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Occurrence of rats and their impacts on colonial waterbirds in a Danish fjord

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Human development around the globe has led to great expansion of the Brown Rat (*Rattus norvegicus*), which has implications for local wildlife and especially ground-breeding birds. In this study, we analyse the colonisation and persistence of rats on small islets important to breeding waterbirds in a Danish fjord, and investigate the effect of rat presence on the number of breeding pairs of eight waterbird species. The islets had an annual rat colonisation probability of 6% and an annual rat population persistence rate of 65% (equalling an annual population survival rate of 62% when adjusting for re-colonisations upon extinctions). Contrary to our hypotheses, rat colonisation and persistence was uncorrelated with islet size, distance from the mainland and the presence of shrub cover. Rat presence had a significant negative effect on the number of breeding pairs of four waterbird species, including Avocet (*Recurvirostra avosetta*, reduced to 30% compared to years without rats), Black-headed Gull (*Chroicocephalus ridibundus*, reduced to 45%) and Common Tern (*Sterna hirundo*, reduced to 52%). The smaller bird species in particular seemed to be affected by the presence of rats, and control efforts aimed at reducing rat presence on important breeding bird islets may consequently have a positive effect on the occurrence and breeding success of these species. We found no evidence of birds acting on a memory of where rats had been present in the previous year, and further research is needed to investigate the precise mechanisms behind the recorded negative effects in the contemporary year, *i.e.* how do prospecting as well as settled breeders detect and behaviourally respond to the presence of rats.

1. Introduction

Anthropogenic expansion to every part of the world has led to severe secondary effects in the form of introductions of commensal species such as Cats (*Felis catus*), Pigs (*Sus domesticus*) and rats (*Rattus* sp.) (Mack *et al.* 2000, Doherty *et al.* 2016). The invasive behaviour of these species threatens avian biodiversity worldwide, and rats have had a major impact on bird populations around the globe (BirdLife International 2008, Jones *et al.* 2008). The Brown Rat (*Rattus* *norvegicus*) originates from eastern Asia, and began to spread worldwide, including Western Europe, during the 18th and 19th centuries (Puckett *et al.* 2016). Since then, rats have demonstrated an exceptional ability to benefit from an increasing human population (Barnett 2002, van Adrichem *et al.* 2013), to the extent that they are now distributed all over Europe as one of the most numerous contemporary species. The increasing human presence in rural areas has led to an expansion of rats in natural habitats, which has again led to increased exposure of native species to rats (Barnett 2002, Banks & Hughes 2012). The growing exposure to rats (*Rattus* spp.) has been shown to have adverse effects on distribution, survival and reproduction for a number of different native taxa around the world, in the form of increased competition, spreading of diseases and direct predation (Jones *et al.* 2008, Chiba 2010, Smith & Banks 2014, Wolf *et al.* 2018).

Among the groups most susceptible to exposure to rats are ground-breeding waterbirds (Atkinson 1985, Jones *et al.* 2008). These birds generally rely on small islands or islets isolated from the mainland as suitable breeding habitats, exploiting the fact that these are largely inaccessible to most native mammalian predators. However, the proximity of their nests to water, in combination with the easy access to eggs and chicks on the ground, render this group especially vulnerable to a mammalian predator with good swimming capabilities such as the Brown Rat (Møller 1983). Due to their generalist feeding strategy and high adaptive capability to new environments (Lee 2002), rats pose an important threat to several coastal waterbird species. Consequently, a number of studies have found rats to be serious predators of adults, eggs and chicks of seabirds and ground nesting colonial waterbirds (*e.g.* Møller 1983, Bertram & Nagorsen 1995, Major *et al.* 2007). The impact is especially severe when affected species are characterised by low annual reproductive output (Martin *et al.* 2000, Owens & Bennett 2000). The many documented examples of negative impacts of rats on coastal-breeding birds have led to management initiatives trying to limit rat abundance in these habitats (Taylor *et al.* 2000, Duron *et al.* 2017).

Ground breeding birds have been under selection to assess and avoid microhabitats exposed to predation from mammalian predators. Birds prospecting for breeding sites on the ground are therefore expected to obtain information about presence/absence of mammalian predators by use of visual, auditory and olfactory cues as well as through presence/absence of conspecifics (Amo *et al.* 2011, Zidar & Løvlie 2012, Stanbury & Briskie 2015). The ability of the birds to detect that rats are present on the islet where they intend to settle to breed is, however, likely to be affected by factors such as the density and/or detectability of rats, which in turn may depend on the diurnal activity patterns of the rats as well as the microhabitat features such as vegetation cover.

During the last couple of decades, coastal-breeding waterbirds have been declining in most of northern Europe, including Denmark (Stroud *et al.* 2006, Laursen & Thorup 2009). The decline seems to result mainly from the effects of loss and degradation of wetland habitats, with knock-on effects on survival and reproduction from increased predation pressure (Stroud *et al.* 2006, MacDonald & Bolton 2008, Rickenbach *et al.* 2011). Larger mammals such as Red Fox (*Vulpes vulpes*) and mustelids (family *Mustelidae*) and avian predators such as corvids (family *Corvidae*) comprise a role as main native predators on eggs and chicks of coastal birds, but increasing exposure to rats may make this invasive predator very important as well – especially given their ability to swim, enabling them to exploit otherwise predator-free islands and islets. Although negative effects of rats on coastal birds have been well documented, most studies have focused on single islands and/or single species, and an actual quantification of the effects has seldom been extracted (Igual *et al.* 2006).

In this study, we analyse the occurrence and abundance patterns of rats and their impacts on numbers of breeding pairs of eight different species of coastal ground-breeding waterbirds across 25 different islets in a Danish fjord (Roskilde Fjord), comprising an important breeding area for these species. We explored the effect of rats on numbers of breeding pairs on individual islets, and investigated whether the extent of negative effects increased with increasing abundance of rats. Furthermore, we examined whether different structural factors of the individual islets (area, distance to mainland and presence of shrub cover) and environmental factors related to weather (average winter temperature and occurrence of ice winters) affected colonization probability of rats. Based on current knowledge, we hypothesized that breeding numbers of smaller species would be negatively affected by the abundance of rats on islets (Avocet *Recurvirostra avosetta*, Common Gull *Larus canus*, Black-headed Gull *Chroicocephalus ridibundus*, Common Tern *Sterna hirundo,* and Arctic Tern *S. paradisaea*), and that larger species would not be affected (Mute Swan *Cygnus olor*, Common Eider *Somateria mollissima*, and Herring Gull *L. argentatus*). We further hypothesized that the number of breeding pairs would be affected by rat abundance in the current year as well as by rat abundance in the previous year. Our reasoning was that:

A) At the time of prospecting and settling, the birds would to some extent be able to detect presence of rats on potential breeding islets, at least if rats occurred in high densities, which would trigger avoidance.

B) The birds would sometimes fail in detecting presence of rats during the time of pre-laying, especially if rats occurred at low density on larger islets covered by vegetation. If this was the case, we anticipated that birds were likely to detect the presence of rats during the incubation or chick rearing period, and that this would lead to avoidance of that specific islet in the following year (a memory effect).

Finally, we modelled the frequency by which rats colonised islets (taken as being recorded one year having not been recorded the previous year) and went extinct (not recorded on an islet having been recorded the year before). We furthermore tested whether these events correlated with islet size, distance to the mainland and winter conditions. The probability of colonisation by rats was hypothesised to correlate negatively with distance to the mainland and positively with the number of days with sea ice cover the preceding winter, as both factors were expected to ease the crossing of open water. Persistence probabilities (*i.e.* opposite of extinction) were hypothesized to relate positively to islet size, presence of shrub cover and rat abundance score the previous year. In the same manner, we expected a negative effect of winter severity on the rats' persistence.

2. Material and methods

2.1. Study area and focal species

Roskilde Fjord (55°48'N, 12°03'E) is situated in the northern part of the island of Zealand in Denmark. The fjord extends 36 km southwards from its mouth to the middle of Zealand, forming an enclosed area with the narrow mouth being the only connection to the open sea of Kattegat (Fig. S1). The fjord depth is generally 0–5 m, but can reach depths up to 30 m. Roskilde Fjord is an important breeding area for substantial numbers of coastal-breeding birds. In particular, Avocet, Common Gull, Black-headed Gull, Common Tern, Arctic Tern, Mute Swan and Herring Gull occupy the area in large numbers (see Tables S3–S10). Several of these species are listed on the EU Birds directive, prompting international obligations to ensure the future of this area as suitable coastal breeding habitat.

In the fjord there are 25 small islets of variable size (range: 0.03–139 ha, median = 0.8, Table S1) and structure, where up to approximately 10,000–20,000 pairs of breeding birds covering 25–30 different species have been breeding every year (Andersen-Harild 2003). The first occurrences of Brown Rats on the islets in Roskilde Fjord were recorded in the late 1980s (E. Hansen & P. Andersen-Harild, pers. obs.), where they were observed to predate on eggs as well as adults of Black-headed Gulls and terns. Since 1989 rat control initiatives (poisoning) were applied whenever rats were detected, but due to the inaccessibility of islets, and to minimize disturbance of breeding birds, there was no systematic data available on the efficacy of control efforts.

2.2. Surveys of breeding birds and rat presence

The breeding populations of waterbirds on islets in Roskilde Fjord were surveyed annually during 1978–2021, and the occurrence of rats was recorded systematically in the years 1988–2009, following the first observation of rats in 1987. In all years included in the present study the surveys of breeding waterbirds were undertaken by the same two experienced observers (E. Hansen &

P. Andersen-Harild), and in the entire period each of the 25 islets were (with few exceptions) visited annually at least once or twice. The most important visit took place between the last week of May and the first week of June during which all the breeding birds present (except for passerines) were recorded. The observers walked over each of the islets, except for a few tiny and low-lying islets, which could be covered by observing from the boat. The two observers attempted to keep disturbance at a minimum. From observation points as well as while walking over the islets the observers estimated the number of breeding pairs of each species either based on counts of all nests found and/or based on counts of the individuals that apparently were involved in breeding activities. In this study, we focus on the species Avocet, Common Gull, Black-headed Gull, Common Tern, Arctic Tern, Mute Swan, Common Eider and Herring Gull. Owing to the small size of the islets, and the high detectability of the breeding colonies, the probability of not detecting the study species included here was very low. The number of annual breeding pairs of all species recorded on the individual islets is given in Table S2–S9.

Surveys of rat occurrence were conducted during the monitoring of breeding waterbirds. Based on these visits, each islet was given a semi-quantitative score for rat abundance representing the situation in the incubation phase of the breeding season. The score ranged from 0 to 3 using the following definitions: 0 = no evidence of rats, 1 = one direct observation of rats and/or other evidence that rats were present in low abundance, 2 = several observations of rats in more than one location on the islet, and/or signs of moderately high numbers of rats, 3 = rats observed several times and many signs of a high abundance of rats. The score was systematically registered on all islets by direct observations of the number of rats, tracks and holes observed as well as the abundance of excrements and carcasses from birds apparently killed by rats. The score was given by the same two persons across all years in this study. The observers knew how to distinguish the signs of presence of European water vole (*Arvicola terrestris*) on the islets from signs of presence of rats. Islets on which rats had been recorded present in May–June were usually revisited in September–October and again in late winter or early spring when rat poison was administered. The persistence of rats in consecutive years is considered most likely to reflect a situation where rats persisted despite management efforts, although we cannot completely rule out the possibility of successful eradication and followed by reinvasion.

2.3. Factors affecting colonization and persistence probability of rats

To investigate whether structural factors at the individual islets affected colonization probability of rats, we collated data on islet size, distance of the islets to the mainland and presence of shrub cover (Table S1). Areas, distances and presence of shrub cover was measured and assessed from orthophotos from spring 2018. Although the extent of shrub cover did change somewhat during the long study period, this variable is useful to distinguish between islets subject to recurrent flooding and islets with persistent vegetation that could make them more attractive to rats and maybe more conducive to persistence of rat populations locally. To explore the importance of winter conditions, we collated data on average winter temperature and occurrence of ice winters during the study period (Table S10). Average winter temperature (December–January) was calculated from data acquired from the Danish Meteorological Institute (DMI), and the occurrence of ice winters in Roskilde Fjord was extracted from annual surveys of local ice cover completed by the Defence Command Denmark (https://www2.forsvaret.dk/omos/organisation/sovarnet/organisation/marinestaben/istjenesten/Pages/Om-Istjenesten.aspx).

2.4. Statistical analyses

2.4.1. Colonisation and extinction rates of rats on islets

The probability of rat colonization on individual islets in individual years was modelled as either 0 (no rats present) or 1 (rats present) for all islet-years, 1989–2009, with a rat score at 0 the previous year in a generalised linear mixed model (GLMM: Glimmix procedure in SAS 9.4) with a logit link function and binomial error distribution. To account for random variation between year and between islets, we stated year and islet as random effects. In this model, we tested the fixed effects of area, distance to mainland and presence of shrubs on individual islets, as well as average winter temperature and days with sea ice the previous winter. All models had a generalised chi-square / df -ratio ranging from 0.48–1.01 (a ratio of 1 indicates a perfect fit), indicating no signs of variance inflation. Models that accounted for spatial autocorrelation generally provided similar predictions as models that did not address spatial autocorrelation, but reached less robust predictions as their estimated G matrix was usually not positive infinite (suggesting less reliable solutions due to overly complex model structure) if converging at all. The same phenomenon occurred when modelling annual variation in rhe number of breeding pairs per islet per year (see below). For these computational (overfitting) as well as biological reasons (the islets were generally closer to the mainland than to each other, so we consider the annual variation in rat presence and bird numbers in reality to be independent between neighbouring islets), we did not incorporate spatial autocorrelation in any of the statistical models to which we refer.

We modelled the general persistence time of rat populations (once established), 1988–2009, as a Kaplan-Meier-survival function (Lifetest procedure in SAS), with the number of consecutive years with rats present as a response variable. Hence, an event where rats were found in a single year only was scored as survival time of 0, whereas an event where rats persisted for four years in a row was scored as survival time of 3. Four rat islet populations still present in 2009 were right-censored. Since the survival curve suggested that annual persistence probability was independent of population age, we subsequently modelled the annual persistence probability as per islet per year (1989–2008) as either 0 (no rats left the following year) or 1 (rats still present the following year) in a GLMM. In the GLMM, islet and year were stated as random effects, and islet area, distance to mainland, presence of shrubs, average winter temperature and days with sea ice as fixed effects. All models had a generalised chi-square / df -ratio ranging from 1.00–1.08 (a ratio of 1 indicates a perfect fit), indicating no signs of variance inflation.

Since the presence of rats on an islet in two subsequent years could be the result of the population surviving as well as a new colonisation event, the annual rat population survival rate (s) was $s = (p - c)/(1 - c)$, where p is the probability that rats would be present from one year to the next and c is the probability that rats would colonise a rat-free islet. The confidence limits of s was estimated from 100,000 bootstrap estimates drawn on the probability distributions of the estimates of p and c.

3.4.2. Effect of rat abundance on numbers of breeding pairs

We modelled the variation in the number of breeding pairs per islet using a GLIMMIX with a log link function and a negative binomial distributed error term). In a few cases (Black-headed Gull data) when models would not converge, we instead used a Poisson distributed error term and corrected for overdispersion ('random _residual_' statement: these models provided similar predictions as those with negative binomial distributed error terms in the other species). We tested for the effect of rat presence and rat abundance score, and included year and islet as random effects. The apparent effects of either rat presence or rat abundance on number of breeding pairs (adjusted for year and islet variation) was modelled as $\exp(B)$, where B was the model coefficient of rat presence (relative to rat absence) or rat abundance (difference between succeeding levels of rat abundance score from 0 to 3). For those species where we found significant effects of rats on the number of breeding pairs, we also conducted post-hoc estimates of the differences between rat score 0 (no rats) and rat scores 1, 2 and 3, respectively. We investigated whether the number of breeding pairs was affected by rat presence in the contemporary year as well as by the presence of rats in the preceding year (a memory effect). We therefore analysed for the effect of rat abundance in the same year as the birds were counted (t) as well as in the previous year (t–1: for the case birds should express a delayed response to rat presence). However, because no cases of delayed effects of rat presence were apparent after we had corrected for effects of immediate presence (same year), while immediate effects persisted even adjusted for effects of rat presence the previous year, we only present results of same-year-effects.

