980, Strøm & Sonerud 2001, Barbaro *et al.* 2016, Morosinotto *et al.* 2017a). Natural tree cavities or artificial nest boxes are used in spring for breeding and late autumn and winter for storing food (Solheim 1984a, 1984b, Morosinotto *et al.* 2017a, Terraube *et al.* 2017). In autumn, all the box-sites were inspected twice (once in late October to early November and once in late November to early December) to collect data on the food stores and on the Pygmy Owl individuals storing the food items (for further details on the study system, see Terraube *et al.* 2017, Masoero *et al.* 2018). The total number of fresh prey items in the two autumn visits was calculated and, to avoid double-counting, prey items in food stores were marked with tail-clipping (mammals) or toe-clipping (birds).

From 2003 to 2017, we collected data for a total of 1018 food stores, of which 643 had an identified food hoarder. On average, the annual percentage (mean ± SD) of food stores with an identified hoarder was 63.2 ± 12.7%. Most owls (82%) at food stores were captured with nest-box traps (a replica of the box equipped with swing door) or with a telescopic fishing pole with a noose at the top, a capture commonly used with larger owl species (*e.g.*, Forsman 1983, Bull 1990) and therefore safe for Pygmy Owls. Captured owls were ringed with an aluminium leg ring for individual identification, weighed, sexed, and aged, and wing and tail lengths were measured. The rest of the identities of hoarders (18%) were obtained using Passive Integrated Transponder (PIT) tags, a small electromagnetic microchip implanted subcutaneously when capturing the owls (Masoero *et al.* 2018). Data on encounters of individual owls were collected by placing the antenna of the reader around the entrance hole of the food-store box. The antenna and reader were set up when the food store was found but capturing the owl with the nest box trap failed. The antenna was then kept in place at least for two weeks or until the reader recorded the identity. As females are larger than males, sex was determined based on wing length, tail length, and body mass (as in Masoero *et al.* 2018). The age was estimated according to wing moult (Lagerström & Syrjänen 1990), and individuals were divided into two classes: individuals at their hatching year (1y = yearlings) and older individuals (Ad = adults).

The abundance of the main prey (bank voles *Myodes glareolus* and *Microtus* voles, the fieldvole *M. agrestis* and the sibling vole *M. rossiaemeridionalis*; Kellomäki 1977, Halonen *et al.* 2007, Masoero *et al.* 2020) was estimated by snap trapping twice a year (early May and mid-September). In two locations 14 km apart within the study area, 50–60 metal mouse snap-traps were set up to cover 0.5 to 0.6 ha and the four main habitat types; agricultural and abandoned fields, and forests dominated by spruce or pine (Korpimäki *et al.* 2005). Live trapping was not feasible due to methodological constraints (see also Ethical approval section). The traps (baited with mixed-grain bread) were placed in vole runways and checked daily for three days. The regional synchrony of vole population cycles and thus indices of small mammals extend up to 80 km (Huitu *et al.* 2003, Korpimäki *et al.* 2005), therefore the validity of this index could be extended to the whole study area. The abundance of vole species in the study area fluctuates in three-year cycles with a 100-200-fold amplitude (see Korpimäki *et al.* 2005 for more details). To obtain an autumn vole abundance index for the analyses, the results from the three-night trapping sessions done in September for both the bank voles and *Microtus* voles (voles only) were pooled and standardised as the number of animals captured per 100 trap nights. For the analysis the continuous vole abundance data was changed into a categorical variable. To consider the actual abundance of main food resources in the current autumn, the variable was divided into three levels: "low" (0.1–3.0 animals captured per 100 trap nights), "intermediate" (3.1–12.0) and "high" (>12.0) abundance (Fig. 1a).

2.2. Owl density

Pygmy Owl density was calculated at a 6000 m radius around a single food store of a focal Pygmy Owl. If the individual had more than one food store, a convex hull, which formed the smallest area that included the buffers around the individual food stores and the area between them, was created. This convex hull reflected the area that an owl individual would have to fly across to move between nest-box sites. The results on a previous study on the same population shows that ca. three-fourths (299 owls out of 412) of the owls had only one store per storing season, whereas the rest had two to six food stores (Masoero *et al.* 2018). The value of 6000 m was chosen based on previous research since the home range size was estimated to be around 2.3 km^2 (range 0.4–6.0 km^2; Strøm & Sonerud 2001). The average distance between two stores of the same individual is known to be 1.5 km and the maximum distance is 5.0 km (Masoero *et al.* 2018). Thus, the chosen 6000 m radius is likely to include all the food stores of an individual. The density values were computed using the function 'density' in the package spatstat (R package v. 1.59-0; Baddeley *et al.* 2015), which computes a kernel smoothed intensity function from a pattern of points. Mean density values within buffers and convex hulls were extracted using the function 'extract' in the package raster

(R package v. 2.5-8; Hijmans & van Etten 2012). The distance between an individual and its nearest neighbour during a particular year was calculated from the coordinates of the boxes using the function 'gDistance' in the package GIStools (R package v. 0.7-4; Brunsdon & Chen 2014).

2.3. Statistical analyses

To be able to detect whether distances between individuals depend on sex, age, and food abundance, we need to estimate the proportional deviance between observed and randomly simulated values and then build a Linear Mixed-effects Model (LMM). Observed values were then compared to randomly distributed owls. Given the owls present each year, we generated 10,000 simulated datasets by re-assigning the owls to different food-hoarding boxes and then checking the identity of the new nearest neighbour (NN) and its distance from the focal owl. Using the average of the simulated values for the NN distance (simulated distance), we calculated the proportional deviance of the observed values as *(obs–sim)/sim*. Using an LMM, we then investigated whether the proportional deviance of the distance between an owl and its NN was related to the vole abundance level (three levels: "low", "intermediate", "high"), to the ages ("1y–Ad", "1y–1y", "Ad–Ad"), and sexes ("F–M", "F–F", "M–M") of the two neighbours. Year was used as a random factor to control for environmental conditions in a certain year.

We then tested the effects of competition on the number of food stores hoarded by an individual and the number of prey items stored (as proxies for hoarding success) using Generalised Linear Mixed-effects Models (GLMMs) with a Poisson family. As independent variables in both models, we considered the neighbouring owls' density (continuous variable), and the categorical variables: vole abundance level, age ("1y" or "Ad") and sex ("F" or "M") of the hoarding owl and of its NN (to understand how characteristics of the NN can affect the hoarder). Continuous variables were standardised ($\mu=0$ and $\sigma^2=1$) using the scale function in R. The identity of the owl and year were used as random factors in the GLMMs to control for multiple stores from the same individual and for environmental conditions in a certain year. We used the dredge function within the package MuMIn (Bartoń 2023) to apply model selection (model selection tables for the number of food stores hoarded by an individual and the number of prey items stored can be found in Supplementary materials S1 and S2, respectively). The optimal model was selected using Akaike Information Criterion corrected for small sample size (AICc) values. If the difference between the model with the lowest AICc and the second one was smaller than two, we decided to keep the most parsimonious model. We fixed vole index, age, and sex of the hoarder to be kept in all models since their significance for the food-hoarding Pygmy Owls is already known (Masoero *et al.* 2018). The three two-way interactions between neighbour density and vole abundance level, age of the hoarder and age of the NN and between sex of the hoarder and sex of its NN were also tested. All analyses were carried out using R v. 4.1.0 (R Core Team 2022), and all GLMMs were run using the package lme4 (Bates *et al.* 2015).

3. Results

3.1. Conspecific density

Variations in both the number of food-hoarding owls and in the conspecific density generally followed variation in vole abundance (Fig. 1). The number of food-hoarding owls varied from a minimum of 13 (2006) to a maximum of 60 (2011) during the 15 years of the study (Fig 1b) in the study area. Conspecific density in the 6000 m radius around the food stores of a focal individual was on average (± SD) 0.05 (± 0.03) and ranged between 0.002–0.150, varying among years (Fig 1c).