3. Results

3.1. Colonisation and extinction rates of rats on islets

The 25 islets in Roskilde Fjord were not equally likely to be populated by rats (Fig. 1). For example, rats were recorded present on Langholm (Lejre Vig) and Kølholm in eight and 13 (respectively) of the 22 study years, whereas 13 of the other islets never had rats (Table S11). In 15 of the 31 instances where rats had immigrated to an islet before the birds settled to breed, the rats had apparently disappeared again before the start of the following breeding season. However, on five islets rats were present without interruption for at least 4–7 years in a row, despite attempts to eradicate them by use of anticoagulant poison (Table S11).

From 1988 through 2009, rats were registered as present on 66 of 493 islet years (13%, Table S11). From 1989 to 2009 we registered 30 colonisation events by rats out of 399 islet years with no rat presence the previous year, equalling an annual colonisation probability of 8% (95% confidence interval: 0.06–0.11) if estimated with plain logistic regression and 6% (95% confidence interval: 0.03–0.12) if adjusting for year and islet ID as random effects. Of 27 islet populations of rats registered for the first time between 1988–2008, 12 (45%) had apparently

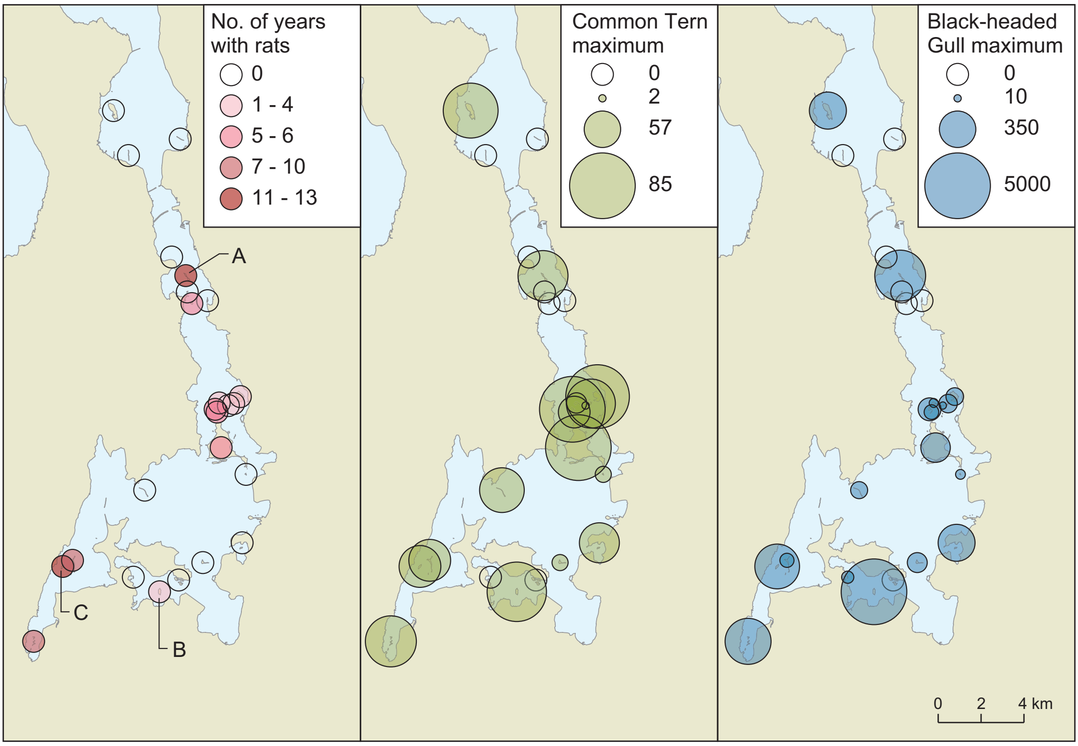

Fig. 1. Distribution of rats and of breeding Common Terns and Black-headed Gulls in Roskilde Fjord 1988–2009. For rats, circles denote the number of years where rats were recorded present during the study period. For birds, circles denote the maximum number of breeding pairs recorded on each islet (note that the scales for the circles differ between the species). The letters A, B and C in the left figure indicate the locations of the islets Kølholm, Ringøen and Hyldeholm for which histograms are shown in Fig. 3.

gone extinct the following year after being registered (Fig. 2). The log-linear shape of the Kaplan-Meier survival curve strongly indicated that the annual persistence probability was constant regardless of population age (Fig. 2). From logistic regression, the annual persistence rate was estimated at 60% (95% confidence interval: 0.47–0.72) in a model without predictor variables, and to 65% (0.45–0.81) if including islet and year as random effects. If adjusting for some apparent persistence observation being due to new colonisations, the latter estimate corresponded to an annual survival probability of 63% (95% confidence interval: 41–82%) for rat populations.

Colonisation, as well as extinction rates, were independent of islet size, distance to mainland, presence of shrubs and winter severity (days with ice cover)(all *P*-values > 0.2).

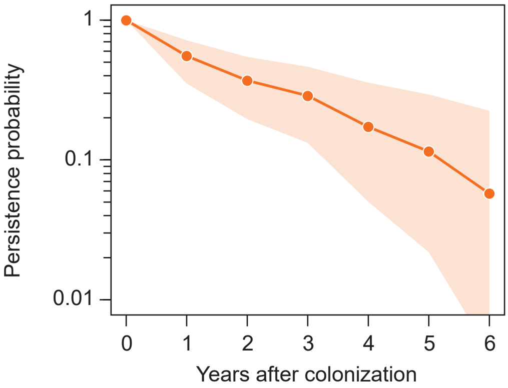

Fig. 2. Survivorship of 27 rat populations established on islets in Roskilde Fjord expressed as a Kaplan-Meier survival function (thin lines indicate 95% confidence zones).

3.2. Observations of rat impacts

The distribution of rats among islets in the fjord greatly overlapped with the distribution of islets holding large numbers of breeding waterbirds (for examples, see Fig. 1). The most dramatic impact of the presence of rats was recorded in 1989 when rats occurred on five of the islets holding colonies of Black-headed Gulls and Common Terns. Rats were particularly abundant on the three islets with the highest numbers of breeding pairs of Black-headed Gulls (*c.* 1,100-1,800 pairs on each islet; the islet 'Ringøen' held approx. 5,000 pairs the year before, see Fig. 3). Based on collection and counts of dead gulls and terns, it was estimated that 500–1,000 adults had been bitten to death and approx. 10,000 eggs and chicks had been lost, eaten or killed. The first adults found bitten to death were recorded before egg-laying had been initiated. Up to 25 corpses of Black-headed Gulls were found at each of the recorded rat holes. The species of breeding birds that had been killed by rats on the five islets included Black-headed Gulls (by far, the most commonly killed species), Common Gulls, Common Terns and Arctic Terns. Later in the season, the rats continued predating eggs and chicks which in several cases led to complete breeding failure for these four gull and tern species. There were no clear documentation of rats predating eggs of Herring Gulls, but there were instances where chicks of this species apparently had been killed and partly eaten by the rats. Eggs of Mallard (*Anas platyrhynchos*) and Tufted Duck (*Aythya fuligula*) were found predated by rats on a few of the islets.

The incidents in the late 1980s with predation from rats in the four largest colonies of Black-headed Gulls in the fjord (5,640 pairs in total) may explain why their numbers declined massively on some of the islets (examples in Fig. 3) and in total declined from approx. 15,000 pairs in the fjord in 1983–1988 to 6,000–8,000 pairs in 1989–1998. Common Tern numbers had increased in the fjord (from 160 pairs in 1978 to 496 pairs in 1988; the largest concentration of breeders of the species in Denmark) but declined almost annually thereafter to just 26 pairs in 2009. Some of the serious incidents with rats probably triggered local population declines, by means of avoidance, increased adult mortality as well as failure in producing new potential recruits. There is some evidence from ringing and counts of other colonies that some of the terns and Black-headed Gulls emigrated to alternative breeding sites in the neighbouring fjord, to lakes on the mainland and to more distant breeding localities.

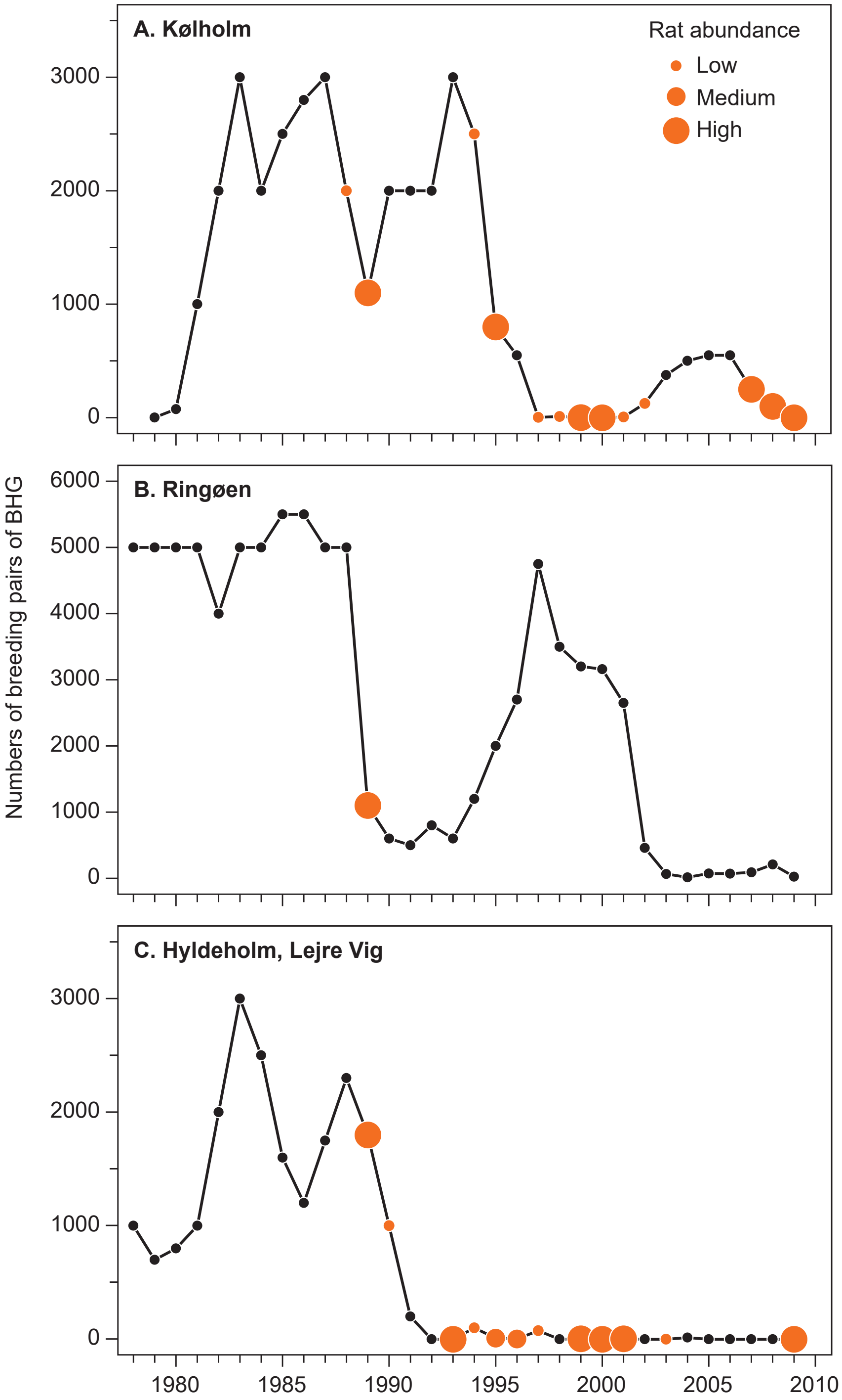

Fig. 3. Examples of the development of numbers of breeding pairs of Black-headed Gulls (BHG) 1978-2009 at three islets in Roskilde Fjord, colonized by rats in the late 1980s. The estimated sizes of the local rat populations are denoted by the three sizes of circles. Note that only two of the y-axes are drawn to the same scale.

3.3. Breeding bird numbers modelled as a function of rat presence and rat abundance

Numbers of breeding pairs of Common Tern, Mute Swan, Avocet and Black-headed Gull correlated negatively with rat presence or abundance (Table 1, Fig. 4). Avocets appeared to be the species most negatively affected by rat presence with an estimated reduction to 30% (95% confidence limits: 16–58%) compared to years without rats, followed by Black-headed Gull (reduced to 45%; 95% confidence limits: 33–60%) and Common Tern (reduced to 52%; 95% confidence limits: 31–89%). Mute Swan numbers were reduced to 81% (95% confidence limits: 60–95%) of the numbers observed in years without rats. Altogether, seven of eight species expressed negative responses to rat presence, and the overall species' response was significantly negatively different from 0 (Table 1: average coefficient = –0.40, *SE* = 0.15, *df* = 7, *P* = 0.028). Analyses of breeding numbers modelled as linear functions of rat score yielded similar results as responses to presence-absence (Table 1). However, post hoc examinations of responses specified to rat score level, suggested that only Common Tern responded more negatively the more rats were present whereas Avocet, Mute Swan and Black-headed Gull responded equally negative no matter whether few or many rats were present (Fig. 4).

4. Discussion

Our findings indicate a clear negative effect of rats on numbers of ground-breeding waterbirds on small islets. This finding supports earlier studies reporting negative impacts of rats on both waterfowl and seabirds (Bertram & Nagorsen 1995, Taylor *et al.* 2000, Angelici *et al.* 2012), and emphasizes that the presence of rats might compromise the availability of suitable breeding sites as well as breeding success among several groups of avifauna. In accordance with our hypothesis, especially the smaller species (Common Tern, Black-headed Gull and Avocet) seemed to be affected by the presence of rats. This relationship has previously been suggested by Martin *et al.* (2000), and may relate to the smaller species' inability to fend off attacks from the approaching predator. The higher impact on small-bodied species was further supported by the finding of adult individuals of Common Terns and Black-headed Gulls that had been killed by rats. We presume that most kills of adult terns and Black-headed Gulls took place at night and that the rats attacked the birds while they were incubating eggs. Following the introduction of infrared cameras on the islets we now know that the rats become particularly active above ground after sunset. For a small but relatively long-lived species like the Common Tern, this adult mortality

Table 1. Effects of presence and abundance of rats on the number of breeding pairs of waterbirds on islets in Roskilde fjord, 1988–2009. The coefficients (*B*) indicate loge-odds ratios of number of breeding pairs as function of rat presence vs. absence or increasing rat abundance score. Relative difference in numbers as function of more rates are thus derived as exp(*B*). Statistical significance levels: °: *P* < 0.1; *: *P* < 0.05; **: *P* < 0.01; ***: *P* < 0.001; ****: *P* < 0.0001.