3.2. Distance to nearest neighbour

Concerning the spatial distribution of Pygmy Owls, we found that the proportional deviance between observed distance of food stores of NNs from the random distances (calculated as *(obs–sim)/sim*) was significantly different according to the sexes of the two NNs. In particular, the

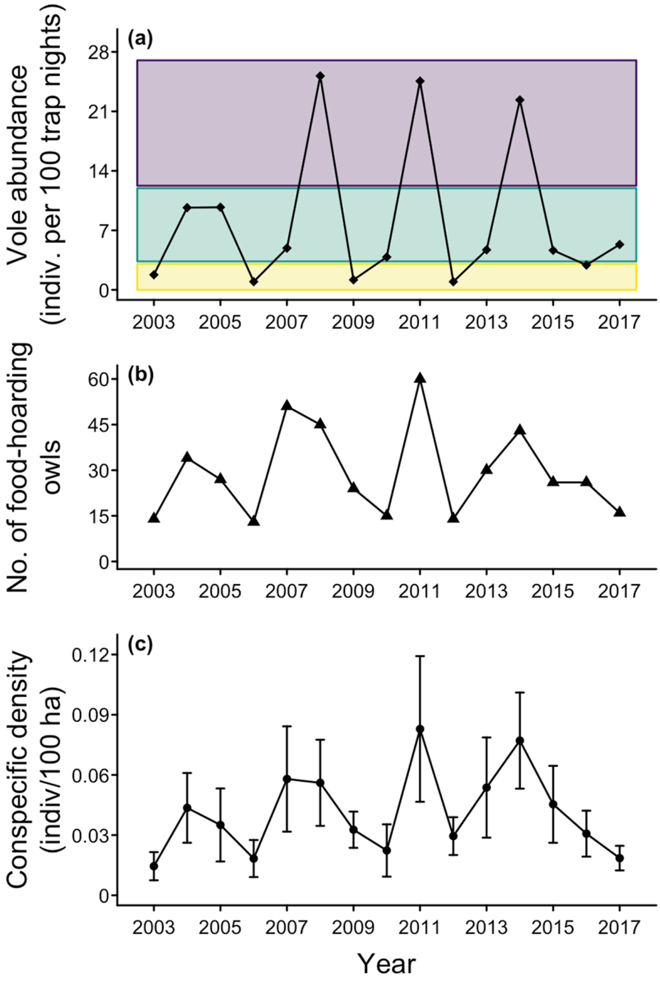

Fig. 1. Among-year variation in (a) autumn vole abundance (number of individuals captured per 100 trap nights), (b) number of food-hoarding individuals and (c) mean (and standard deviation) conspecific density in the 6000 m radius around the food stores of a focal individual in the study area during 2003–2017. In panel (a), the colours represent the subdivision of the vole abundance in 3 levels: low (0–3) in yellow, intermediate (3–12) in green, and high (>12) in purple. Colour figure is available in the online version of the article at https://doi.org/10.51812/of.130326.

distance between stores of neighbouring owls was similar to what simulated by random (values of proportional deviance ~ 0) if the two owls were both females (Fig. 2; mean linear distance ± SD: 3.6 ± 2.3 km), whereas stores between male neighbours (2.8 ± 1.8 km) and different sex neighbours (2.7 ± 1.8 km) were closer than simulated by random (proportional deviance < 0) (Table 1, Fig. 2).

3.3. Number of stores per individual

The top model for the number of stores per individual included only a significant effect of conspecific density (see Supplementary materials Table S1 for the model selection table). This means that the number of food stores hoarded by a focal individual increased with increasing density of surrounding Pygmy Owls (Table 2, Fig. 3), but was not affected by level of vole abundance, age, or sex of the hoarding individual.

3.4. Hoarding success

The top model for the total number of prey items stored by an owl (hoarding success) included all the variables and two of the tested two-way interactions (Table 3; see Supplementary materials Table S2). The interaction between conspecific density and level of vole abundance (Fig. 4a)

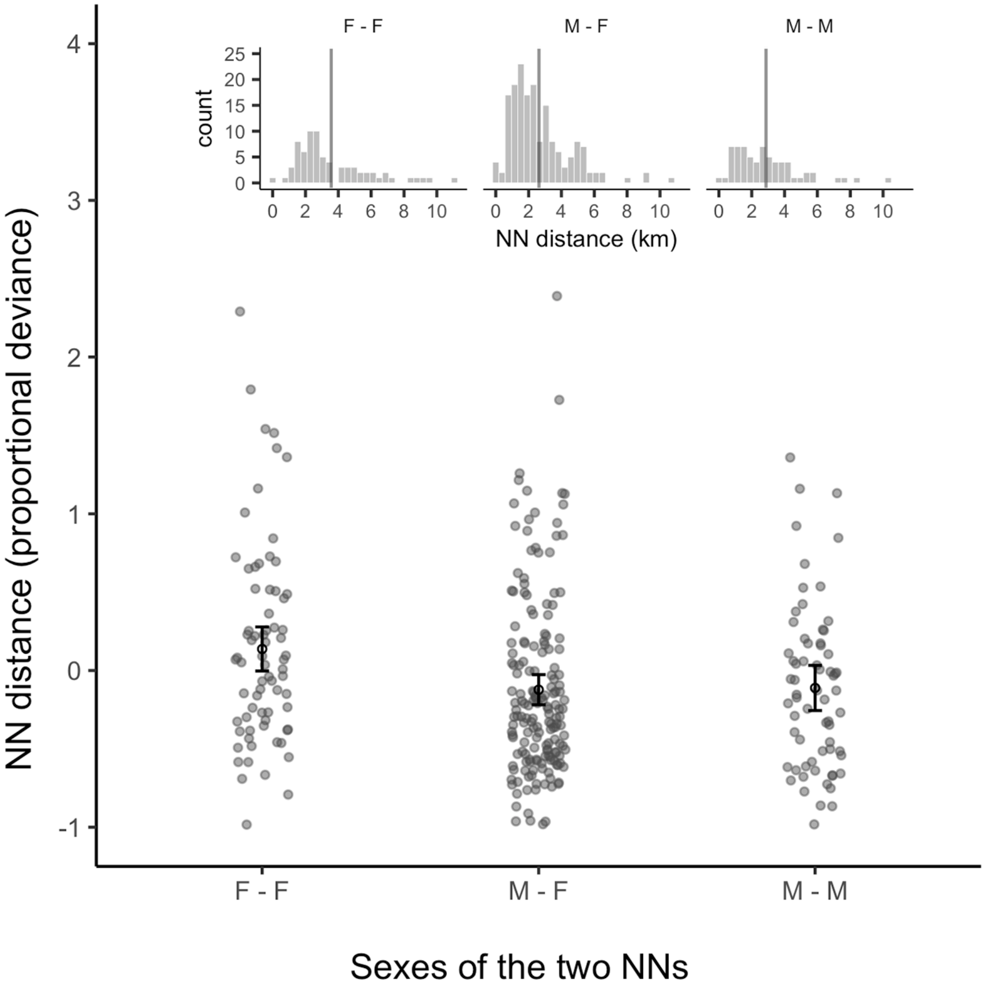

Fig. 2. Predicted values (and 95% CI) of the proportional deviance for the distance between nearest neighbours (NN) in relation to the sexes of the NNs (see Table 1). Observed values are represented with jittered semi-transparent dots, with darker colours meaning a higher number of observations. The histograms on top of the panel represent the distribution of the actual distances between NNs in km (light grey bars), with the mean value for each group represented with a dark grey vertical line. N = 295 NNs.

indicates that when vole abundance is low, the increasing density of conspecifics is associated with a decreasing amount of food stored. In intermediate and high years of vole abundance, increasing density of conspecifics is associated with, respectively, either no relationship or increased number of food items stored (Table 3). The interaction between the age of the hoarder and the age of its NN was not significant and was not present in the best model. Yearlings showed a tendency to store more prey items than adults (Fig. 4b), and owls with a yearling NN stored more prey items that owls with an adult NN (Fig. 4c). The interaction between the sex of the hoarder and the sex of the NN indicates that there were some significant differences between groups (Fig. 4d) that were tested using post-hoc Tukey tests. Female hoarders with a female NN hoarded more prey than females with a male NN ($z = -7.20$, $p<0.0001$), or male hoarders independently of the sex of their NN (with female NN: $z = -4.60$, $p<0.0001$; with male NN: $z = 5.27$, $p<0.0001$).