	Presence vs. absence of rats					Rat score tested as covariate (0–3)				
	B	Exp(*B*)	SE(*B*)	t_{446}	*P*	*B*	Exp(*B*)	SE(*B*)	t_{446}	*P*
Common Tern	–0.65	0.52	0.27	–2.43	*	–0.51	0.60	0.13	–3.81	°
Arctic Tern	–0.09	0.91	0.24	–0.38		–0.20	0.82	0.13	–1.56	
Mute Swan	–0.21	0.81	0.08	–2.60	**	–0.07	0.93	0.04	–1.78	°
Avocet	–1.20	0.30	0.33	–3.60	***	–0.67	0.51	0.17	–3.88	***
Common Eider	0.09	1.10	0.19	0.49		0.08	1.08	0.09	0.92	
Common Gull	–0.14	0.87	0.13	–1.10		–0.09	0.92	0.06	–1.40	
Herring Gull	–0.20	0.82	0.12	–1.71	°	–0.11	0.90	0.06	–1.91	°
Black-headed Gull	–0.80	0.45	0.15	–5.39	****	–0.38	0.68	0.08	–4.90	****

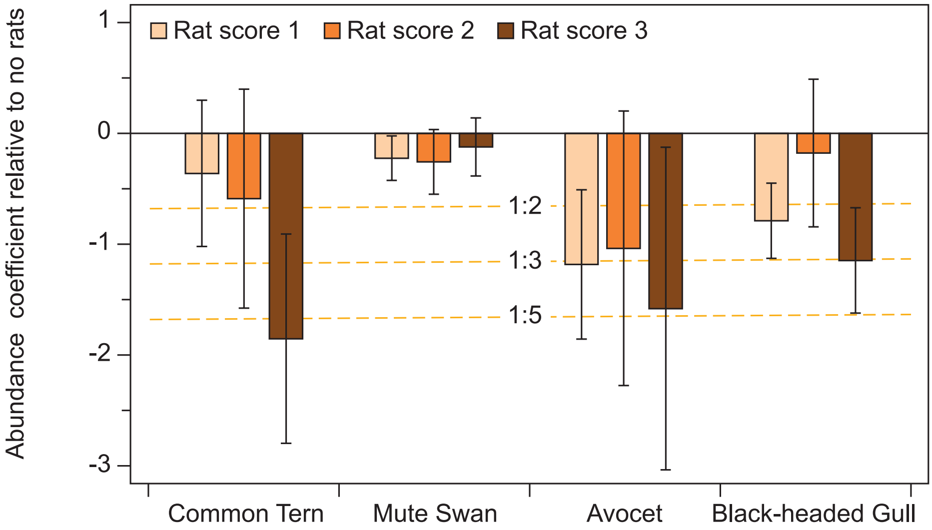

Fig. 4. Differences (with 95% confidence intervals) in number of breeding pairs at different rat abundance levels (score 1–3 from few to many rats) relative to no rats being present in the four bird species that responded negatively to rat presence (Table 1). The horizontal, stippled lines indicate odds-ratios of the difference in breeding pairs relative to no rats being present (1:2 indicate a halving of the number of breeding pairs compared to no rats being present).

is likely to have a large negative impact on population dynamics (Lebreton 2005, Cabot & Nisbet 2013). Our analysis also indicated a negative effect of rats on the number of breeding Mute Swans on individual islets, suggesting that even birds more than 20 times the size of rats were impacted. It is also known from other islets in Denmark that even though rats do not attack incubating birds of the size of Herring Gulls they may predate heavily on their chicks causing a more or less complete breeding failure in an entire colony (own observations). We find it noteworthy that even Mute Swans appeared to avoid nesting on islets with rats. Rats have been observed crawling up on nests of Mute Swans but being repelled repeatedly by the incubating parent that remained lying on the nest (Davies 2020). Our results could thus be an indication that the mere stress caused by rat harassment is sufficient to drive ground-nesting birds away from their breeding grounds.

Only Common Tern expressed a clear negative relation between numbers of breeding pairs and rat abundance. This may indicate that for some species of breeding birds the presence or absence of rats is more crucial than actual rat numbers. The birds' experience of rat presence may also have differed from the perception of the observers in the present study, *i.e.* observers and birds do not necessarily use the same cues and may interpret these differently when 'estimating' rat abundance.

We found an immediate negative effect of presence of rats on the numbers of breeding pairs of the smaller species (Avocets, Common Terns and Black-headed Gulls), *i.e.* breeding numbers dropped significantly in the year when rats had immigrated before the birds settled to breed. This immediate response may appear because potential breeders detect rats when prospecting prior to egg-laying and/or because birds experience that rats are present after they have settled and initiated breeding and then decide to abandon the islet before the monitoring of breeding birds took place. We find it likely that most of the colonial coastal birds such as the terns and gulls did try to prospect for presence of predators at the time of settling (*cf.* Cabot & Nisbet 2013), and probably some individuals experienced that rats were present and consequently gave up their first choice and instead selected another islet in the fjord or maybe even outside the fjord. Rats are normally not very active above the ground during day-time (which was also the case in our study area), and this may make it difficult for prospecting breeding birds to detect presence of rats and other nocturnal predators during the time of pre-laying (*cf.* Ratcliffe *et al.* 2008), especially if the rats occur at low density and the islet is covered by vegetation and is fairly large. It is unclear to what extent birds are able to detect the presence of rats, and what environmental cues or sensory perceptions might trigger abandonment of a breeding site. Several studies have documented that visual and auditory signals aid birds to detect potential predators (*e.g.* Quinn *et al.* 2006, Fernandez-Juricic 2012), and a study by Stanbury and Briskie (2015) report indications that Common Starlings (*Sturnus vulgaris*) are able to detect rats by means of olfactory cues. We find it likely that it commonly occurred that individuals were unaware of the presence of rats at the time of settling, maybe because they used the presence of already settled breeders as a cue for safety or were site faithful to previous breeding sites. Subsequently, rats might have become attracted to the specific site where the birds were nesting, whereby the incubating birds experienced that they and their eggs were at a real risk of being predated, and this then triggered abandonment of the islet, in some cases before the breeding survey took place. Overall, the results clearly indicate that the birds' ability to avoid rats was not super-efficient, given that there are several documented cases of birds breeding on islets with rats despite availability of rat-free and apparently suitable islets nearby.

Taken together, the collective impact of rats on numbers of ground-breeding birds is considered likely to have arisen both because some birds responded to rat presence by leaving the islet entirely and by the increased vulnerability of the birds that decided to stay or failed to detect rats and consequently were at risk of being killed during incubation as well as by losing their eggs and/or young due to predation from the rats.

We anticipated that a significant proportion of the breeding birds would avoid returning to and settling on islets where rats had been present in the previous breeding season. There were certainly instances where Black-headed Gulls and Common Terns apparently abstained from returning to breed on an islet where rats had been numerous in the previous year or over several previous years (examples in Fig. 3). However, overall we did not find significant evidence to support the hypothesis that birds would skip an islet as a breeding site if rats had been present in the previous year. Based on the clumped distribution of the breeding birds present inside the fjord, we find it very likely that many of the individuals that settled to breed on an islet on which rats had been present in the previous year were site faithful individuals which had nested on the same islet the year before. It was a surprising finding that birds reappeared on islets which had rats the previous year, especially considering that the species covered by this study – in almost all instances – had opportunities to settle on other islets free of rats. Other studies have demonstrated how islands and islets are skipped completely as breeding sites in years following immigration of predators (Nordström & Korpimäki 2004, Hilton & Cuthbert 2010), but there are also studies documenting how colonial coastal birds may continue for years to return to specific islets despite deteriorating breeding conditions that are linked to the islet itself and despite availability of suitable alternative islets (*e.g.* Heinänen *et al.* 2008). The recorded behaviour of breeding birds returning to islets in our study area which had been populated by rats in the previous year (as well as in the current year) is likely to have amplified the negative impact of the rats on the overall breeding populations of the smaller species of colonial waterbirds in the fjord. It is unknown whether the observed 'tolerance' of rat presence reflect that the historical selection pressures for strong behavioural avoidance of sites populated by this species of rodent has been fairly weak despite the coexistence of the species for almost 2000 years.

Contrary to our expectations, colonisation rate of rats on individual islets seemed unrelated to distance to the mainland and winter severity. We expected that shorter distances to the mainland and the presence of ice cover would increase the probability of colonisation. Acknowledging that the power of the analysis is limited (30 colonisation events), absence of any effects of winter severity could indicate that the rats primarily reached the islets by swimming. The absence of a relationship with distance from the mainland may indicate that, within distances of 875 m from the mainland (maximum distance among all the included islets), rats are fully capable of colonizing islets under most circumstances – at least in a relatively protected water body like Roskilde Fjord. Lodal (2008) report that rats are capable of swimming at least 750 m, and that they are able to survive for 3 days in water, and Russell *et al.* (2008b) found rats to regularly swim up to 1 km. This demonstrates that most, if not all, islets in Roskilde Fjord are probably within colonization distance. To this end, the distances between several of the individual islets were substantially less than the distance to the mainland, and rats may therefore have used the islands and islets as stepping-stones when colonizing new areas. Periods with low water levels are likely to increase movements to other islets, as rats have been observed running across the mudflats between the islets (S. Christensen, H. Jørgensen & H. Aare pers. comm.). Interestingly, Møller (1983) also found no effects of island size and distance to the mainland, but suggested that the presence (and size) of larid colonies might increase the probability of an island being occupied by rats. As such, the mere presence of terns and gulls on specific islets in Roskilde Fjord might have been a driver of rat colonisation events. The presence of birds might also have affected rat persistence locally, but the larid colonies are only present during the breeding season in spring and early summer, whereas the bottleneck in terms of rat food availability (and hence persistence) is likely to be in winter. In addition, the colonization with rats of islets in Roskilde Fjord is certainly not limited to the period when terns and gulls are present, and the birds are therefore unlikely to be the sole driver of rat presence. In our data set, there is a high risk that eradication efforts on the individual islets obscured the possible positive effect that the presence of breeding birds might have had on local rat populations, and the data we have available are therefore unsuitable to shed further light on the importance of birds as drivers for local rat population dynamics.

The persistence of rats was unaffected by the size of individual islets, presence of shrubs and winter severity. While this may lead to the conclusion that rats can survive on even very small and bare islets under most conditions in this area, it may also reflect that most colonisation events of rats on small islands are relatively short-lived (see Møller 1983). In all cases, the potential population regulatory effects of these factors may well have been obfuscated by the systematic implementation of control measures upon the detection of rats on an islet. Hence, persistence should not be interpreted as ‘natural’, but rather as the ability to persist despite control efforts. Although rats were generally subject to control whenever detected, there were no systematic data available to evaluate the efficacy of these initiatives.

In terms of management implications, it is clear that some species of waterbirds suffer from the presence of rats on their breeding islets. Consequently, eradication of rats is likely to have a positive effect on breeding numbers if successful. Currently, pest control of rats in Roskilde Fjord is severely hampered by a national ban since 2016 on the use of poison to kill rats in natural habitats. The current methods applied on the islets in the Roskilde Fjord include use of traps and trained dogs as well as shooting of rats by use of a rimfire rifle combined with a night vision scope. These methods have turned out to be far less efficient and very time consuming compared with the former use of poison. The recently developed automatic self-resetting Goodnature A24 rat traps were also in use, and these were not costly in use in terms of time and man power. However, they were effective only in a few cases, apparently because the rats were difficult to attract to the traps, possibly because the rats had easy access to alternative food resources. Consequently, the control of rats on the islets has become increasingly ineffective. Nonetheless the most sensitive species being terns and Black-headed Gulls are still breeding on a few of the islets but now in far lower numbers than they used to (T. Bregnballe, P. Andersen-Harild & E. Mandrup-Jacobsen in prep.).

In all cases, the recurring problem with rats on the islets in Roskilde Fjord clearly indicate that sustained eradication will be very challenging. Some of the lessons learned during the ‘control to zero’ campaigns on islands in New Zealand include that for control to zero density to be feasible, the following three rules must be met: (1) all pest animals must be put at risk; (2) pests must be removed faster than they reproduce; and (3) immigration must be stopped or new invaders captured before they reproduce (Anderson *et al.* 2014). In an environment like Roskilde Fjord, near-shore pest management will be regularly counteracted by reinvasion from the mainland. So, effective pest control may require multiple different control measures, including a simultaneous effort in mainland source populations and frequent surveillance in the islets (*cf.* Russell *et al.* 2008a, 2008b).

To conclude, the presence of rats on breeding islets can have substantial negative effects on their value as breeding sites for colonial waterbirds. Although the effects were most pronounced for the smaller species, our findings indicate that even large species of waterbirds might potentially be affected. Our analysis suggested that the presence or absence of rats was more important than rat abundance and that, at least in sheltered waters like bays and fjords, rats were able to colonise islets irrespective of their size, the extent of vegetation cover and their distance to the mainland.

Förekomst av råttor och deras påverkan påkoloniala vattenfåglar i en dansk fjord

Människans verksamhet har lett till en omfattande global utbredning av brunråttan (*Rattus norvegicus*) med konsekvenser för djurlivet, speciellt för markhäckande fåglar. I denna studie analyserar vi kolonisering och fortlevande av brunråttor på små öar i en Dansk fjord som är av stor betydelse för häckande vattenfåglar. Sannolikheten att öarna kolonsierades av brunråttor var 6% och sannolikheten att de fortlevde på öarna var 65% (motsvarande en 62% årlig överlevnad när återkolonisering efter utdöende beaktas). I motsats till våra hypoteser var brunråttans kolonisering oberoende av öarnas storlek, deras distans från fastlandet eller förekomsten av buskvegetation på öarna. Brunråttans närvaro hade en signifikant negativ effekt på antalet häckande par hos fyra vattenfågelarter. Antalet häckande skärfläckor (*Recurvirostra avosetta*) minskade till 30% under år med brunråttor, skrattmåsar (*Chroicocephalus ridibundus*) minskade till 45% och fisktärnor (*Sterna hirundo*) minskade till 52%. Främst de mindre vattenfågelarterna påverkades negativt av brunråttans närvaro. Kontrolleringsinsatser för att minska brunråttans närvaro på de viktigaste häckningsöarna kan ha en positiv effekt på fågelarternas förekomst och häckningsframgång. Vi fann inga bevis för att fåglarna skulle utnyttja sitt minne för att veta var brunråttorna fanns året innan. Mera forskning behövs för att undersöka beteendemekanismerna bakom de omedelbara negativa effekterna i fågelpopulationerna samma år som råttorna observerades, med andra ord, hur iakttar och reagerar prospekterande och etablerade häckande individer på närvaro av brunråttor.

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Online supplementary material

Supplementary material available in the online version includes Tables S1–S3 and Fig. S1.

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Tutoring new song elements to male birds in the wild: Lessons learnt from playback tests with the collared flycatcher

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Many vocalisations of songbirds are sexually selected and socially learnt behavioural traits that are subject to cultural evolution. For cultural inheritance, it is required that individuals imitate the song elements and build them into their repertoire, but little is known about how such learning mechanisms take place in natural populations of birds with large repertoire size. Using a Hungarian population of the collared flycatcher (*Ficedula albicollis*) as a model, we tested how often adult males can build new song elements (artificially modified or originated from distant populations) into their repertoire during mating season by using a playback approach. We predicted that when individuals incorporate new elements into their repertoire, the formerly unfamiliar elements from the playback songs would be recovered in the recorded songs of the focal males. We performed a teaching procedure with 26 males, in which we played back song sequences containing three artificially modified and three foreign syllables for each male. We recorded the song of the focal males twice a day for 2–6 days long. Then, we applied a thorough search based on a combined automatic and manual identification method to detect the tutorial syllables in the recorded songs. We found one foreign syllable type in the recordings from one male which indicates that male collared flycatchers may learn new syllable types in the courtship season. As our study has some limits, we highlight some general challenges concerning the use of playback approaches in the field for demonstrating the incidences of learning of particular song elements.

1. Introduction

Cultural transmission can be defined as the inheritance of phenotypic traits through the process of social learning (Jenkins 1978, Slater 1986, Luther & Baptista 2010, Garland *et al.* 2011). Consequently, individuals can accumulate and use information from others concerning food preference, sexual behaviour, predator avoidance and habitat choice. Such learning helps individuals gain their fitness by adapting to the quickly changing environment and lead to processes of cultural evolution (Mesoudi *et al.* 2016, Aplin 2019). Cultural evolution has been shown to affect the communication system of many animal species, of which birdsong is the most studied model. Several studies have identified local dialects (Harbison *et al.* 1999, Nelson *et al.* 2004, Podos & Warren 2007) or the change of repertoire composition in a population over time (Byers *et al.* 2010, Williams *et al.* 2013) suggesting that cultural evolution takes place. However, the underlying assumption of individual learning remains to be proven in many cases.

Few studies have demonstrated experimentally that individual birds are able to copy song elements from tutor songs, most of which were performed in captivity. These experiments revealed that song learning is often linked to a specific sensory phase, when tutees need to be exposed to tutor songs, while the production of the learnt elements corresponds to a sensorimotor phase when birds sing the learned songs (Marler 1970, Baptista & Petrinovich 1986, Baptista & Morton 1988, Slater *et al.* 1988, Beecher & Brenowitz 2005). In songbirds, there is a considerable interspecific variance concerning the timing of learning: closed-ended learners have a restricted sensitive phase (Nottebohm 1984, Böhner 1990, Beecher & Brenowitz 2005, Kiefer *et al.* 2014), while open-ended learners remain sensitive throughout their lifetime (McGregor & Krebs 1989, Chaiken *et al.* 1994, Brainard & Doupe 2002, Eriksen *et al.* 2011, Araya-Salas & Wright 2013). Laboratory studies are biased towards closed-ended learners with simple songs (small repertoire of syllables in repeated sequences), and most of the field experiments were also conducted on such birds (Jenkins 1978, Mennill *et al.* 2018). Meanwhile, evidence for the learning of particular song elements is scarce for species with complex song (large repertoire of syllables in various orders). For example, in case of the pied flycatcher (*Ficedula hypoleuca*), it has been shown that adult males were able to imitate unfamiliar syllables in playback tests in the field (Eriksen *et al.* 2011). Further studies on similar species would be of particular importance because the underlying learning mechanisms in open-ended learners with complex songs potentially involve many elements with potentially different functions (Garamszegi *et al.* 2012).