Table 1. LMMs analysing the proportional deviation from random distances between the food stores of two nearest neighbours (NN) according to the level of vole abundance, age, and sex of the NNs. All models included 'year' as a random factor. Significant variables (p<0.05) are shown in bold. N=295 NNs.

Explanatory		Estimate ± SE	Chisq	p
Intercept		0.100 ± 0.106		
Vole abundance			1.05	0.5903
	Low	0 ± 0		
	Intermediate	0.056 ± 0.095		
	High	–0.018 ± 0.103		
NNs - ages			0.29	0.8658
	Ad – Ad	0 ± 0		
	1y – Ad	–0.003 ± 0.086		
	1y – 1y	0.079 ± 0.093		
NNs - sexes			10.64	**0.0049**
	F – F	0 ± 0		
	M – F	–0.260 ± 0.082		
	M – M	–0.249 ± 0.101		

Table 2. GLMMs on the total number of food stores per individual in relation to conspecific density at 6000 m. Explanatory variables also included vole abundance level (Low, Intermediate, High), age (1y = yearlings and Ad = Adults) and sex (M = males and F = females) of the hoarder. All models included year and individual identity of the owl as random factors. Significant variables (p< 0.05) are shown in bold. N=428 cases for 327 individuals in 15 years.

Explanatory		Estimate ± SE	Chisq	p
Intercept		0.471 ± 0.119		
Conspecific density		0.181 ± 0.048	14.09	**0.0002**
Vole abundance	Low	0 ± 0	1.43	0.4883
	Intermediate	–0.091 ± 0.124		
	High	–0.181 ± 0.152		
Hoarder age	Ad	0 ± 0	0.07	0.7894
	1y	0.022 ± 0.084		
Hoarder sex	F	0 ± 0	0	0.9999
	M	0 ± 0.081		

4. Discussion

We expected Pygmy Owls to avoid neighbours with similar hunting strategies (same sex or same age) to reduce exploitative intraspecific competition. In accordance with this expectation, the observed distance between stores of nearest neighbours was larger when the neighbours were both females. According to proportional deviance, male-male and male-female pairs seemed to be closer to each other than expected by random. Despite this spatial distribution, food stores were mostly larger when the hoarder was a female and especially so when the nearest neighbour was also female. In contrast, we found no age-specific spatial distribution but having yearlings as neighbours led to overall higher hoarding success, suggesting a benefit from having neighbours with modest hunting experience. The number of prey items stored by an owl depended on vole abundance as well as conspecific density, suggesting high costs of exploitative competition when food is scarce. However, in high years of vole abundance, increasing conspecific density resulted in a larger number of stored prey items, probably indicating an overall positive effect of food abundance on population densities. As expected, the number of stores hoarded by an owl increased with increasing conspecific densities to decentralize stored prey items to avoid potential

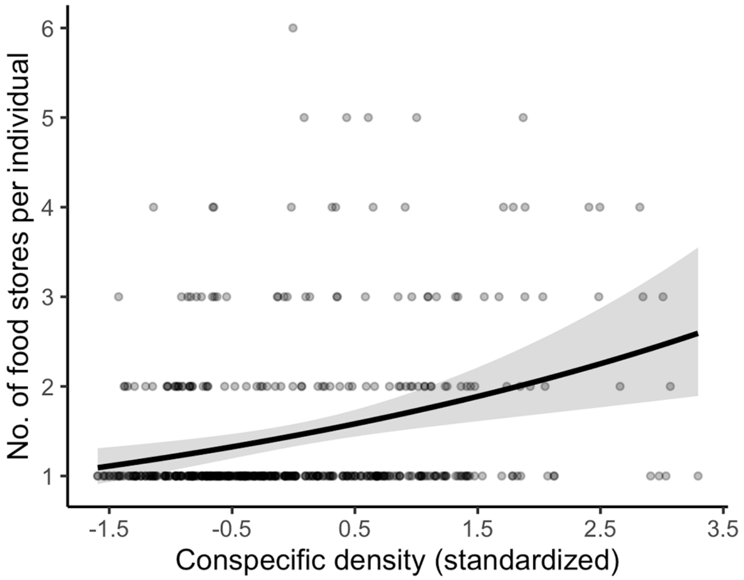

Fig. 3. Predicted values (and 95% CI) of the total number of food stores per individual in relation to conspecific density in a 6000 m radius based on the models in Table 2. Observed values are represented with semi-transparent dots, with darker colours meaning a higher number of observations.

Table 3. GLMMs analysing the variation in hoarding success (as total number of prey items stored by one individual) in relation to conspecific density in a 6000 m radius from its store(s), vole abundance level (Low, Intermediate, High), age (1y = yearlings and Ad = adults) and sex (M = males and F = females) of the hoarder and of the nearest neighbour (NN). The symbol “X” denotes an interaction. All models included year and owl identity as random factors. Significant variables (p<0.05) are shown in bold. N=428 cases for 327 individuals in 15 years.

Explanatory		Estimate ± SE	Chisq	p
Intercept		1.694 ± 0.246		
Conspecific density X Vole abundance	Low	0 ± 0	53.22	**<0.0001**
	Intermediate	1.101 ± 0.168		
	High	1.225 ± 0.169		
Conspecific density		–1.041 ± 0.178	14.64	**0.0001**
Vole abundance	Low	0 ± 0	5.69	0.0581
	Intermediate	1.443 ± 0.272		
	High	1.593 ± 0.334		
Hoarder age	1yr	0.084 ± 0.045	3.52	0.0605
	Ad	0 ± 0		
NN age	1y	0.237 ± 0.050	22.16	**<0.0001**
	Ad	0 ± 0		
Hoarder sex X NN sex	M–M	0.430 ± 0.093	21.35	**<0.0001**
	others	0 ± 0		
Hoarder sex	M	–0.526 ± 0.114	8.81	**0.0030**
	F	0 ± 0		
NN sex	M	–0.521 ± 0.072	33.05	**<0.0001**
	F	0 ± 0		