The demonstration of vocal imitation in species with complex songs is a challenging task for at least two reasons. First, ideally one should study natural systems, because individuals may not sing the whole repertoire in captivity, and/or may not be as responsive to social stimuli in the laboratory as in the wild (Rivera-Gutierrez *et al.* 2011). Second, learning should be proven experimentally, otherwise, it is impossible to disentangle if a newly detected element in the repertoire is a result of learning from an immediate vocal interaction, or it was already known, and the current stimulus recalled it from the memory. The collared flycatcher (Ficedula albicollis) as an oscine, is strongly assumed to learn its song elements (Kroodsma & Miller 2016). Furthermore, in case of the strongly related pied flycatcher it was experimentally proven, that it learns its song (Eriksen *et al.* 2011). We also know that both temporal and spatial variations in repertoire content exist at the population level, which implies roles for social learning in this species (Vaskuti *et al.* 2016), but alternative explanations (such as genetic drift) cannot be ruled out. Here, we aim to study how frequently collared flycatcher males imitate syllables in territorial interactions using a playback design. We played back modified songs of the same species that included syllables unknown for the population. We predicted that when imitation occurs, then the novel elements would be detectable in the song of the focal males.

2. Materials and methods

2.1. Preparation of playback sequences

Each playback tutorial sequence was built based on three different sources of syllables: recordings from 2017 on the experimental site (Source 1); foreign syllables originating from recordings in other distant places (Source 2); and artificially modified syllables (Source 3). We considered the syllables from Source 1 as known and Source 2 and 3 as unknown for the focal population (Fig. 1). All of these syllables were taken from recordings with the best available quality (low background noise and without vocal disturbance from other birds). Source 1 recordings were used to generate the baseline sequence of the syllables in which tutorial syllables from Sources 2 and 3 were inserted (Fig. 1a).

The syllables from Source 2 were obtained from the song recordings downloaded from the Xeno-Canto website (www.xeno-canto.org) and originating from several countries of Europe (Supplementary Table 1). The minimum distance of these recordings from our study sites was *ca.* 400 km and the maximum distance was *ca.* 1300 km (871 ± 291 km in mean ± SD). We assumed that the syllables from these recordings have species-specific characteristics and contain population-specific syllables that are unknown for the males in the studied Hungarian population.

The modified syllables (Source 3) originated from the same area as Source 1 syllables, but they were modified to create novel syllable types. To carry out this manipulation we used the "Pitch shifter" function of Adobe Audition 3.0 (Adobe Systems Inc.). With this tool we shifted the frequency of the syllables, meanwhile length remained the same. The modified syllables remained within the frequency range that is typical for the species but resulted in a particular frequency profile for the modified syllable that are unknown for the population.

To ensure that the tutorial syllables (Sources 2 and 3) were not present in the repertoire of the local population, we conducted thorough search in our long-term syllable library (see supplementary material). Altogether 39 syllable types from 16 recordings (Source 2 and Source 3) were used in our experiment.

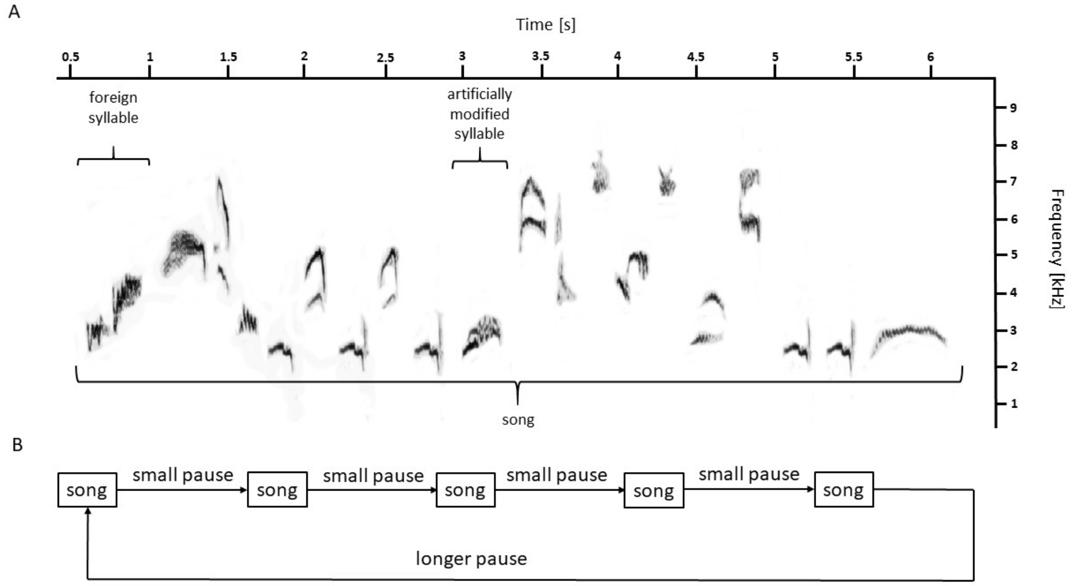

Fig. 1. Playback sequences used for tutoring: (A) Spectrogram of a song we played back. Each song contained syllables originating from the local population, tutorial syllables originating from a foreign population and syllables that were modified artificially. (B) The block diagram of the song sequences. The sequences of the songs were arranged in a natural way including shorter and longer pauses.

2.2. Field procedure

The playback tests were performed in April and May of 2018–2019 in the Pilis-Visegrádi Mts., Hungary (47°43’16’’N, 18°59’56’’E) in a range of around eight kilometers. Males involved in the study were free-living individuals occupying natural tree holes. Males were identified as unpaired males by their conspicuous courtship behaviour (*i.e.* singing and displaying). After finding a suitable male, we placed the playback installations 4–6 m high on a tree trunk about 20 meters away from the nest hole of the focal male. With this setup, we imitated a newly arrived singing conspecific neighbour. The volume of the speaker was set up by a human listener in a way to obtain a natural sound intensity similar to the singing males. After starting the playback (around 6–8 AM), we simultaneously recorded around 50 good quality songs from the focal male and then we left the area and kept the playback to continue. We returned to the focal territory in 4–5 hours and recorded another set of *ca.* 50 songs, just before remounting the installation and terminating the playback for that given day. In the subsequent days, we repeated this procedure until the focal male has paired and stopped singing. This approach resulted in recordings from 26 males, spanning 2–6 days per males (3.8 ± 1.5 days in mean ± SD) including 2-16 successful recordings (7.9 ± 3.7 recordings in mean ± SD) from each male.

2.3. Detection of the tutorial syllable types in the recordings

In the first step of syllable detection, we scanned the recordings for the presence of the tutorial syllable types. We first used a spectrographic cross-correlation approach with the library of ‘monitoR’ (Hafner & Katz 2018) in R (R Core Team 2019) to detect candidate syllables that could potentially represent learned syllables. To do so, for each tutorial syllable type, we built a filter window relying on the minimum and maximum frequency of the template syllable to narrow down the automatic scanning into the appropriate frequency range and to remove the effect of the background noise outside of this frequency range. To determine the detection threshold, we used the part of the recordings that contained the playback songs from the speaker, so we were certain that the tutorial syllable appears in the recording. The detected cross-correlation values between the template syllables and their correspondent syllables retained from the recordings were between 0.55 and 0.88 (0.68 ± 0.09 in mean ± SD). Therefore, we defined a detection threshold at a cross-correlation cut-off value of 0.55 for the automatic selection of candidate syllables potentially representing incidences of true copies (see supplementary material in the online version of this article).

In the second step, we manually screened the candidate syllables to eliminate the false positives by the visual inspection of the spectrographic representation of the syllables. The final judgement by human observers was necessary for making conclusions about qualitative matches by also appreciating some level of variance within the same syllable type. The conclusions of the visual inspection were finally confirmed by the three authors to reach a consensus for incidences for learnt syllable types.

3. Results

Based on our screening routine, we found that one tutorial syllable type appeared in the recordings at one out of 26 males involved in the tutoring tests. We could detect 11 instances of this template-like tutorial syllable type in the given individual (Fig. 2). The first instance appeared in the songs from the second recording of the first day. Similarly to the original, all the copied syllables were between 4–6 kHz in frequency, 0.2–0.25 seconds long and has similar structure with a shorter higher frequency part (5–6 kHz), and a longer lower frequency part (4–5 kHz). Differences arose mainly in the relative duration of these parts or the duration of the whole syllable and in the frequency track of parts slightly decreasing or increasing. The cross-correlational scores between the instances and the template were between 0.590 and 0.652 (0.14 ± 0.020 in mean ± SD).

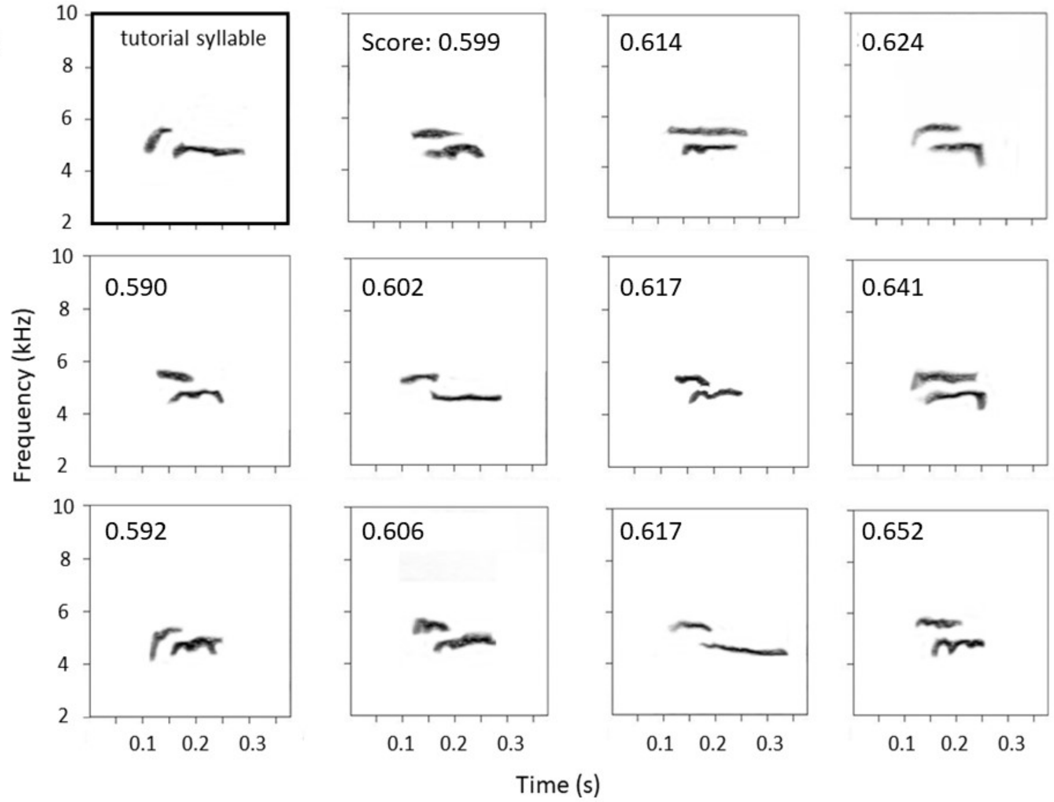

Fig. 2. Spectrograms of the tutorial syllable originated from an Italian population (recording number in Xeno-Canto: XC375479) and its potential copies found in the songs in one tutored individual. The tutorial syllable type is indicated with bold frame in the upper left corner.

4. Discussion

In general, we found weak evidence for the learning of new syllable types in the collared flycatcher, as most of the tested males did not incorporate novel elements from the playback recordings into their songs. Below, we provide a critical interpretation for these results, then – based on the experienced shortcomings – we provide some methodological recommendations that can be used to improve future studies.

We cannot be sure that the individual that produced similar syllables to one of the playback stimuli actually learnt the template syllable. In the process of learning, syllables go through the crystallization and thereafter they are sung by relatively low variation (Read & Weary 1992, Tumer & Brainard 2007). As our test examines a nearby period of the imitative learning of some syllables, one can appreciate that the learnt element would not have the exact representation on the sonograms to the tutorial syllable type. Therefore, upon the detection of imitation events, such learning mistakes should be considered (Marler 1970, Slater *et al.* 1988). This may warrant more permissive approaches for syllable categorization allowing a certain degree of within-individual variation of the same syllable type, however, the extent of that mistakes remains unknown in our model species. Accordingly, we cannot be sure that the detected similarity between the template syllable and the 11 template-like syllables is due to true learning (variations in Fig. 2 capture the variance of the same syllable type) or due to observer effect (variations in Fig. 1 capture the among-syllable type variance).

Even if we accept the above incidences

for a single male as evidence for successful learning of the template syllable type, we can conclude that the success rate of our tutoring test was relatively low (it would mean that only the 3.8% of males were able to pick up a new syllable type from a playback). There are several reasons that can explain the low rate of learning of novel syllable types by the males in our tests. First, it is possible that the chosen stimulus did not achieve a sufficiently natural effect and so the constructed playback sequences may be not suitable to induce biological response from the focal birds. For example, although we aimed to mimic a natural situation with the structure of the playback sequences, we have repeated the same set of sequences several times. Furthermore, the playback songs were played back from exactly the same location and at the same volume, which may have also represented unnatural situation. Also, we performed the tests in the absence of a visual stimulus that would establish a particular social context, while for a successful learning the presence of a live tutor might be necessary (Rice & Thompson 1968, Kroodsma & Pickert 1984, Baptista & Petrinovich 1984, 1986, Chaiken *et al.* 1993). Playback sequences that reflect better the natural variance of song content or the better elaboration of playback conditions (visual stimulus, various volume and direction of playback) may have led to better results (Beecher & Burt 2004).

We believe that our recording regime was sufficient to recover the learnt syllables as previous studies showed that 20 songs are feasible to reliably describe the song repertoire of a male collared flycatcher, particularly, the vast majority of the syllables known by an individual are produced already in 15 songs (Garamszegi *et al.* 2002, Garamszegi *et al.* 2012). We recorded 100 songs daily for 2–6 days to reveal the repertoire of each collared flycatcher male, nonetheless, it is plausible, that rarely sang, newly acquired syllables might occur only later, after the playback procedure (Chaiken *et al.* 1994, Kiefer *et al.* 2010). We cannot exclude the possibility that collared flycatcher males do not copy syllables from each other during the courtship period, but they might study novel song elements out of the breeding sites (Sorensen *et al.* 2016).

Despite the above remarks, our study points out some important phenomena that should be considered in similar tutoring tests in species with complex songs and could be used to design firm experiments. We would like to emphasise especially the problem of the learning mistakes that may lead to some extra variation in the physical structure of the learned syllable, which can raise some uncertainty around judgements about the imitative learning. Additional data processing techniques, like cluster analysis of syllables (*e.g.* software KOE https://koe.io.ac.nz, Fukuzawa *et al.* 2020), might reveal the learnt syllables in a more sensitive way than the spectrographic cross-correlation technique we used. Also the structural variation of syllables could be analysed along the sequences of recordings from each male under the prediction that learning mistakes decrease as the male practices the acquired syllables, thus within-individual variance of the same syllable type should be decreased by time. Future studies along this direction may warrant insights on the detailed mechanisms of vocal learning in general.