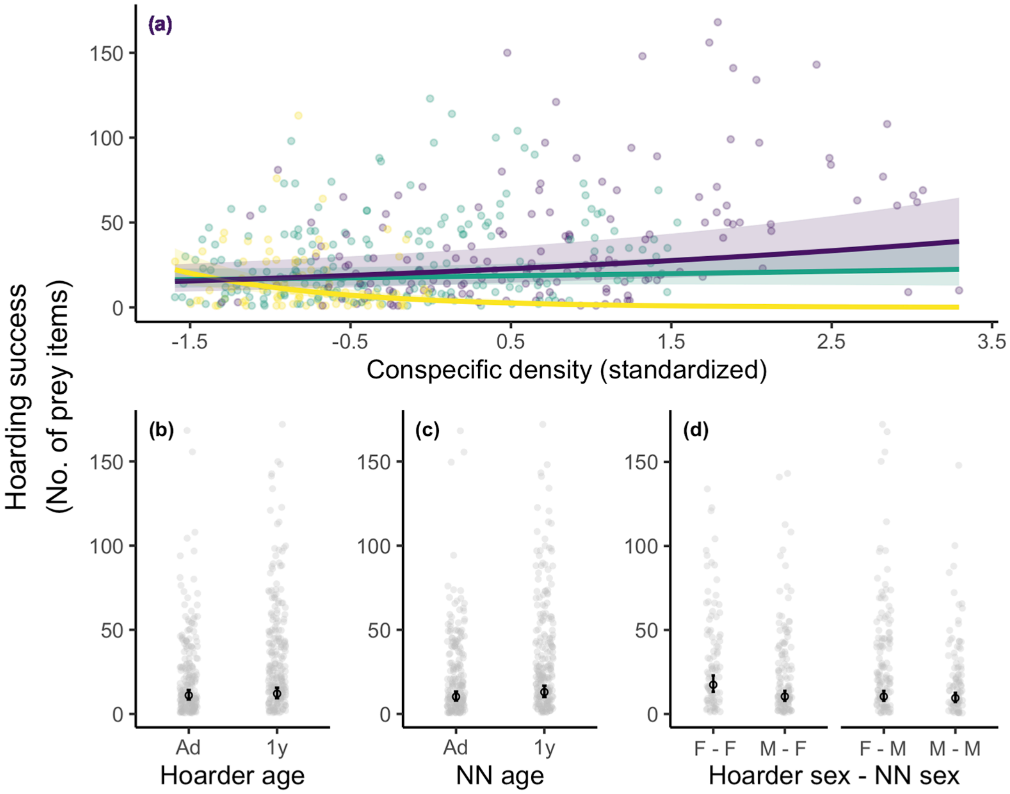

Fig. 4. Predicted values (and 95% CI) of total number of prey items stored (hoarding success) in all the food stores of one individual Pygmy Owl in relation to (a) the conspecific density in a 6000 m radius, (b) age of the hoarder, (c) of its NN, and (d) the interaction sex of the hoarder and of its NN. Predicted values are based on the models in Table 3. In plot (a), the three lines represent the different levels of vole abundance: low in yellow, intermediate in green, high in purple. Observed values are represented with dots, with darker colours meaning a higher number of observations. Colour figure is available in the online version of the article at https://doi.org/10.51812/of.130326.

pilfering and interference competition. These results suggest that high conspecific density overall inflames interference competition when food availability is low and leads to sex-specific spatial distribution.

4.1. Sex-specific competition

Pygmy Owls showed sex-specific spatial distribution. Females had overall larger distances to same-sex neighbours compared to male-male neighbours or neighbours of the opposite sex, which were instead closer to each other than expected at random. Close distances between the stores of male-male and opposite-sex neighbours were associated which led to higher conspecific density, but their different hoarding strategies and diverse diet could reduce the costs of exploitative competition. Males can hunt a large array of prey including small birds along with small mammals while females mostly hunt voles (Masoero *et al.* 2020). Therefore, the intrasexual exploitative competition among males, or between sexes, may be reduced since individuals may specialize on different prey groups. Interference competition and especially conspecific aggression could also be reduced if the neighbours are of opposite sex, or both are males. Female Pygmy Owls are larger and likely need more food than males and indeed store larger food hoards (Masoero *et al.* 2018). The energy requirement of an individual increases together with body size (Schmidt-Nielsen & Knut 1984), and therefore leads to a consequent increase in space used (Jetz *et al.* 2004). Indeed, females are known to be more aggressive toward conspecifics at least during the breeding season (Mikusek 2019). During the hoarding season their aggressive behaviour could lead females to occupy wider territories, and thus to have stores further away from each other. These results suggest that there is an asymmetry in the competitive abilities of males and females. This supports previous studies which show that individuals of the larger sex (females in our case) exert stronger competition by acquiring resources at the expense of others (Oddie 2000, Bedhomme *et al.* 2003), and they can respond more strongly than males to the presence of a competing female (Iglesias-Carrasco *et al.* 2020).

The sex-specific spatial distribution that we observed here is thus probably a combined result of exploitative and interference competition. The role of interference competition is suggested by the fact that the hoarding success of female owls with a same-sex neighbour was higher than owls with different-sex neighbours or male owls. The larger territories of females with same-sex neighbours, being in average 1 km further apart from their neighbours compared to individuals with opposite-sex neighbours or male-male neighbours (see results), probably derive from the high intrasexual aggression. These large territories could be beneficial not only to reduce interference competition but also as they reduce exploitative competition due to higher prey availability. On the other hand, being closer than expected to a neighbour with different hoarding strategy could also be beneficial in terms of reduced interference competition, while the diverse diet can help to reduce the costs of living at closer distance and thus alleviate exploitative competition. Different individuals thus seem to adopt different strategies to cope with the cost of aggressive interactions (interference competition) and the cost of exploitative completion at high densities, thus resulting in a sex-specific spatial distribution of stores.

Overall, our findings indicate that Pygmy Owls show sex-specific responses to competitor sex, supporting previous studies showing that under resource limitation, the larger sex is at a disadvantage due to the costs of producing and maintaining a large body (Wikelski & Thom 2000, Benito & González-Solís 2007). Our results also confirm the importance of considering not only the age and sex characteristics of the focal owl but also of their competitors when evaluating competition (Bonisoli-Alquati *et al.* 2011, Iglesias-Carrasco *et al.* 2020). We also suggest that Pygmy Owls might avoid same-sex nearest neighbours to further release the intrasexual interference competition and resource depression (sensu Charnov *et al.* 1976). In general, interference competition can be exhausting by reducing food availability and the energy allocated in competition is then unavailable for other functions (Jaeger *et al.* 1983, Cresswell 1997), which in turn can lead to reduced fitness (Eccard & Ylönen 2002). Therefore, intraspecific competition and resource depression are probably among the main drivers in regulating wintering population of Pygmy Owls, as suggested for other predators (*e.g.*, Cubaynes *et al.* 2014), and behavioural mechanisms releasing this competition can thus be highly beneficial. In addition, interspecific competition with other predators subsisting small mammals may also be important, because Pygmy Owls are able to store less food in the presence of larger Tengmalm's Owls (*Aegolius funereus*; Suhonen *et al.* 2007).

4.2. Conspecific density and resource abundance

The number of stores hoarded by an owl increased with increasing conspecific densities. Allocating prey in several food stores can reduce transportation distance and, thus, energetic costs. Distributing prey items to multiple store-sites instead of one (shifting from larder-hoarding towards scatter-hoarding) can help to reduce the overall loss to potential pilfering when the conspecific density is high (Vander Wall & Jenkins 2003). Pygmy Owls can visit each other's food stores (Masoero *et al.* 2018) and multiple food stores likely reduce pilfering from conspecifics or other small predators, such as small mustelids (*Mustela* sp.), which also increase in numbers during years of vole abundance (Korpimäki *et al.* 1991). When food is abundant, the variance in competitive abilities might be higher, because also more inexperienced or inferior competitors may be able to survive in the population and be more prone to conduct pilfering, as shown in other food-hoarding species (*e.g.*, American red squirrels *Tamiasciurus hudsonicus*; Donald & Boutin 2011). A high density of competitors will increase both exploitative and interference competition and having several hunting grounds might dilute this effect. It has been found that animals can adjust their behavioural patterns according to the assessed population density (Dantzer *et al.* 2012), so it can be suggested that showing activity in multiple store locations could also be a way for Pygmy Owls to strengthen their territory ownership, which can, in turn, reduce the confrontations from intruders.

In low vole abundance years, conspecific density decreased the total prey number stored by an owl, showing high costs of competition. This is in line with previous studies showing that when resources are scarce, intraspecific exploitative competition is stronger (*e.g.*, Amundsen 2007, Morosinotto *et al.* 2017a). Hoarding success increased with conspecific density in high vole years in early winter, which is consistent with an earlier finding that Pygmy Owls avoided breeding close to each other but less so when food was plentiful (Morosinotto *et al.* 2017a). When voles are abundant, also the number of Pygmy Owls over-wintering in the area is high (Masoero *et al.* 2020) but, due to the good food availability, the intraspecific competition *per se* appeared to be relaxed. This shows the crucial role of the high-amplitude vole cycles for the predator community in northern areas. Voles are keystone herbivores in boreal landscapes and the main food source for a whole predator community, consisting of several avian and mammalian predators (*e.g.*, Korpimäki 1987, Korpimäki *et al.* 1991). Accordingly, Dhondt (2012) highlights the importance of resource availability for intraspecific competition. It is often difficult to disentangle the effects of food availability and population density when they are highly intertwined (Dantzer *et al.* 2012). For example, and consistently with our results, in breeding Eagle Owls (*Bubo bubo*) the population growth rate is positive in low conspecific abundance, whereas it tends to be negative when conspecific abundance is high (Fernandez-de-Simon *et al.* 2014). Population growth was also positively related to the density of Eagle Owls' main prey (rabbits *Oryctolagus cuniculus*), when considering Eagle Owl conspecific abundance (Fernandez-de-Simon *et al.* 2014). Especially in systems with drastically varying food supply from year to year, the focus of the competition can fluctuate between food (when food is scarce) and space, like roosting sites during winter, when food is not the limiting factor.

4.3. Age-specific effects

Pygmy Owls did not seem to spatially avoid individuals according to age, because the age of the nearest neighbour only slightly affected hoarding success. Hoarders with a yearling neighbour had larger food stores than hoarders with an adult neighbour, but independently from the hoarder's age. Young competitors likely lack the same experience in hunting as adults have, as shown in numerous other species (Marchetti & Price 1989, Wunderle 1991), and they are usually at a disadvantage when having to compete with adult individuals (Donázar *et al.* 1999, Smallegange & van der Meer 2006, Breed *at al.* 2013). Among food-hoarding species as well, young individuals face a higher risk of pilfering than adult individuals due to their lower experience (Beck *et al.* 2020). Furthermore, adults appear to be able to hunt a wider variety of prey (Masoero *et al.* 2020) and therefore might suffer less from competition. As adult owls cache also more small birds, they could be more mobbed. Intra and interspecific collaborative mobbing/antipredator behaviours from prey (Bshary & NoË 1997, Templeton *et al.* 2005, Dutour *et al.* 2016) may interfere with the hunting of many predators in the same forest patch and induce depression of food resources (sensu Charnov *et al.* 1976). Individuals may therefore be favoured by competing with a young neighbour and avoid food depletion by an adult neighbour due to intense mobbing of small birds.

4.4. Concluding remarks

Our results highlight the importance of intraspecific competition during a non-breeding season. We found that in food-hoarding predators high wintertime conspecific densities can lead to a lowered food-storing success, which can, in turn, decline the chances for over-winter survival or reduce breeding success in the following year. Therefore, in harsh winter conditions, sex-specific spatial segregation in species with sex-dependent hunting differences could have evolved to reduce the costs of interference competition rather than exploitative competition. Having the right neighbour can help to reduce the severity of intraspecific competition locally, as sexes are known to have differences in diet and hunting behaviour (Mills *et al.* 2019, Masoero *et al.* 2020). When predators are in question, the outcome of their interactions will also indirectly impact prey populations (Ritchie & Johnson 2009), because prey will modify their habitat choice according to the spatial distribution of predators (Korpimäki *et al.* 1996, Morosinotto *et al.* 2010, Byholm *et al.* 2012). As male Pygmy Owls hunt more birds than females do, the sex-specific spatial settlement patterns of wintering Pygmy Owls can further modify the habitat selection of their main and alternative prey, voles, and small passerine birds, respectively. Since harsh winter months are critical for the abundance and condition of small birds in boreal forests (*e.g.*, Morosinotto *et al.* 2017b), even small-scale habitat decisions made by predators can have severe consequences on a wintering animal. Thus, understanding how conspecific predators interact and how this can impact their spatial distribution and hunting success is crucial to investigate predator effects at a landscape scale.

Lajinsisäinen tiheys ohjaa varpuspöllön sukupuolikohtaista alueellista talvilevittäytymistä ja ravinnonkeräämiskäyttäytymistä

Useimmat tutkimukset lajinsisäisestä kilpailusta on tehty pesimäkaudella. Pohjoisilla leveysasteilla lajinsisäisen kilpailun kuitenkin odotetaan olevan erityisen voimakasta pesimäkauden ulkopuolella, kun sääolosuhteet ovat ankarat ja resursseja on tarjolla rajallisesti. Tässä tutkimuksessa tarkastelimme talvehtivien varpuspöllöjen (*Glaucidium passerinum*) ravinnonkeräämiskäyttäytymistä 15 vuoden ajalta. Lisäksi analysoimme sekä sukupuoli- että ikäkohtaista alueellista levittäytymistä suhteessa vaihtelevaan pääsaaliin (myyrien) runsauteen ja lajinsisäiseen tiheyteen.

Huonoina myyrävuosina korkeampi lajinsisäinen tiheys vähensi varpuspöllöjen varastoiman saaliin kokonaismäärää, mikä voi johtua epäsuoran resurssikilpailun korkeista kustannuksista. Etäisyydet ruokavarastojen välillä olivat pidempiä silloin, kun lähimmät naapurit olivat naaraita, mikä viittaa alueellisen käyttäytymisen liittyvän sukupuolikohtaiseen kilpailuun. Naarasvarpuspöllöjen varastot sisälsivät kuitenkin enemmän saalista erityisesti silloin, kun lähin naapuri oli samaa sukupuolta. Yksilöt varastoivat enemmän saalista varpuspöllöpopulaation tiheyden kasvaessa. Saaliiden jakaminen useille varastopaikoille yhden sijasta voi auttaa vähentämään mahdollisia varkauksia pöllöpopulaation tiheyden ollessa suuri.

Nämä tulokset yhdistettyinä viittaavat siihen, että suuri lajinsisäinen tiheys kärjistää sukupuolisidonnaista suoraa häirintäkilpailua (eikä pelkästään epäsuoraa resurssikilpailua), mikä puolestaan voi johtaa havaitsemaamme sukupuolikohtaiseen alueelliseen levittäytymiseen. Ravinnonkeräämis- ja häirintäkäyttäytymisen perusteella sukupuolikohtainen alueellinen levittäytyminen voi olla keino vähentää lajinsisäisen kilpailun voimakkuutta paikallisesti. Sillä voi olla myös kerrannaisvaikutuksia saalisyhteisöön.

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Author contributions statement. EKoi, CM, GM and EKor conceived the ideas and designed methodology; EKor, GM and CM collected the data;

GM and ELT analysed the data; EKoi, GM and CM led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data Availability Statement. The data (https://doi.org/10.17605/OSF.IO/ACWKS) is available at the following link: https://osf.io/acwks/.

Please note that the location data are not included to avoid endangering the nesting sites of the Pygmy Owls.

Ethical approval. Trapping and ringing of Pygmy Owls were executed under the ringing licence (no. 524 to EKor) by Ringing Centre of the Finnish Museum of the Natural History. Pit-tags were used in accordance with Finnish and EU Laws and regulations and under the approval of the Animal Experiment Committee of the State Provincial Office (Etelä-Suomen aluehallintovirasto ESAVI; permit numbers: ESAVI-2010-05480/Ym-23, ESAVI/3221/04.10.07/2013, ESAVI/3021/04.10.07/2017). Ethical approval from ethics committee for involving animals in this study was not required. All applicable international, national and/or institutional guidelines for the use of animals were followed and all methodologies adopted in this manuscript were in line with Finnish law, including snap trapping of small rodents.