Handledning av nya sångelement för hanfåglar i det vilda: lärdomar från uppspelningstester med halsbandsflugsnapparen

Vokalisering hos sångfåglar är ofta socialt inlärda beteenden som uppstått genom sexual selektion och som kan modifieras genom kulturell evolution. För att kulturell nedärvning ska ske bör individer imitera beståndsdelarna i sången och bygga in dem i sin egen repertoar, men kunskapen om dylika inlärningsmekanismer hos fåglar med bred repertoar i naturliga populationer är bristfällig. Vi använde playback av konstgjort modifierade sånger samt sånger från avlägsna populationer för att undersöka hur ofta vuxna halsbandsflugsnapparhannar (*Ficedula albicollis*) kan bygga in nya beståndsdelar i sångrepertoaren under parningssäsongen. Vi förväntade oss att inlärning förekommer när tidigare obekanta beståndsdelar från playbacksången integreras i individens repertoar. Vi utförde en inlärningsprocedur med 26 hannar där vi spelade upp sångsekvenser som innehöll tre konstgjorda och tre avlägsna stavelser enskilt för varje individ. Vi spelade in sångerna från

hannarna två gånger per dag under två till sex dagar. Vi kombinderade automatiska och manuella identifieringsmetoder för att identifiera om uppspelade stavelser kunde hittas i inspelningarna. Vi hittade en stavelsetyp från en avlägsen population i inspelningarna från en hanne, vilket indikerar att halsbandsflugsnapparhannar kan lära sig nya stavelser under parningssäsongen. Eftersom vår studie har begränsningar vill vi markera några allmänna utmaningar när man använder playback i fältstudier för att demonstrera inlärning av sångstavelser.

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Online supplementary material

Supplementary material available in the online version includes descriptions of preparation of playback tutorial songs, and fieldwork, and supplementary Table S1.

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Diet shifting of tortoise-eating Golden Eagles (*Aquila chrysaetos*) in southeastern Bulgaria

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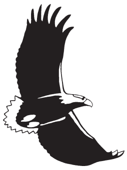

Top predators may adapt their diets to changes in prey availability where human-induced environmental changes are intense. This long-term study of the breeding-season diet of Golden Eagle (*Aquila chrysaetos*) in the Strandzha Mountains analyzed shifts in diet caused by the population decline in principal prey species, the tortoises (*Testudo hermanni* and *T. graeca*). Tortoises comprised 50.0% of the eagle diet by prey number in the 1990s, but that share collapsed to 5.8% in 2014–2021. During this later interval, Golden Eagles preyed more intensively on lighter-weight prey such as Northern White-breasted Hedgehog (*Erinaceus roumanicus*, an increase of 28.2% by number) and Edible Dormouse (*Glis glis*, an increase of 14.9% by number). Hedgehogs predominated in the diet of an individual eagle nest site for the first time in 1998 and became the principal prey in 2014–2021. Differences in food niche breadth and proportions of mesopredators between tortoise- and hedgehog-dominated individual annual diets were not significant, corresponding to a low level of food stress. The only eagle with an annual diet dominated by Squamata (snakes and lizards) was an exception, having the widest food niche. Young domestic ungulates have almost completely disappeared from eagle diets at the same as the reduction of tortoises, corresponding to a concurrent decline of livestock farming. The results obtained here have relevance to conservation management of both predator and prey populations.

1. Introduction

Adaptability of predators to changes in food supply and accessibility to prey largely determine the degree of plasticity of predator populations in a changing environment. A shift in diet to alternate prey species when preferred prey populations decrease is a common response of opportunistic birds of prey including owls (Newton 1979, Mebs & Schmidt 2014, Scherzinger & Mebs 2020). In this way predators survive periods of scarce supply of favored prey (Steenhof & Kochert 1988, Taylor 1994, Rutz & Bijlsma 2006, Penteriani & Delgado 2019). Some opportunistic top predators even occupy new territories and improve the condition of their populations by adjusting their diet to locally available food supplies (Tofft 2002, Clouet *et al*. 2015, Horváth *et al*. 2018).

The Golden Eagle (*Aquila chrysaetos*) hunts a large variety of prey across its vast range in the Northern Hemisphere, but its diet depends on mostly medium-size mammals and birds weighing 0.5–4 kg (review in Watson 2010). The local populations of rabbits and hares (Lagomorpha), marmots and squirrels (Rodentia), young ungulates including domestic livestock (Cetartiodactyla) and gallinaceous birds (Galliformes) comprise the principal prey, in varying proportions according to the specific food supply (Watson 2010, Mebs & Schmidt 2014). Carrion can be significant in winter (Haller 1996, Watson 2010). The predominance of tortoises is one of the exceptions to the breeding-season diet of the Golden Eagle typical of the Balkan Peninsula (Fischer *et al.* 1975, Grubač 1987, Miltschew & Georgiewa 1992, Georgiev 2009, Sidiropoulos *et al.* 2022). Tortoises (Hermann's Tortoise *Testudo hermanni*, Common Tortoise *T. graeca*) comprised 70.5% of the prey (n = 227) in the Strandzha Mountains, SE Bulgaria, in the late 1980s (Miltschew & Georgiewa 1992). Both tortoise species are currently listed as "endangered" in the Bulgarian Red Data Book due to the marked reduction in their number and distribution in recent decades (Golemanski 2015). Consumption of tortoises by local residents and fires set in pastures, forests and abandoned arable lands are among the main negative factors still relevant today (Petrov *et al.* 2004, Popgeorgiev 2008, Tzankov & Milchev 2014). Adaptation by Golden Eagles to the declining supply of their former main prey, tortoises, is expected to transition opportunistically to alternative prey and a wider food niche (Fernàndez 1993, Sulkava *et al.* 1998, Collins & Latta 2009, Clouet *et al.* 2015, Bedrosian *et al.* 2017, Heath *et al.* 2021). A hypothesized change would be to more mesopredator mammals and birds in the top predator's diet as an adaptive strategy to reduced supply of the principal prey in response to an increased food stress (Lourenço *et al.* 2011).

This study (i) describes the breeding-season diet of Golden Eagle during the shift in principal prey and (ii) investigates the fluctuations of dietary breadth within the study population as the main prey categories change.

2. Material and methods

2.1. Study area

The study area covers the Bulgarian part of the Strandzha Mountains, a landscape with strongly folded hill relief up to 300–400 m a.s.l. (2950 km², N42°11' S27° 26'; Fig. 1). The climate is continental-Mediterranean characterized with hot and dry summers, mild winters and annual rainfall of 600–800 mm. Deciduous forests dominated by oaks (*Quercus* spp.) and less often beech (*Fagus orientalis*) characterizes the forested landscape. Scattered open areas on flattened ridges especially at the northern and western periphery of the mountain range diversify the landscape. The Strandzha Mountains are sparsely inhabited by an aging population living in scattered villages. Malko Tarnovo municipality (747.4 km²) in the central Strandzha Mountains averages 5.1 people/km². Economic activity in the area was historically based on logging, extensive livestock husbandry and farming (see also Milchev & Georgiev 2014). Arable land was abandoned with the restitution of private land ownership after 1991/1992. Agricultural subsidies attempted but failed to restore farming after Bulgaria's accession to the EU in 2007. At the same time, the number of grazing livestock declined by more than 90% and has not recovered. The last remnants of traditional grazing pig farming disappeared following the spread of African swine fever in 2019.

Fig. 1. Study area in southeastern Bulgaria.

Tortoise populations in the Strandzha Mountains were in good condition, according to a questionnaire circulated throuout Bulgaria in the 1980s (Beshkov 1984). Both species are only slighly impacted in the study area by otherwise major negative factors at the national level such as intensification in agriculture, fires and replacement of native deciduous forests and shrubs by conifer plantations (Stojanov *et al*. 2011, Golemanski 2015). Human consumption continues to be the negative factor (Tzankov & Milchev 2014, Golemanski 2015) that has affected the tortoises in the Strandzha Mountains (Petrov *et al*. 2004, author's unpubl. data). People's unrestricted access to the Strandzha Mountains was allowed after the democratic changes of the 1990s and appears to have increased the human consumption of tortoises.

2.2. Data collection

Data on Golden Eagle diets were collected over two periods: (1) 1991–2005 with two visits in late June to early July, and again in late August to early September each year; and (2) 2014–2021 with a third intervening visit in late July. To minimize disturbance to nest sites, the visits occurred after the young eagles were over 45–50 days old. This delayed first visit probably led to the omission of some prey that could be important in the early nestling period (Collopy 1983). Eagle pairs nesting unsuccessfully in June–July were usually dropped from subsequent visits. Golden Eagles nested only in trees in about ten nesting territories (terminology follows Steenhof *et al*. 2017) in the Strandzha Mountains (Miltschew & Georgiewa 1992). Diet data were collected from eight nesting territories, and occupied nests were found in six of them during the first study period. Their number decreased to five territories with three known occupied nests in the second period; two territories were excluded as unoccupied and one pair built a nest in a densely wooded valley that precluded the possibility of tracking the eagles. The lack of open sites with visibility to the nests in the heavily wooded, rugged landscape made it difficult to find occupied nests in all nesting territories. Food remains (parts of prey, skin, feathers, bones, 312 intact and disintegrated pellets, *etc.*) were collected beneath occupied nests and at sites where eagles were resting, feeding, or consuming prey. One nest was climbed to collect food remains in 1994–2003 and nine fallen nests were inspected; Golden Eagles leave relatively few remains in their nests (Whitfield *et al*. 2009, Preston *et al*. 2017, and author's observation). Clearly recognizable remains, such as a tortoise shell and a leaf-filled stomach left next to it by the Golden Eagle, skinned hedgehog hides or legs of a hare, were described on the spot and removed so that they would not be counted again on the next visit. Other food remains were examined more closely in the laboratory to determine prey to the lowest taxonomic level possible using the published technical references (Görner & Hackethal 1987, März 1987, Peshev *et al*. 2004, Stojanov *et al*. 2011), comparative material from the National Museum of Natural History, Sofia, and the author's own reference collection. A minimum number of individuals was estimated for each taxon based on the number of the most frequent anatomical part in food remains or the pairing of anatomical parts. Bird feathers identified to species were compared to the list of bone determinations from the same sample, and the missing species from bone samples were added to the species list. The number of snakes and lizards corresponded to the number of pellets with their scales (Seguin *et al*. 1998).

Food niche breadth (FNB) was computed after Levins (1968):

$$\mathrm{FNB} = 1/\Sigma\, p_{\mathrm{i}}^{\,2} \qquad (1)$$

where p_{i} is the proportion of prey category i by number in the actual diet. The larger values indicate a higher dietary diversity. To obtain results comparable to those of Watson (2010), mammals and birds were classified by family, reptiles by order. Birds unidentified at the family level were excluded from the prey lists.

The large number of prey taxa is categorized for the analyses into seven main prey categories. The dominant prey species, (1) tortoises and (2) hedgehog, are in separate categories. The other four categories include at least one species with significant variations in its diet proportions: (3) hare (*Lepus europaeus*) and all small mammals; (4) ungulates; (5) birds; (6) lizards and snakes, Squamata. The last prey category (7) mesopredators incorporates predatory mammals (Carnivora) and birds (Accipitriformes and Strigiformes), whose share in the diet of top predators is an indicator of the level of food stress (Lourenço *et al*. 2011).

2.3. Statistical analysis

Differences between the diets of the Golden Eagle populations from the two study periods were tested with a chi-square contingency table. The annual diets (food caught by a successfully breeding pair raising at least one fledgling during one breeding season) in individual nesting territories with at least 25 prey specimens presented the dietary range within the study population. The Product Moment Correlation Coefficient measured the relations between proportions (arcsine-transformed data) of the main prey categories in the annual diets and FNB. The significance level was $p < 0.05$. All means are reported as the arithmetic mean ± standard deviation. The analyses were carried out with PAST 3.01 software (Hammer *et al*. 2001). Principal component analysis was used for studying the pattern of distribution of the prey categories in annual diets (CANOCO v. 4.5; ter Braak 1995). The samples were the annual diets, while the variables were the proportions of the main prey categories (% by number) in the respective diets. The variables are represented by arrows and the annual diets by circles on the ordination chart. The arrows show the weightings of the variables in the first two principal components. The angles between the arrows approximate the correlations among variables. Most important in the analysis with the ordination axes were species with longer arrows and sharper angles (ter Braak 1995, Lepš & Šmilauer 2003)

3. Results

3.1. Food composition

The feeding range includes 1417 prey specimens distributed among 56 identified vertebrate taxa (Supplementary Table S1). Mammals and reptiles dominated the diet in number (cumulative 87.5% by number), and birds were the most diverse class with 23 prey species. Six prey species accounted for 81.8% of the total prey number (Northern White-breasted Hedgehog *Erinaceus roumanicus* 33.6%, tortoises 23.6%, Edible Dormouse *Glis glis* 12.7%, Aesculapian Ratsnake *Zamenis longissimus* 5.7%, Common Woodpigeon *Columba palumbus* 3.1% and European Hare 3%).

Diet differed very significantly in the frequency of prey across the main categories

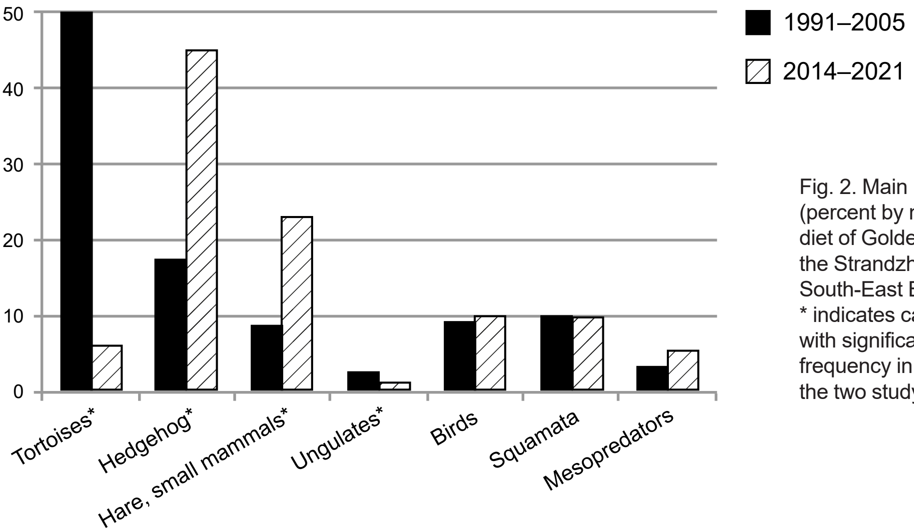

Fig. 2. Main prey categories (percent by number) in the diet of Golden Eagles in the Strandzha Mountains, South-East Bulgaria: * indicates categories with significantly different frequency in the diet during the two study periods.

between the two study periods ($\chi^2 = 420.9$, *df* = 6, $p < 0.001$; Fig. 2). Tortoises were predated much less frequently in the second period, when their proportions in the diet collapsed to 5.8% by number (*n* = 845; a decrease of 44.2%). The ratio between the two tortoise species in the diet also changed, but with a similar proportion of unidentified tortoises to species (Supplementary Table S1): the number of Hermann‘s Tortoise versus Common Tortoise was 1.6 : 1 in the first period and 5.3 : 1 in the second one. Ungulates significantly decreased to a few items (0.5% by number, *n* = 845). The resinous black color of the fur from the birth of local domestic pigs showed that they were the only ones present in the food with one exception. The prey list included wild boar (*Sus scrofa*) according to a hole from a gunshot wound in a scapula of a subadult specimen.

Frequency of Northern White-breasted Hedgehog as the eagle prey increased and this species became the dominant prey with an increase in 28.2% by number in the second period. A similar change occurred in the frequency of the category “hare, small mammals” (an increase of 14% by number). Edible Dormice in this category were responsible for the increase (a growth of 14.9% by number). Thus, species not traditionally consumed by local people accounted for 40.9% (*n* = 572) of the prey number in the Golden Eagle diet in the first study period but reached 86% (*n* = 845) of the diet after 2014. The shift to hunting White-breasted Hedgehogs and Edible Dormice corresponded to a slight widening of the food niche (3.40 in 1991–2005, 3.84 in 2014–2021).

3.2. Analysis of individual diets of eagles

The 22 analyzed annual diets of successful pairs comprised 86% of the total number of prey collected (*n* = 1417). Tortoises were the most numerous prey in 11 diets (50%, *n* = 22), while Northern White-breasted Hedgehogs predominated 10 diets (45%, Table 1). Snakes and lizards, category “Squamata”, were the most frequent prey in one diet (5%). Tortoise-dominated and hedgehog-dominated diets differed significantly in median prey numbers ($U = 1.5$, $p < 0.001$), being higher in hedgehog-dominated diets. The proportions of the three dominant categories varied greatly in annual diets, but hedgehogs were the only prey among them represented in all diets.