References

Abramsky, Z., Rosenzweig, M.L. & Subach, A. 2001: The cost of interspecific competition in two gerbil species. — Journal of Animal Ecology 70: 561–567. https://doi.org/10.1046/j.1365-2656.2001.00520.x

Amundsen, P.-A., Knudsen, R. & Klemetsen, A. 2007: Intraspecific competition and density dependence of food consumption and growth in Arctic charr. — Journal of Animal Ecology 76: 149–158. https://doi.org/10.1111/j.1365-2656.2006.01179.x

Armstrong, D.P., Davidson, R.S., Dimond, W.J., Perrott, J.K., Castro, I., Ewen, J.G., Griffiths, R. & Taylor, J. 2002: Population dynamics of reintroduced forest birds on New Zealand islands. — Journal of Biogeography 29: 609–621. https://doi.org/10.1046/j.1365-2699.2002.00710.x

Avgar, T., Betini, G.S. & Fryxell, J.M. 2020: Habitat selection patterns are density-dependent under the Ideal Free Distribution. — Journal of Animal Ecology 89: 2777–2787. https://doi.org/10.1111/1365-2656.13352

Baddeley, A., Rubak, E. & Turner, R. 2015: Spatial Point Patterns: Methodology and Applications with R. — Chapman and Hall/CRC Press, London. http://www.crcpress.com/Spatial-Point-Patterns-Methodology-and-Applications-with-R/Baddeley-Rubak-Turner/9781482210200/

Barbaro, L., Blache, S., Trochard, G., Arlaud, C., de Lacoste, N. & Kayser, Y. 2016: Hierarchical habitat selection by Eurasian pygmy owls *Glaucidium passerinum* in old-growth forests of the southern French Prealps. — Journal of Ornithology 157: 333–342. https://doi.org/10.1007/s10336-015-1285-3

Baroni, D., Masoero, G., Korpimäki, E., Morosinotto, C. & Laaksonen, T. 2021: Habitat choice of a secondary cavity user indicates higher avoidance of disturbed habitat during breeding than during food-hoarding. — Forest Ecology and Management 483: 118925. https://doi.org/10.1016/j.foreco.2021.118925

Bartoń, K. 2023: MuMIn: Multi-Model Inference. R package version 1.47.5. https://cran.hafro.is/web/packages/MuMIn/MuMIn.pdf

Bates, D., Maechler, M., Bolker, B. & Walker, S. 2015: Fitting Linear Mixed-Effects Models using lme4. R package v. 1.1-15. — Journal of Statistical Software 67: 1–48. https://doi.org/10.18637/jss.v067.i01

Beck, K.B., Loretto, M.-C. & Bugnyar, T. 2020: Effects of site fidelity, group size and age on food-caching behaviour of common ravens, *Corvus corax*. — Animal Behavior 164: 51–64. https://doi.org/10.1016/j.anbehav.2020.03.015

Bedhomme, S., Agnew, P., Sidobre, C. & Michalakis, Y. 2003: Sex-specific reaction norms to intraspecific larval competition in the mosquito *Aedes aegypti*. — Journal of Evolutionary Biology 16: 721–730. https://doi.org/10.1046/j.1420-9101.2003.00576.x

Benito, M.M. & González-Solís, J. 2007: Sex ratio, sex-specific chick mortality and sexual size dimorphism in birds. — Journal of Evolutionary Biology 20: 1522–1530.https://doi.org/10.1111/j.1420-9101.2007.01327.x

Bonisoli-Alquati, A., Boncoraglio, G., Caprioli, M. & Saino, N. 2011: Birth order, individual sex and sex of competitors determine the outcome of conflict among siblings over parental care. — Proceedings of the Royal Society B: Biological Sciences 278: 1273–1279. https://doi.org/https://doi.org/10.1098/rspb.2010.1741

Both, C. 1998: Experimental evidence for density dependence reproduction in great tits. — Journal of Animal Ecology 67: 667–674. https://www.jstor.org/stable/2647286

Breed, G.A., Bowen, W.D. & Leonard, M.L. 2013: Behavioral signature of intraspecific competition and density dependence in colony-breeding marine predators. — Ecology and Evolution 3: 3838–3854. https://doi.org/10.1002/ece3.754

Brunsdon, C. & Chen, H. 2014: GISTools: Some further GIS capabilities for R. http://CRAN.R-project.org/

packageGISTools

Bshary, R. & NoË, R. 1997: Red colobus and Diana monkeys provide mutual protection against predators. — Animal Behaviour 54: 1461–1474. https://doi.org/10.1006/anbe.1997.0553

Bull, E.L. 1990: Ecology of the great gray owl. — US Department of Agriculture, Forest Service, Pacific Northwest Research Station. https://doi.org/10.2737/PNW-GTR-265

Byholm, P., Burgas, D., Virtanen, T. & Valkama, J. 2012: Competitive exclusion within the predator community influences the distribution of a threatened prey species. — Ecology 93: 1802–1808. https://doi.org/10.1890/12-0285.1

Calsbeek, R. & Sinervo, B. 2002: An experimental test of the ideal despotic distribution. — Journal of Animal Ecology 71: 513–523. https://doi.org/10.1046/j.1365-2656.2002.00619.x

Carrete, M., Sánchez-Zapata, J.A. & Tella, J.L. 2006: Components of breeding performance in two competing species: habitat heterogeneity, individual quality and density-dependence. — Oikos 112: 680–690. https://doi.org/10.1111/j.0030-1299.2006.14528.x

Chang, A.M. & Wiebe, K.L. 2016: Body condition in Snowy Owls wintering on the prairies is greater in females and older individuals and may contribute to sex-biased mortality. — The Auk 133: 738–746. https://doi.org/10.1642/AUK-16-60.1

Charnov, E.L., Orians, G.H. & Hyatt, K. 1976: Ecological implications of resource depression. — American Naturalist 110: 247–259. https://doi.org/10.1086/283062

Coulson, T., Catchpole, E.A., Albon, S.D., Morgan, B.J.T., Pemberton, J.M., Clutton-Brock, T.H., Crawley, M.J. & Grenfell, B.T. 2001: Age, Sex, Density, Winter Weather, and Population Crashes in Soay Sheep. — Science 292: 1528–1531. https://doi.org/10.1126/science.292.5521.1528

Cresswell, W. 1997: Interference Competition at Low Competitor Densities in Blackbirds *Turdus merula*. — Journal of Animal Ecology 66: 461–471. https://doi.org/10.2307/5941

Cubaynes, S., MacNulty, D.R., Stahler, D.R., Quimby, K.A., Smith, D.W. & Coulson, T. 2014: Density-dependent intraspecific aggression regulates survival in northern Yellowstone wolves (*Canis lupus*). — Journal of Animal Ecology 83: 1344–1356. https://doi.org/10.1111/1365-2656.12238

Dann, P. & Norman, F.I. 2006: Population regulation in Little Penguins (*Eudyptula minor*): the role of intraspecific competition for nesting sites and food during breeding. — Emu - Austral Ornithology 106: 289–296. https://doi.org/10.1071/MU06011

Dantzer, B., Boutin, S., Humphries, M.M. & McAdam, A.G. 2012: Behavioral responses of territorial red squirrels to natural and experimental variation in population density. — Behavioral Ecology and Sociobiology 66: 865–878. https://doi.org/10.1007/s00265-012-1335-2

Denac, D. 2006: Intraspecific Exploitation Competition as Cause for Density Dependent Breeding Success in the White Stork. — Waterbirds 29: 391–394. https://doi.org/10.1675/1524-4695(2006)29[391:IECACF]2.0.CO;2

Dhondt, A.A. 2012: Interspecific competition in birds. — Oxford University Press, Oxford.

Donald, J.L. & Boutin, S. 2011: Intraspecific cache pilferage by larder-hoarding red squirrels (*Tamiasciurus hudsonicus*). — Journal of Mammalogy 92: 1013–1020. https://doi.org/10.1644/10-MAMM-A-340.1

Donázar, J.A., Travaini, A., Ceballos, O., Rodríguez, A., Delipes, M. & Hiraldo, F. 1999: Effects of sex-associated competitive asymmetries on foraging group structure and despotic distribution in Andean condors. — Behavioral Ecology and Sociobiology 45: 55–65. https://doi.org/10.1007/s002650050539

Dutour, M., Lena, J.P. & Lengagne, T. 2016: Mobbing behaviour varies according to predator dangerousness and occurrence. — Animal Behaviour 119: 119–124. https://doi.org/10.1016/j.anbehav.2016.06.024

Eccard, J.A. & Ylönen, H. 2002: Direct interference or indirect exploitation? An experimental study of fitness costs of interspecific competition in voles. — Oikos 99: 580–590. https://doi.org/10.1034/j.1600-0706.2002.11833.x

Faegre, S.K., Nietmann, L., Hannon, P., Ha, J.C. & Ha, R.R. 2020: Age−related differences in diet and foraging behavior of the critically endangered Mariana Crow (*Corvus kubaryi*), with notes on the predation of *Coenobita* hermit crabs. — Journal of Ornithology 161: 149–158. https://doi.org/10.1007/s10336-019-01705-3

Fernandez-de-Simon, J., Díaz-Ruiz, F., Cirilli, F., Tortosa, F.S., Villafuerte, R. & Ferreras, P. 2014: Role of prey and intraspecific density dependence on the population growth of an avian top predator. — Acta Oecologica 60: 1–6. https://doi.org/10.1016/j.actao.2014.06.006

Ferrer, M. & Donazar, J.A. 1996: Density-dependent fecundity by habitat heterogeneity in an increasing population of Spanish imperial eagles. — Ecology 77: 69–74. https://doi.org/10.2307/2265655

Field, I.C., Bradshaw, C.J.A., van den Hoff, J., Burton, H.R. & Hindell, M.A. 2007: Age-related shifts in the diet composition of southern elephant seals expand overall foraging niche. — Marine Biology 150: 1441–1452. https://doi.org/10.1007/s00227-006-0417-y

Fretwell, S.D. 1972: Populations in a seasonal environment. — Princeton University Press, Princeton.

Forsman, E.D. 1983: Methods and materials for locating and studying spotted owls. — US Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. https://doi.org/10.2737/PNW-GTR-162

Garabedian, J.E., Moorman, C.E., Peterson, M.N. & Kilgo, J.C. 2022: Group size mediates effects of intraspecific competition and forest structure on productivity in a recovering social woodpecker population. — Animal Conservation 25: 438–452. https://doi.org/10.1111/acv.12757

Gurevitch, J., Morrison, J.A. & Hedges, L.V. 2000: The interaction between competition and predation: a meta-analysis of field experiments. — American Naturalist 155: 435–453. https://doi.org/10.1086/303337

Hakkarainen, H. & Korpimäki, E. 1991: Reversed sexual size dimorphism in Tengmalm’s Owl: is small male size adaptive? — Oikos 61: 337–346. https://doi.org/10.2307/3545241

Hakkarainen, H., Korpimäki, E., Koivunen, V. & Ydenberg, R. 2002: Survival of male Tengmalm's owls under temporally varying food conditions. — Oecologia 131: 83–88. https://doi.org/10.1007/s00442-001-0865-5

Hakkarainen, H., Mykrä, S., Kurki, S., Korpimäki, E., Nikula, A. & Koivunen, V. 2003: Habitat composition as a determinant of reproductive success of Tengmalm’s owls under fluctuating food conditions. — Oikos 100: 162–171. https://doi.org/10.1034/j.1600-0706.2003.11906.x

Halonen, M., Mappes, T., Meri, T. & Suhonen, J. 2007: Influence of snow cover on food hoarding in pygmy owls *Glaucidium passerinum*. — Ornis Fennica 84: 105–111. https://ornisfennica.journal.fi/article/view/133686

Hijmans, R.J. & van Etten, J. 2012: raster: Geographic analysis and modelling with raster data. R package version 2.5–8. http://CRAN.R-project.org/package=raster

Huitu, O., Norrdahl, K. & Korpimäki, E. 2003: Landscape effects on temporal and spatial properties of vole population fluctuations. — Oecologia 135: 209–220. https://doi.org/10.1007/s00442-002-1171-6

Iglesias-Carrasco, M., Brookes, S., Kruuk, L.E.B. & Head, M.L. 2020: The effects of competition on fitness depend on the sex of both competitors. — Ecology and Evolution 10: 9808–9826. https://doi.org/10.1002/ece3.6620

Ishikawa, K. & Watanuki, Y. 2002: Sex and individual differences in foraging behavior of Japanese cormorants in years of different prey availability. — Journal of Ethology 20: 49–54. https://doi.org/10.1007/s10164-002-0053- z

Jaeger, R.G., Nishikawa, K.C.B. & Barnard, D.E. 1983: Foraging tactics of a terrestrial salamander: Costs of territorial defence. — Animal Behaviour 31: 191–198. https://doi.org/10.1016/S0003-3472(83)80188-2

Jetz, W., Carbone, C., Fulford, J. & Brown, J.H. 2004: The Scaling of Animal Space Use. — Science 306: 266–268. https://doi.org/10.1126/science.1102138

Kellomäki, E. 1977: Food of the pygmy owl *Glaucidium passerinum* in the breeding season. — Ornis Fennica 54: 1–29. https://ornisfennica.journal.fi/article/view/132921

Korpimäki, E. 1987: Dietary shifts, niche relationships and reproductive output of coexisting Kestrels and Long eared Owls. — Oecologia (Berlin) 74: 277–285. https://doi.org/10.1007/BF00379371

Korpimäki, E., Norrdahl, K. & Rinta-Jaskari, T. 1991: Responses of stoats and least weasels to fluctuating vole abundances: is the low phase of the vole cycle due to mustelid predation? — Oecologia 88: 552–561. https://doi.org/10.1007/BF00317719

Korpimäki, E., Koivunen, V. & Hakkarainen, H. 1996: Microhabitat use and behavior of voles under weasel and raptor predation risk: predator facilitation? — Behavioral Ecology 7: 30–34. https://doi.org/10.1093/beheco/7.1.30

Korpimäki, E., Norrdahl, K., Huitu, O. & Klemola, T. 2005: Predator-induced synchrony in population oscillations of coexisting small mammal species. — Proceedings of the Royal Society B: Biological Sciences 272: 193–202. https://doi.org/10.1098/rspb.2004.2860 Korpimäki, E. & Hakkarainen, H. 2012: The Boreal owl: ecology, behaviour and conservation of a forest-dwelling predator. — Cambridge University Press, Cambridge. https://doi.org/10.1017/CBO9780511844164

Korpimäki, E., Hongisto, K., Masoero, G. & Laaksonen, T. 2020: The difference between generalist and specialist: the effects of wide fluctuations in main food abundance on numbers and reproduction of two co-existing predators. — Journal of Avian Biology 51: 1–13. https://doi.org/https://doi.org/10.1111/jav.02508

Krüger, O. 2005: The evolution of reversed sexual size dimorphism in hawks, falcons and owls: a comparative study. — Evolutionary Ecology 19: 467–486. https://doi.org/10.1007/s10682-005-0293-9

Lagerström, M. & Syrjänen, J. 1990: Ageing Pygmy Owls. — Lintumies 25: 291–194. (In Finnish with English summary)

Marchetti, K., & Price, T. 1989: Differences in the foraging of juvenile and adult birds: the importance of developmental constraints. — Biological Reviews 64: 51–70. https://doi.org/10.1111/j.1469-185X.1989.tb00638.x

Massemin, S., Korpimäki, E. & Wiehn, J. 2000: Reversed sexual size dimorphism in raptors: evaluation of the hypothesis in kestrels breeding in a temporally changing environment. — Oecologia 124: 26–32. https://doi.org/10.1007/s004420050021

Masoero, G., Morosinotto, C., Laaksonen, T. & Korpimäki, E. 2018: Food hoarding of an avian predator: sex- and age-related differences under fluctuating food conditions. — Behavioral Ecology and Sociobiology 72: 159. https://doi.org/10.1007/s00265-018-2571-x

Masoero, G., Laaksonen, T., Morosinotto, C. & Korpimäki, E. 2020: Age and sex differences in numerical responses, dietary shifts, and total responses of a generalist predator to population dynamics of main prey. — Oecologia 192: 699–711. https://doi.org/10.1007/s00442-020-04607-x

Mikusek, R. 2019: The role of caches in the Eurasian Pygmy Owl *Glaucidium passerinum* during the breeding season. — Ornis Polonica 60: 1–15. http://ornis-polonica.pl/_pdf/OP-60-1-Mikusek.pdf

Miller, R.S. 1967: Pattern and process in competition. —

Advances in Ecological Research 4: 1–74.