The proportions of the three dominant prey categories and the categories “ungulates” and “hare, small mammals” correlated significantly with each other in the annual diets (Table 2). The strongest correlations were negative between the proportions of tortoises and those of “hare, small mammals” ($r = –0.815$, $p < 0.001$) and hedgehogs

Table 1. Variations of diet characteristics in 22 individual annual diets of Golden Eagles in the Strandzha Mountains, SE Bulgaria: n = number of annual diets; %N = percent by prey number; FNB = food niche breadth; average ± standard deviation (minimum–maximum).

Prey categories		Tortoise-dominated diets (*n* = 11)	Hedgehog-dominated diets (*n* = 10)	Squamata dominated diet (*n* = 1)
Tortoises	%N	53.7 ± 12.5 (38.7–79.2)	8.2 ± 9.9 (0–34.6)	5.8
Hedgehog	%N	15.4 ± 6.5 (8.0–30.2)	47.3 ± 13.5 (34.1–68.4)	19.2
Hare, small mammals	%N	4.0 ± 3.9 (0–14.0)	21.0 ± 11.3 (6.6–35.1)	28.8
Birds	%N	9.4 ± 5.3 (3.0–18.5)	9.0 ± 2.2 (6.7–12.7)	13.5
Squamata	%N	10.4 ± 4.8 (0–15.2)	9.1 ± 3.3 (3.8–13.3)	30.8
Ungulates	%N	3.0 ± 3.3 (0–8.3)	0.8 ± 1.2 (0–3.8)	0
Mesopredators	%N	4.0 ± 4.0 (0–11.1)	4.6 ± 2.7 (0–8.6)	1.9
Prey number		31 ± 7 (25–44)	83 ± 25 (43–135)	53
FNB		3.12 ± 0.94 (1.57–4.31)	3.46 ± 1.01 (2.01–4.69)	5.28

Table 2. Significant correlations between the proportions of the prey categories (% by number) and the food niche breadth (FNB) in the individual annual diets of Golden Eagles in the Strandzha Mountains, SE Bulgaria: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, ns = not significant.

Prey categories	Tortoises	Hedgehog	Hare, small mammals	Squamata	Birds
Hedgehog	–0.790***		0.475*	ns	ns
Hare, small mammals	–0.815***	0.475*		ns	ns
Ungulates	0.477*	–0.457*	–0.465*	–0.543**	ns
FNB	ns	ns	0.593**	0.457*	0.483*

($r = –0.790, p < 0.001$). FNB correlated positively with the proportions of “hare, small mammals”, “birds” and “Squamata” (Table 2) and peaked at 5.28 for the Squamata-dominated diet. Mean FNB values did not differ significantly between tortoise- and hedgehog-dominated diets.

Principal component analysis determined the main regularities in the food composition of 22 annual diets. The first and second ordination axes explain 80.1% and 12.0% of the total variation in the data. The first gradient distributes diets according to the proportions of tortoises versus proportions of hedgehogs and “hare, small mammals” (Fig. 3). The categories “Squamata” and “hare, small mammals” correlate with the positive part of the second axis, while the categories “hedgehog”, “ungulates” and “mesopredators” respectively with the negative part of the axis. Tortoise-dominated diets fall in the left half of the chart and form a group of diets from all nesting territiries in 1991–1999. Only diets from the nesting territory 1 from 1994, 1996 (both tortoise-dominated) and 1998 (hedgehog-dominated) displayed the gradual transition to a diet with decreasing tortoise proportion. Mostly the prey categories “ungulates”, “mesopredators” and “hedgehog” replaced the tortoises in these diets. The 1996 and 1998 diets in territory 1 included 83% of the smallest tortoises as Golden Eagle prey ($n = 6$ Hermann‘s Tortoises, carapace lengh 11.2 ± 2.3 cm, range 8.5–14.4 cm).

The squamata-dominated diet (4-00, Fig. 3) in 2000 stood out from the rest by the high share of snakes, small mammals, and birds (cumulative 73.1% by number) and a drop of tortoises to 5.8% by number. All hedgehog-dominated diets since 2016 are positioned in the right half of the chart in two groups. One group included diets in nesting territory 3 with the highest hedgehog dominance (62.1 ± 7.2% by number). The category “hare, small mammals” complemented these diets the most with 10.7 ± 7.2% by number at FNB 2.4 ± 0.5. More diverse prey replaced the tortoises in the second group with diets at FNB 4.5 ± 0.2 of territories 4 and 5 (37.2 ± 2.3% hedgehogs, 31.1 ± 3.9% “hare, small mammals” and 10.6 ± 3.8% “Squamata “). The diet of territory 4 in 2019 was the only one without tortoises.

4. Discussion

Data from breeding-season Golden Eagle diets confirmed the expected change with the replacement of tortoises as the most numerous prey by the Northern White-breasted Hedgehog. This new dominant prey occupied the second position by number in previous Bulgarian studies (Miltschew & Georgiewa 1992, Georgiev 2009) and in the non-breeding diet in Greece (Sidiropoulos *et al.* 2022). Hedgehogs dominated as an exception the Golden Eagle food in Estonia (Zastrov 1946, in Watson 2010) and Gotland, Sweden (Högström & Wiss 1992). The third numerical position of the Edible Dormouse in the eagle diets in the Strandzha Mountains has an analogue only in the forested Italian pre-Alps (Pedrini & Sergio 2002). The uniqueness of the present study’s diets was reinforced by the substantial share of snakes that were important in some diets in southern Europe (Clouet 1981, Seguin *et al.* 1998), Kazakhstan (Karyakin *et al.* 2011) and Japan (Takeuchi *et al.* 2006). Ungulates were the final category with a significantly changed frequency in eagle diets during the second study period. The observed decline corresponds to the collapse of grazing

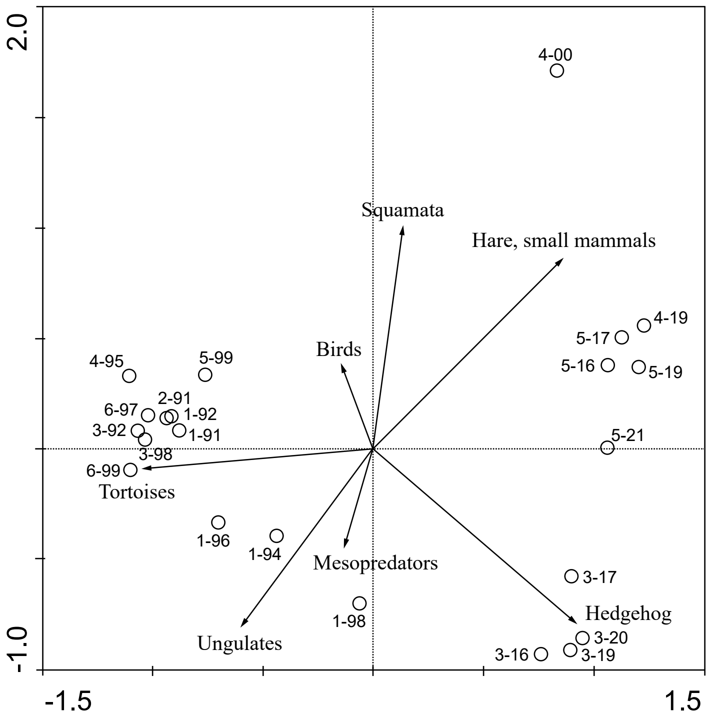

Fig. 3. PCA ordination of seven main prey categories (arrows) and 22 annual diets (circles) of Golden Eagle pairs in the Strandzha Mountains, SE Bulgaria: the category names are given at the arrowheads; individual diets are marked with a combination of two numbers, where the first is a serial number on the nesting territory according to Miltschew, Georgiewa (1992), and the latter are the last two digits of the year of the diet collection.

livestock in recent decades and the complete ban on pig farming in 2019.

Diets of Golden Eagles respond to the local supply and availability of prey from the preferred weight group. Diet changes follow Schluter's (1981) optimal diet theory (Bedrosian *et al.* 2017, Preston *et al.* 2017, Roemer & Collins 2019). Northern White-breasted Hedgehog (about 750 g, Glutz von Blotzheim & Bauer 1994) falls within the favorable weight group for Golden Eagle prey. Edible Dormouse (about 125 g, Glutz von Blotzheim & Bauer 1994) is a night climber on trees and shrubs, much lighter than the preferred prey weight group. Both prey species are significantly lighter than the predominant size group in the Bulgarian tortoise populations with 20–25 cm carapace lengh (Stojanov *et al.* 2011) and a biomass of about 2100 g (Jackson 1980). The Golden Eagles likely compensate for the lighter-weight alternative prey by increasing the total prey number in annual diets. No data on the populations of the Golden Eagle prey in the Strandzha Mountains have shown estimates that the Northern White-breasted Hedgehog and the Edible Dormouse are the most profitable prey. But indirect confirmation of flourishing populations of both mammals could explain their dominance in the opportunistic diet of a sympatric top predator such as the Eagle Owl (*Bubo bubo*) (cluster 7 in Milchev & Georgiev 2020). The Northern White-breasted Hedgehog was also the principal prey of the Eastern Imperial Eagle (*Aquila heliaca*), another opportunistic top predator breeding in neighboring more open landscapes to the west and southwest of the Golden Eagle population studied here (Demerdzhiev *et al.* 2014).

The food niche expanded slightly after the decline of tortoises in the diet, but remained below the average of 4.03 ± 2.07 in Eurasia (*n* = 24 diets, Watson 2010). Large birds such as two young Great Cormorants (*Phalacrocorax carbo*) and White Storks (*Ciconia ciconia*) were found in the food subsequently. Neither species breed in the nesting territories of the predator eagles (author's unpub. data). Golden Eagles have benefited little from the dispersal of young Great Cormorants in the Strandzha Mountain River Network and from White Storks migrating over the mountains on the main western Black Sea Flyway. Migratory bird predation was as low as that found by Clouet *et al*. (2015) for trans-Pyrenean migrants, although the migration of the numerous White Storks largely coincides with the nesting period of the Golden Eagles in the Strandzha Mountains (Milchev & Kovachev 1995).

Proportion of mesopredators also rose insignificantly and remained below the average 6.6 ± 5.6% in Europe (*n* = 21 diets, Lourenço *et al*. 2011). The predominance of owls (3.3% by number in the second period) among eaten predators in the present study was atypical for Golden Eagles (0.5 ± 0.6% owls, Lourenço *et al*. 2011) and included resident and vagrant forest owls (Menzel & Miltschev 2001). The food niche breadth and the share of mesopredators did not show extreme values nor a high level of food stress after changes in the breeding-season diet of the study population.

The analysis of annual diets between and within nesting territories shows that populations of preferred tortoises were large enough in the 1990s. Tortoise-dominated diets had a very similar structure in all territories during this period. The exception was the westernmost territory 1, where the first data on mass consumption of tortoises by humans in 1991 and 1992 were obtained (author's data, Petrov *et al*. 2004). This territory was the only one with a gradual transition to a hedgehog-dominated diet and compensatory predation of ungulates and mesopredators over the years. The collection of large adult tortoises for food by humans in the post-1990 economic crisis was the most likely explanation for the appearance of smaller young tortoises in the eagles‘ diet. The two tortoise species differ in their habitat preferences. Hermann's Tortoise prefers forest-shrub habitats, and the Common Tortoise inhabits mainly open grasslands (Stojanov *et al*. 2011). Hermann‘s Tortoise predominated over the Common Tortoise in the eagle‘s diet in the forested Strandzha Mountains in both periods, but three times more in the second period. I speculate that easier collection of tortoises by humans in open habitats has more strongly reduced the population of Common Tortoises and has been reflected in the Golden Eagle diet. Tortoise populations have dropped below some threshold level and have been replaced by alternative prey in all diets since 2000.

The shift in Golden Eagles‘ specialization to a new main prey, hedgehogs, has not led to significant differences in the food niche breadth within the study population over the years. Additional prey from the categories of small mammals, birds, and Squamata correlated positively with the width of the niche. Snakes have dominated the most diverse annual diet, but they do not seem to have furnished a stable enough supply over the years to be a diet alternative equivalent to hedgehogs and Edible Dormice. The observed transition with diversification of the diet is similar to the processes that took place in the diet of other Golden Eagle populations (Fernàndez 1993, Nyström *et al*. 2006, Bedrosian *et al*. 2017, Preston *et al*. 2017) including even subsequent specialization in new principal prey (Collins & Latta 2009, Watson & Davies 2015, Heath *et al*. 2021). Seasonal changes in food supply and availability cause usually alterations in the non-breeding-season diet of Golden Eagles (Watson 2010, Mebs & Schmidt 2014). Sidiropoulos *et al*. (2022) reported such seasonal dietary changes in neighboring northern Greece as the first in the Balkans. The Golden Eagles in the Strandzha Mountains have to change their diet during the cold half of the year much more markedly than in Greece, due to the obligatory hibernation of their main prey, hedgehogs, Edible Dormice and reptiles. The nonbreeding-season diet is important for overwinter survival and its study is needed for developing a complete Golden Eagle conservation strategy in the context of both global climate and socio-economic changes.

One of the most troubling findings from this study is the indirect confirmation of the ineffectiveness of conservation for tortoises in the Strandzha Mountains. Both tortoise species have been strictly protected under national law since

1961 (Golemanski 2015). The Strandzha Natural Park established in 1995 covers nesting territories 4 and 5, while the other Golden Eagle territories with analyzed annual diets remain outside park boundaries. However, the Natura 2000 protected-area network has covered most of the mountain range since 2007 and only nesting territory 3 has remained unprotected. Tortoises are the only reptiles with a national conservation action plan (Petrov *et al*. 2004). Nevertheless, the tortoises diminished as a prominent prey source for the Golden Eagle both in protected and unprotected territories. Both tortoise species are now among the ineffectively protected and managed wildlife populations in the Strandzha Mountains, joining extirpated and declining breeding birds (Milchev & Georgiev 2014, 2021, Demerdzhiev *et al*. 2019). The adaptive abilities of the Golden Eagle population in this study to adapt to new food sources could guide future actions to preserve both the predator and its prey.

Ruokavaliomuutos kilpikonniin erikoistuneissa maakotkissa (*Aquila chrysaetos)* Bulgarian lounaisosassa

Huippusaalistajat saattavat muokata ruokavaliotansa saalistarjonnan mukaan ympäristön muuttuessa. Tässä pitkäaikaistutkimuksessa analysoimme maakotkan (*Aquila chrysaetos*) ruokavaliomuutoksia Strandzhan vuoristossa, jossa pääsaaliin eli kilpikonnien (*Testudo hermanni* ja *T. graeca*) populaatiokoot ovat pienentyneet. Kilpikonnien osuus maakotkan saalistamasta ruokavaliosta oli 50.0% 1990-luvulla, mutta tämä osuus on pienentynyt 5.8% 2014–2021 tutkimusjaksolla. Tällä myöhemmällä tutkimusjaksolla maakotkat saalistivat voimakkaammin kevyempiä saaliita, kuten siilejä (*Erinaceus roumanicus*), joiden osuus kasvoi 28.2%, ja unikekoja (*Glis glis*), joiden osuus kasvoi 14.9%. Siilit olivat tärkeimpiä saaliita yhdessä maakotkapesässä ensimmäisen kerran 1998, ja vuosina 2014–2021 siitä tuli vallitseva saalislaji maakotkien pesissä. Ruokavalion laajuuden ja piensaalistajien osuuden vaihtelu kilpikonna- ja siilivaltaisissa pesissä ei eronnut, mikä viittaa siihen, että ravinnon saatavuus ei ole rajoittava tekijä. Ainoastaan yksi käärmeihin ja liskoihin (Squamata) erikoistunut maakotka erottui joukosta muita selvästi laajemmalla ruokavaliolla. Nuorten kotieläiminä pidettyjen sorkkaeläinten osuus saaliista on vähentynyt samaan aikaan kilpikonnien kanssa, mikä johtuu karjanhoidon vähenemisestä kyseisessä maanosassa. Tutkimuksen tulokset ovat tärkeitä sekä peto- että saalislajien suojelussa.

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Online supplementary material

Supplementary material available in the online version includes Table S1.

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Field selection of greylag geese (*Anser anser*): Implications for management of set-aside fields to alleviate crop damage

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Greylag geese (*Anser anser*) have been increasing in numbers in Europe during the last decades. They forage and roost in agricultural landscapes and may cause damage to sensitive crops. We studied field selection of greylag geese around lake Sörfjärden in south central Sweden where geese aggregate during the growing season. In this area a set-aside field was established in 2010, *i.e.*, a field where geese can graze undisturbed, with the aim to reduce damage in surrounding conventional fields. The goal of our study was to investigate the general selection of the different field types as well as the specific set-aside field. We used a point survey count to estimate goose numbers and regression analyses to evaluate the relationship between presence or absence of greylag geese and field characteristics such as crop type, distance to roost site and field size. According to the top-ranked model, the probability of presence of foraging greylag geese was higher in spring and in grass fields, while the probability decreased with distance to roost site. Our results also show that the set-aside field in general was used more than other fields in the area during spring and summer but not during autumn. We conclude that it is important to consider variables affecting the probability of field selection by geese, such as season, crop type and distance to roosts to understand the behaviour of geese when establishing set-aside fields.

1. Introduction

During the past 60 years the number of geese (Anatidae) has increased throughout Europe (McKay *et al.* 2006, Fox *et al.* 2010, Fox & Madsen 2017). Although the recovery from previously over-harvested and dwindling goose populations can be viewed as a conservation success, their increase also comes with a downside. Today's superabundant goose populations frequently cause conflicts between different human interests, such as conservation and farming (Eythórsson *et al.* 2017, Fox & Madsen 2017). Geese cause crop damage by grazing, grubbing and trampling when foraging, and this problem has increased particularly in agricultural areas where birds aggregate in large numbers for longer periods of time (Fox *et al.* 2017, Montràs-Janer *et al.* 2019).

To manage this conflict and to mitigate damage, a palette of both lethal and non-lethal preventive tools is available, such as culling, scaring, and altered farming strategies (Fox *et al.* 2017). However, given how widely these strategies are used worldwide, surprisingly few attempts have been made to scientifically evaluate their efficiency (Hake *et al.* 2010, Johnson *et al.* 2014, Koffijberg *et al.* 2017). One common non-lethal strategy is to attract and divert geese to set-aside fields, *i.e.* areas where they can graze undisturbed (also referred to as lure crops, alternative feeding areas, sacrificial crops, diversionary fields or accommodation fields in the literature) (McKay *et al.* 2001, Hake *et al.* 2010, Tombre *et al.* 2013, Nilsson *et al.* 2016, Koffijberg *et al.* 2017). It is key to adapt management in accordance with the selection patterns of geese, so that the latter are attracted to the set-aside fields and kept away from sensitive crops (Gill 1996, Hake *et al.* 2010). Set-aside fields can consist of protected natural grass fields, stubble fields left unplowed, but also conventional fields with crops managed to attract geese (Vickery & Gill 1999, Merkens *et al.* 2012). Other characteristics such as distance to roost and sward height, may also affect field selection. In Sweden set-aside fields are sometimes combined with scaring geese off sensitive crops, as scaring otherwise just tends to move the problem between fields and farmers (Hake *et al.* 2010). Still, quite few set-aside fields have been established on productive agricultural land in Sweden, a fact making their effectiveness hard to evaluate, and even more so because geese may select different crop types and fields in different areas and seasons (Montràs-Janer *et al.* 2019).

Crop type, nutritional content, and crop stage (*e.g.*, newly sown, growing crop, or stubble with spilled grain) are examples of variables affecting field selection of geese (Fox *et al.* 2017, McKay *et al.* 2006, Merkens *et al.* 2012, Vickery and Gill 1999). Generally speaking, geese prefer crops high in protein, digestibility, and energy, but low in fiber, in order to meet daily energetic needs, (Fox *et al.* 2017). Field selection may also change between seasons, as the nutritional demands of geese change over the year, as does the availability of different food types (Newton & Campbell 1973, Jensen *et al.* 2008, Fox *et al.* 2017). Moreover, previous research shows that flight distance between roost sites and fields also affects field selection by geese. There is a trade-off between energy gained from foraging in a certain field and energy lost when flying to and from it. Consequently, geese show a general preference for fields closer to roost sites (Newton and Campbell 1973, Gill 1996, McKay *et al.* 2006, Amano *et al.* 2007). Geese also prefer larger fields from where it is easier to spot and avoid predators and humans (Newton & Campbell 1973, Jensen *et al.* 2008, Wisz *et al.* 2008).

Selection patterns by geese can be studied by comparing actual use of a certain crop type or habitat in relation to their availability in the landscape. By comparing the selection of set-aside fields and conventional fields it is also possible to evaluate whether the former are preferred compared to other fields in the surrounding landscape. Such knowledge is of value for management, as it can be used to increase the attractiveness of set-aside field and thereby reduce or prevent crop damage and conflicts (Gill 1996, Vickery & Gill 1999, McKay *et al.* 2006, Merkens *et al.* 2012).

In Sweden, the breeding and autumn staging population of greylag geese (*Anser anser*) has been increasing since annual September counts started in 1984, from 20,000 to approximately 170,000 in 2018 (Liljebäck *et al.* 2021, Nilsson & Haas 2019). During this period, the greylag goose population and crop damage have increased more or less in parallel (Montràs-Janer *et al.* 2019).

Barley, wheat and ley are the crop types most reported as damaged by greylag geese in the south of Sweden; ley in spring and barley and wheat during most of the summer (Montràs-Janer *et al.* 2020). Reimbursements paid to Swedish farmers for crop damage caused by large grazing birds have increased since 1995 and were *ca.* 550,000 euros in 2020 (Frank *et al.* 2021).

Farmers and other stakeholders are actively working to reduce crop damage and use several measures to accomplish this (Hake *et al.* 2010). Yet, the understanding of the effectiveness of certain measures is limited. We studied field selection patterns by greylag geese in an area where a set-aside field was established in 2010. By considering factors known to affect selection patterns by geese, such as crop type, distance to roost, season, and field size we were able to gain insights about general selection patterns, but also to compare selection of set-aside versus conventional fields. We predicted that the set-aside field would have a higher presence of greylag geese than other fields (crop types) in the study area. We also predicted that the set-aside area would be more frequently selected in spring than in summer and fall. Finally, we predicted that fields closer to roost sites and larger fields would have a higher presence of geese than distant and smaller fields.

2. Material and methods

2.1. Study area

The study was carried out 2010–2012 in south-central Sweden in the surroundings of lake Sörfjärden (59°25′52″N, 16°46′57″E; Fig. 1), situated in the boreonemoral biotic zone, which is a transition between the boreal and nemoral biotic zones, and characterized by a mosaic of coniferous and broad-leaved forest. The study area consists of agricultural land, forests, wet

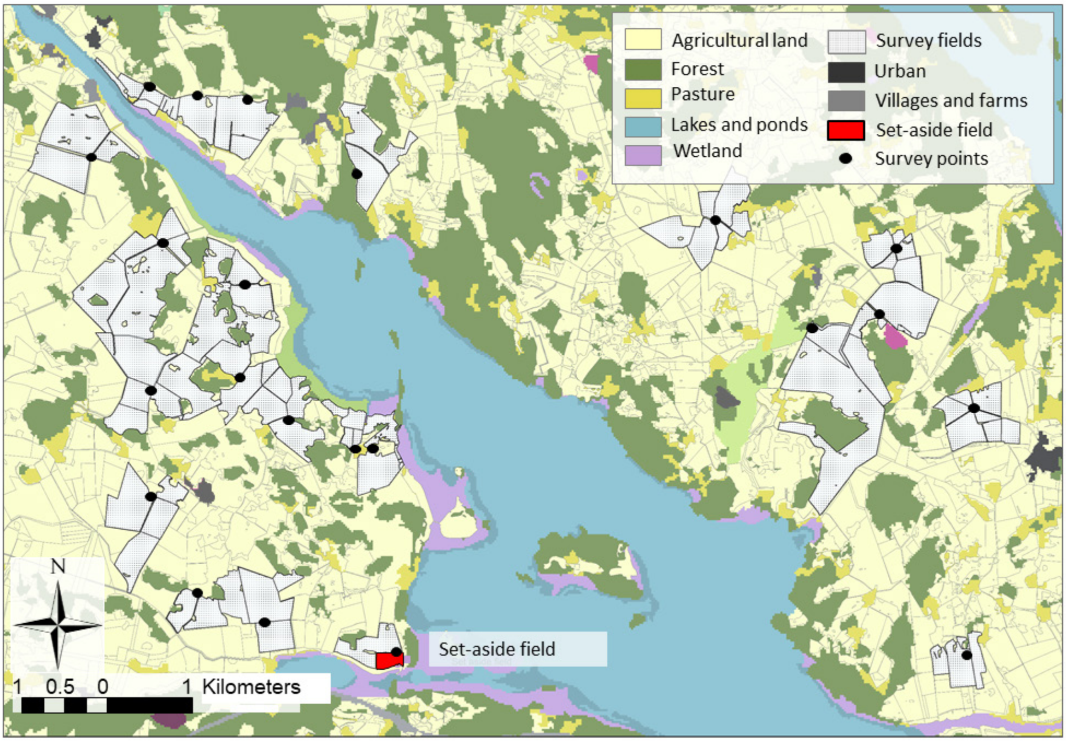

Fig. 1. Map of the study area. Grey fields were included in the study and the red field in the south is the set-aside field. Black circles show the survey points from which geese were counted. Only the fields or the part of a field that was visible from any survey point were considered.

meadows, dense reed-beds, and open water. The agricultural land is used for intensive farming of mainly cereals such as wheat, oats, barley, and rye, but also grass for hay and silage, potatoes, and oil rapeseed. Crops are sown in both fall and spring. Lake Sörfjärden and its surroundings have been partly protected since 2001 by the RAMSAR Convention since 2001 and hold several nature reserves (209 ha of reed beds and wet meadows) and Natura 2000 sites based on the European Bird Directive (SPA) and the Habitat Directive (SAC/SCI) (EC 2009). The area hosts a generally rich birdlife and many breeding species.

Lake Sörfjärden is usually covered by ice and snow from January to mid-March or early April. The growing season lasts from April to September. Annual precipitation ranges between 600 and 800 mm (Swedish Meteorological and Hydrological Institute, www.SMHI.se). Growing crop in spring such as wheat and ley fields are most sensitive to damage by geese. Harvest takes place from late June (ley fields) to September (ley, cereals, potatoes, and rapeseed). Spill grain from harvested fields is attractive to geese, however geese do not cause damage on these fields.

2.2. Data on goose numbers

Greylag geese in the agricultural landscape surrounding lake Sörfjärden were counted using a point survey method, in which the visible fields were scanned for geese at each point without any pre-set time limit for searching. Surveys were conducted by volunteers every week from March to October 2010–2012, with a two-week break in the beginning of June (during the molting period when most geese are flightless and remain on the lake). Geese were counted from sunrise to mid-day (latest 14:30 hrs) using a telescope from 22 points, from which a total of 65 agricultural fields were surveyed (1–6 fields per point; Fig. 1). The initial distribution of survey points along available roads was randomly selected, but the precise location was adjusted in some cases (<300 m) to maximize the number of fields visible from the car, to avoid unnecessary disturbance when leaving it. Points were visited in a different order on each survey occasion to avoid bias of daily movements/behavioural patterns. Other 'large grazing birds' such as Canada geese (*Branta canadensis*), barnacle geese, (*Branta leucopsis*), taiga bean geese (*Anser fabalis*), greater white-fronted geese (*Anser albifrons*), common cranes (*Grus grus*), and whooper swans (*Cygnus cygnus*) also occur in the area, although in lesser numbers than greylag geese (Ödman *et al.* 2013).

2.3. Set-aside field

The set-aside field was established in March 2010 with the aim to attract greylag geese and reduce crop damage, particularly in spring when most damage occurs to fall-sown cereals. The location of the set-aside field was based on previous observations of foraging geese in the area, indicating that this specific field was selected by many geese. The size of the field was 5.7 ha, and it was sown with a seed mix containing 25% alfalfa (*Medicago sativa*), 23% timothy (*Phleum pratense*), 15% bird's-foot trefoil (*Lotus corniculatus*), 12% meadow fescue (*Festuca pratensis*), 10% white clover (*Trifolium repens*), 10% chicory (*Cichorium intybus*), and 5% caraway (*Carum carvi*). The field was managed by harvesting to keep the grass sward low, in accordance with preference by geese (0–10 cm, Strong *et al.* 2021). In 2010, the set-aside field was harvested in August. In 2011 it was harvested in June, July, and August, and in 2012 once in June (Ödman *et al.* 2013, 2012, 2011). Manure fertilizer was applied in spring every year.

Our aim was to relate the probability of goose presence to explanatory variables such as field size, crop type, and distance to roost. We measured distance to water from the center-point of each field to the nearest water edge by using the function "Near" in ArcGIS version 10.5. The distance from surveyed fields to the surrounding roost sites varied from 150 to 3,100 meters. We obtained data on crop type and field size from the database "SAM" provided by the County Administrative board of Södermanland and the Swedish Board of Agriculture. This database builds on farmers´ annual reports of used crop type for obtaining EU and government subsidies (in accordance with the European Common Agriculture Policy, CAP). We pooled some crop types to obtain eight categories for our analyses (wheat, barley, rye, rapeseed, oats, set-aside, grass, and other). Potatoes, linseed, fallow land, and mixed cereal were merged into the category ‘other’ and pasture, ley, meadows, and mowed pasture into the ‘grass’ category.

2.4. Data analysis

Presence (1) or absence (0) of greylag geese was used as a binary response variable, whilst field and landscape characteristics were explanatory variables (Table S1). To estimate relationships between the presence of geese and field characteristics (crop type, distance to roost, and field size; Table S1) we used multiple regression analysis, with season added as covariate (see below). Three years of survey data were merged into one data set. We also grouped data into three seasons: spring, summer, and fall (Table S1). Spring (March–May) refers to the period when geese return from wintering areas and feed to restore muscle mass after the migration flight, build nutrient reserves, and start breeding (Fox *et al.* 2017). The main crops available in spring are those sown the previous autumn (fall-sown cereals and rape seed), spring sown crops, and ley fields. Summer (June–August) is when geese rear goslings and adults molt; hence they forage more in wetlands in June but start visiting the fields again in mid-July (Fig. 2). There is a larger variation in the availability of preferred forage during summer. At this time, crops in the area are either growing, being harvested, or growing for a second/third harvest (*e.g.*, ley fields). Fall (September–October) is when geese build up reserves for migrating south again, and most crops have been harvested and stubble fields with spilled grain are available (Fox *et al.* 2017).

Field id was set as a random factor to account for dependency of repeated observations within individual fields (Zuur *et al.* 2010). The response variable was over-dispersed with an excess of zeroes, so we used a zero-inflated binomial model with a logit link function, in the glmmTMB package (Bolker 2019) in program R (R Core Team 2021).

We used the Akaike Information Criterion (AICc) for small sample size, ΔAICc and AICc weights (w_i) for model comparison to find the most parsimonious models by using the dredge function in the package MuMIn (Barton 2022). We used the conditional R-square (Nakagawa *et al.* 2017) as a measure of the overall model fit.

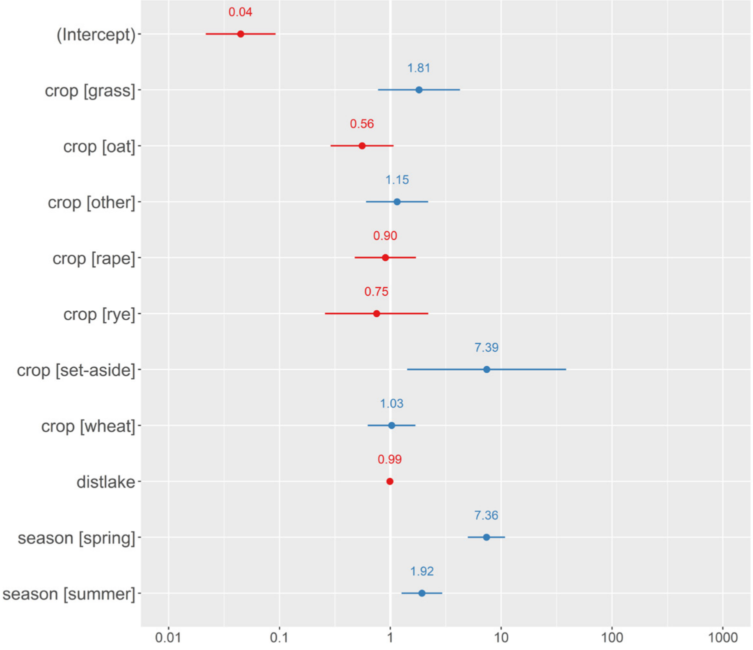

Fig. 2. Forest plot of the probability of goose presence, based on the top model estimates. Intercept corresponds to barley and fall. Whiskers are 95% confidence intervals. The vertical intercept (x=1; thick white line) is the neutral line which indicates no effect. Odds ratios greater than 1 indicate positive associations (blue dots), whereas odds ratios smaller than 1 indicate negative associations (red dots).