Mills, R., Taylor, G.K. & Hemelrijk, C.K. 2019: Sexual size dimorphism, prey morphology and catch success in relation to flight mechanics in the peregrine falcon: a simulation study. — Journal of Avian Biology 2019: e01979. https://doi.org/10.1111/jav.01979

Morosinotto, C., Thomson, R.L. & Korpimäki, E. 2010: Habitat selection as an antipredator behaviour in a multi-predator landscape: all enemies are not equal. — Journal of Animal Ecology 79: 327–333. https://doi.org/10.1111/j.1365-2656.2009.01638.x

Morosinotto, C., Villers, A., Thomson, R.L., Varjonen, R. & Korpimäki, E. 2017a: Competitors and predators alter settlement patterns and reproductive success of an intraguild prey. — Ecological Monographs 87: 4–20. https://doi.org/10.1002/ecm.1238

Morosinotto, C., Villers, A., Varjonen, R. & Korpimäki, E. 2017b: Food supplementation and predation risk in harsh climate: interactive effects on abundance and body condition of tit species. — Oikos 126: 863–873. https://doi.org/10.1111/oik.03476.

Oddie, K.R. 2000: Size matters: Competition between male and female great tit offspring. — Journal of Animal Ecology 69: 903–912. https://doi.org/10.1046/j.1365-2656.2000.00438.x

Pérez-Camacho, L., García-Salgado, G., Rebollo, S., Martínez-Hesterkamp, S. & Fernández-Pereira, J.M. 2015: Higher reproductive success of small males and greater recruitment of large females may explain strong reversed sexual dimorphism (RSD) in the northern goshawk. — Oecologia 177: 379–387. https://doi.org/10.1007/s00442-014-3146-9

Pérez-Camacho, L., Martínez-Hesterkamp, S., Rebollo, S., García-Salgado, G. & Morales-Castilla, I. 2018: Structural complexity of hunting habitat and territoriality increase the reversed sexual size dimorphism in diurnal raptors. — Journal of Avian Biology 49: e01745. https://doi.org/10.1111/jav.01745

Pulliam, H.R. & Danielson, B.J. 1991: Sources, sinks, and habitat selection: a landscape perspective on population dynamics. — American Naturalist 137: 50–66. https://doi.org/10.1086/285139

R Core Team 2022: R: A language and environment for statistical computing. — R Foundation for Statistical Computing.

Reigert, J. & Fuchs, R. 2011: Fidelity to roost sites and diet composition of wintering male urban Common Kestrels *Falco tinnunculus*. — Acta Ornithology 46: 183–189. https://doi.org/10.3161/000164511X625955

Ritchie, E.G. & Johnson, C.N. 2009: Predator interactions, mesopredator release and biodiversity conservation. — Ecology Letters 12: 982–998. https://doi.org/10.1111/j.1461-0248.2009.01347.x

Schmidt-Nielsen, K. & Knut, S.N. 1984: Scaling: why is animal size so important? — Cambridge university press, Cambridge.

Schoener, T.W. 1974: Resource partitioning in ecological communities. — Science 185: 27–39. https://doi.org/10.1126/science.185.4145.27

Schoener, T.W. 1983: Field experiments on interspecific competition. — American Naturalist 122: 240–285. https://www.jstor.org/stable/2461233

Schönn, S. 1980: Der Sperlingskauz. — Die Neue Brehm-Bücherei, Wittenberg-Luthesstadt. (In German)

Sih, A., Crowley, P., McPeek, M., Petranka, J. & Strohmeier, K. 1985: Predation, competition and prey communities: a review of field experiments. — Annual Review of Ecology, Evolution, and Systematics 16: 269–311. https://doi.org/10.1146/annurev.es.16.110185.001413

Smallegange, I.M. & van der Meer, J. 2006: Interference from a game theoretical perspective: shore crabs suffer most from equal competitors. — Behavioral Ecology 18: 215–221. https://doi.org/10.1093/beheco/arl071

Smith, R.D. & Metcalfe, N.B. 1994: Age, Sex and Prior Site Experience Have Independent Effects on the Foraging Success of Wintering Snow Buntings. — Behaviour 129:99–111.https://doi.org/10.1163/156853994X00370

Solheim, R. 1984a: Caching behaviour, prey choice and surplus killing by pygmy owls *Glaucidium passerinum* during winter, a functional response of a generalist predator. — Annales Zoologici Fennici 21: 301–308. https://www.jstor.org/stable/23734162

Solheim, R. 1984b: Breeding biology of the pygmy owl *Glaucidium passerinum* in two biogeographical zones in southeastern Norway. — Annales Zoologici Fennici 21: 295–300. https://www.jstor.org/stable/23734161

Strøm, H. & Sonerud, G.A. 2001: Home range and habitat selection in the pygmy owl *Glaucidium passerinum*. — Ornis Fennica 78: 145–158. https://ornisfennica.journal.fi/article/view/133558

Suhonen, J., Halonen, M., Mappes, T. & Korpimäki, E. 2007: Interspecific competition limits larders of pygmy owls. — Journal of Avian Biology 38: 630–634. https://doi.org/10.1111/j.2007.0908-8857.03960.x

Svanbäck, R. & Bolnick, D.I. 2007: Intraspecific competition drives increased resource use diversity within a natural population. — Proceedings of the Royal Society B: Biological Sciences 274: 839–844. https://doi.org/10.1098/rspb.2006.0198

Svanbäck, R., Eklöv, P., Fransson, R. & Holmgren, K. 2008: Intraspecific competition drives multiple species resource polymorphism in fish communities. — Oikos 117: 114–124. https://doi.org/10.1111/j.2007.0030-1299.16267.x

Taylor, I.R. 1994: Barn Owls. Predator-prey relationships and conservation. — Cambridge University Press, Cambridge.

Templeton, C.N., Greene, E. & Davis, K. 2005: Allometry of Alarm Calls: Black-Capped Chickadees Encode Information About Predator Size. — Science 308: 1934. https://doi.org/10.1126/science.1108841

Terraube, J., Villers, A., Poudré, L., Varjonen, R. & Korpimäki, E. 2017: Increased autumn rainfall disrupts predator-prey interactions in fragmented boreal forests.

— Global Change Biology 23: 1361–1373. https://doi.org/doi.org/10.1111/gcb.13408

Valeix, M., Chamaillé-Jammes, S. & Fritz, H. 2007: Interference competition and temporal niche shifts: elephants and herbivore communities at waterholes. — Oecologia 153: 739–748. https://doi.org/10.1007/s00442-007-0764-5

Vander Wall, S.B. 1990: Food Hoarding in Animals. — University of Chicago Press, Chicago. https://doi.org/10.1016/0169-5347(90)90034-B

Vander Wall, S.B. & Jenkins, S.H. 2003: Reciprocal pilferage and the evolution of food-hoarding behaviour. — Behavioral Ecology 14: 656–667. https://doi.org/10.1093/beheco/arg064

Wikelski, M. & Thom, C. 2000: Marine iguanas shrink to survive El Niño. — Nature 403: 37–38. https://doi.org/10.1038/47396

Wunderle, J.M. Jr 1991: Age-specific foraging proficiency in birds. — In Current ornithology vol. 8 (Ed. Power, D.M.): 273–324, Plenum Publishing Corporation, New York.

Ziv, Y., Abramsky, Z., Kotler, B.P. & Subach, A. 1993: Interference competition and temporal and habitat partitioning in two gerbil species. — Oikos 66: 237–246. https://doi.org/10.2307/3544810

Online supplementary material

Supplementary material available in the online version (https://doi.org/10.51812/of.130326) includes Tables S1–S2 with information on model selection.

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