3. Results

3.1. Distribution and number of greylag geese

The number of greylag geese at Sörfjärden in September varied between 1,200 and 5,000 in 2010–2012 (mean number 4,060 individuals, mainly non-local staging birds) according to local counts (Ödman *et al.* 2013). The number of breeding greylag geese at Sörfjärden was estimated at an average of 175 pairs in 2007–2009. A total of 21,573 greylag geese were counted in the surveyed fields during the three years of study, with peaks in April and September (Fig. S1). In most cases (92%) of the survey events, there was no geese on the observed fields. The highest number of geese counted in one field was 2,100. The median number of greylag geese on the fields, when excluding the zero counts, was 12.

3.2. Factors influencing goose presence

The top ranked model to explain probability of goose presence included crop type, season, and distance to roost (conditional $R^2 = 0.42$; Table 1). Field size was not included in the top ranked model. The top ranked model predicted that the probability of geese presence was higher in the set-aside field than for the rest of the crop types, but it also had a larger error with a higher uncertainty (Fig. 2 & Fig. 3). There was a negative relationship between goose presence and distance to nearest roost site (Fig. 2 & Fig. 3). The model showed that geese were more likely to be present in surveyed fields in spring than in summer and fall (Fig. 2 & Fig. 3).

3.3. Probability of goose presence

To illustrate how the distance to roost affects the probability of goose presence, we here compare the probability of goose presence for fields at two different distances, 150 meters representing the shortest distance to roost, and 1,300 meters representing the average distance. According to the prediction of the top ranked model, the probability of goose presence on the set-aside field, during spring and at a distance from 150 meters from the roost site, was 0.68 (CI: 0.31–0.91). At the same distance and season the probability was lower for the category grass fields (second highest probability; 0.34 (CI: 0.21–0.49) followed by the category other 0.25 (CI: 0.15–0.37). At 1,300 meters from the roost site the probability for goose presence in spring was again highest for the set-aside field 0.39 (0.12–0.76), second highest for grass 0.14 (0.07–0.24) followed by other 0.09 (0.06–0.14) and wheat 0.08 (0.06–0.11).

In fall, the predicted probability to find geese on the set-aside field (150 meters from the nearest roost site) was 0.22 (0.6–0.58) and in summer for the same distance 0.35 (0.10–0.72). Grass fields ranked second in fall, 0.07 (0.03–0.12) and summer, 0.12 (0.07–0.20), at the same distance from the roost site. At 1,300 meters from the roost site in fall the set-aside was more prone to host geese 0.08 (0.02–0.30), second was grass 0.02 (0.01–0.04). In summer at 1,300 meters from the roost, set-aside had a predicted probability of goose presence of 0.14 (0.03–0.45), the second highest probability was for grass, 0.04 (0.02–0.08).

4. Discussion

Our results show that field selection of foraging greylag geese in the study area is influenced by a combination of factors such as crop type, season, and distance from the roost site. This implies that all these variables need to be considered when deciding where to place and what agricultural practices to use when establishing set-aside fields. Though our study concerned only one set-aside field it still indicates that its management made it more attractive to geese than were the adjacent conventional fields.

We found a low predicted probability for greylag goose presence on grass crops, but higher than for barley and wheat. A preference for ley grass and harvested root crops over cereals was found in migratory greylag geese in England (Newton & Campbell 1973). Wisz *et al.* (2008) modeled the probability of goose presence along the north European flyway and found an increased probability of pink-footed goose (Anser brachyrhynchus) occurrence on grassland compared to other crop types. Similarly, Strong *et al.* (2021)

Table 1. Multiple regression models used to evaluate field and landscape characteristics in relation to greylag goose presence at Sörfjärden in 2010–2012. Models are ranked according to Akaike's Information Criterion (AICc). The number of parameters (NP), AICc, changes in AICc (Δ AICc) relative to the top model and AICc weights (w_i) are listed for the 16 models considered as well as log likelihood. All models include field id as random effect. Only the top ranked model is considered in the results.

Model variables	NP	Log likelihood	AICc	ΔAICc	w_i
Crop + Distance to roost + Season	12	–1123.30	2270.7	0.00	0.456
Distance to roost + Season	5	–1130.85	2271.7	1.06	0.268
Size + Crop + Distance to roost + season	13	–1123.30	2272.7	2.01	0.167
Size + Distance to roost + Season	6	–1130.74	2273.5	2.84	0.110
Crop + Season	11	–1140.69	2303.4	32.78	0.000
Size + Crop + Season	12	–1140.37	2304.8	34.15	0.000
Season	4	–1152.86	2313.7	43.07	0.000
Size + Season	5	–1152.82	2315.6	44.99	0.000
Crop + Distance to roost	10	–1220.74	2461.5	190.86	0.000
Distance to roost	3	–1227.79	2461.6	190.92	0.000
Size + Distance to roost	4	–1227.68	2463.4	192.71	0.000
Size + Crop +Distance to roost	11	–1220.74	2463.5	192.87	0.000
Crop	9	–1238.52	2495.1	224.42	0.000
Size + Crop	10	–1238.21	2496.5	225.82	0.000
Null	2	–1250.06	2504.1	233.47	0.000
Size	3	–1250.01	2506.0	235.38	0.000

found that ley fields, and particularly those with short swards, were preferred by greylag geese in spring and summer in the surroundings of lake Hornborga (Sweden). Fox *et al.* (2017) concluded that geese prefer grass in spring, a pattern also reported from Scotland, where greylag geese appeared to select grass fields more often in spring than in fall and winter (Newton & Campbell 1973). Montràs-Janer *et al.* (2019) found that ley fields were one of the most reported damaged crops, second to barley, by geese in south-central Sweden.

In line with previous studies showing increased field selection and grazing pressure closer to roost sites (Gill 1996, McKay *et al.* 2006, Amano *et al.* 2008, Baveco *et al.* Nolet 2011), probability of presence of graylag geese in our study increased close to the roost. We found a 5 % decrease in probability of goose presence 1 km away from the roost site, compared to fields closest to it. Fox *et al.* (2017) concluded that fields with minimal disturbance and close to roosts are a success recipe for set-aside fields. Amano *et al.* (2007) showed that damage-prone crops such as wheat should be placed farther away from roosts to avoid damage. Vickery & Gill, (1999) recommended placing set-aside fields within a preferred distance of 2–5 km from the roost site for Icelandic greylag geese. However, we saw a continuously decreasing predicted probability for fields with distance to the roost site, with no such threshold.

Undisturbed sites in the agricultural landscape where geese can forage have been pointed out as important for conservation purposes, but also to reduce damage and thereby manage possible conflict between conservation and agriculture (McKenzie 2014, Fox & Madsen 2017). In areas where geese are simply scared away to prevent crop damage, set-aside fields are even more important in order to avoid just 'moving the problem around' (Jensen *et al.* 2008). Previous studies have shown that set-aside fields can attract geese if managed in the right way; *e.g.* by ensuring short sward height, using a preferred crop, and by

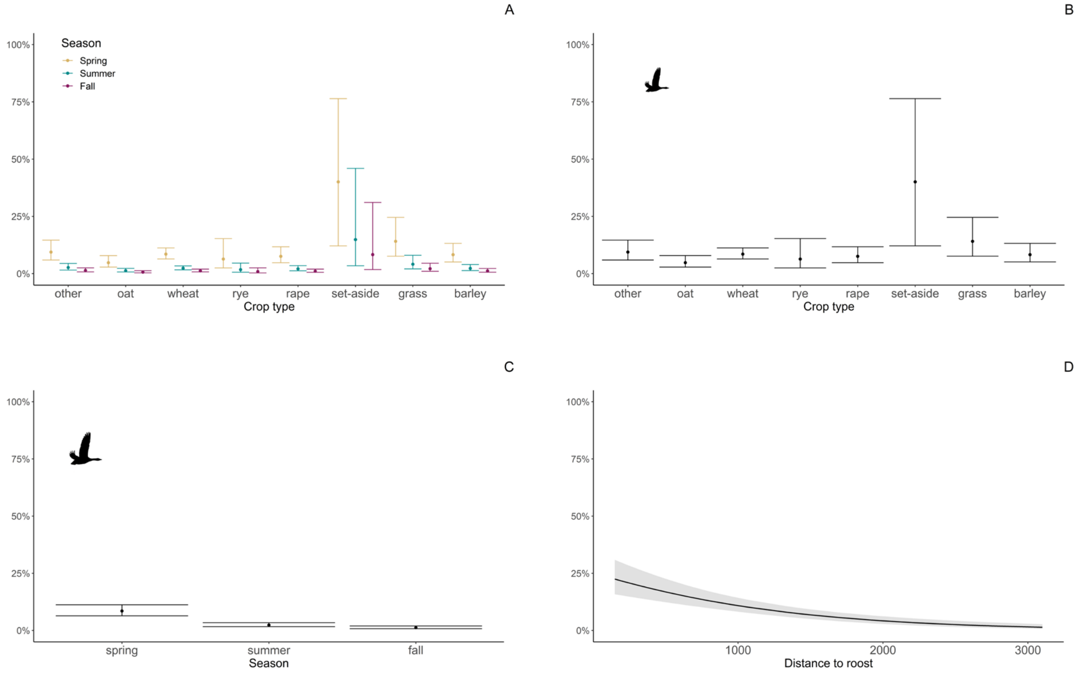

Fig. 3. Predicted mean probability of greylag goose presence (y axis) in study fields based on the top ranked model estimates, relative to crop type and season (A), crop type for all seasons (B), seasons (C), and distance to roost site (D). The error bars in the A, B, and C graphs and the grey area in D show confidence intervals (CI). Distance to roost site is held constant in the predictions to its mean (1300 meters) in plot A, B and C, and for plot D barley is the crop type held constant.

applying fertilizer (Aerts *et al.* 1996, Merkens *et al.* 2012, Fox *et al.* 2017). In our study area, most damage from geese occurs in spring and early summer, during the early growth phase of many crops. Later in summer and in autumn more stubble fields are available, where geese can feed without affecting unharvested fields. The aim with the set-aside field in our study was to divert greylag geese from conventional fields in spring and early summer by using a seed mix with grass and herbs known, from practical experience, to attract geese. According to our results and in line with our prediction, the probability of goose presence was higher on the set-aside field in spring compared to the other seasons. This indicates that the management of this field was appropriate.

Even though the set-aside was preferred compared to other available fields, it attracted only 28% of the total number of counted geese in the surveyed area during spring, and 12% for the whole period. One reason could be that the food availability on the set-aside field was limited in relation to the number of geese present in the area so that they needed to forage elsewhere. Another possible reason, as also shown in our study, is that the probability of geese visiting the fields decrease with distance to roost. Additional set-aside fields evenly distributed within the study area may therefore be needed to attract a larger proportion of geese. Increasing the size of the existing set-aside field might be another way to divert a higher proportion of geese from conventional fields. The size of the set-aside field in relation to the overall number of geese in the area should therefore be considered (Vickery & Gill 1999). Scaring efforts to reduce goose presence on surrounding fields could decrease their attractiveness in relation to the set-aside field. Scaring, open hunting and derogation shooting were indeed carried out in the study area to reduce crop damage, but the extent and frequency are unknown and thus not possible to consider when interpreting our results.

However, they are all likely additional factors affecting the distribution of geese and a reason for the high use of the set-aside field where geese are allowed to graze undisturbed

Our study did not reveal any increased selection for wheat and barley fields in late summer and fall, when the cereals have been harvested. Such an increase has previously been shown by Nilsson & Persson (1992) who found that geese foraged on cereal stubble fields during autumn. The energetic return from spilled grain is substantial (Clausen *et al.* 2018) and it should be an ideal food resource for geese at a time when they need to prepare physiologically for autumn migration (Fox *et al.* 2017). These results underline the importance of considering season when choosing crop type for a set-aside field. During spring and early summer, a well-managed ley field seems to work for attracting greylag geese in our study area, but cereal stubble fields may be a better option for set-aside fields in late summer and fall.

Our study shows that the probability of goose presence in the fields varied among seasons. There was a higher probability of goose presence in spring compared to in fall and summer, even though the total number of geese was lower in spring. As we used a binary predictor in our models, we interpret this as geese being more scattered in the landscape in spring than in summer and fall (Fig. S1). Other studies of geese have shown a similar pattern *i.e.* a more aggregated distribution and larger flocks in fall and winter than in spring and summer (Newton & Campbell 1973, McKay *et al.* 2006). We find two possible explanations for this pattern; greylag geese may be more prone to occur in pairs than in flocks during the breeding period, and/or food resources are less clumped in spring.

Contrary to earlier studies showing that field selection by geese increases with field size (Newton & Campbell 1973, Nilsson & Persson 1991, Gill 1996, McKay *et al.* 2006, Vickery & Gill 1999) our study did not find any such effect. Fox *et al.* (2017) recommended that set-aside fields should be larger than 5 ha, whereas Gill, (1996) concluded that smaller fields than 6 ha were never selected by pink-footed geese. The conventional fields we surveyed were 1–45 ha and the set-aside field was 5.7 ha. However, the mere size of fields can have different effect on the selection by geese depending on other landscape features such as hedges, ditches with reeds, trees etc. These features may block the view for geese and smaller fields with an open view may still be as preferred as larger fields. According to McKay *et al.* (1996) field size was of less importance to brent geese (*Branta bernicla bernicla*) when they were using pastures compared to when they were using crop fields. In that study, pasture fields differed from crop fields by being surrounded by lower hedges, located closer to water, and having less disturbance than crop fields. The multitude of factors influencing the selection of geese could be an explanation for why field size did not play an important role in our study.

We decided to present the results of the top ranked model according to AICc (Fig 2 & 3), however the ΔAICc of the second best model was <2, indicating that these two models are comparable in predicting goose presence. We motivate to present the top ranked model, which included the variable crop, as previous studies point out the importance of this variable explaining field selection of geese (Fox *et al.* 2017, McKay *et al.* 2006, Merkens *et al.* 2012, Vickery and Gill 1999). On the other hand, field size has also been pointed out as an important variable, however in our study, field size was not included in the models with ΔAICc <2 and also explained less variation than the null model as a single variable (Table 1).

Our study was based on one set-aside field and one species. This might limit the generality of the results. However, we are confident that our findings still may be useful in terms of crop protection because: a) there are very few previous studies evaluating the effect of established set-aside fields and b) our results are largely in line with previous studies on field selection patterns by geese in general. We did not assess the actual damage level caused by goose grazing but is reasonable to assume that when geese are foraging in a field, they indeed impact crops. Estimating and comparing damage levels could be an important next step to evaluate the effectiveness of preventive measures such as set-aside fields.

We found that field selection by greylag geese in the Sörfjärden study area was influenced by several factors such as distance to the roost site, season, and crop type. We argue this knowledge is important to understand selection patterns when managing geese in agricultural landscapes to minimize damage and conflict.

Fältval hos grågäss (*Anser anser*): implikationer för anläggande och skötsel av avledningsåkrar för att minska skador på gröda

Antalet grågäss (*Anser anser*) har ökat i Europa under de senaste decennierna. De söker föda och rastar i jordbrukslandskapet och kan orsaka skador på känsliga grödor. Vi studerade fältval av grågäss i området kring sjön Sörfjärden i södra Mellansverige och där gässen samlas under växtsäsongen. I detta område anlades en avledningsåker 2010, det vill säga en åker där gässen tillåts beta ostört, i syfte att minska skadorna på konventionella grödor. Målet med vår studie var att studera gässens fältval med fokus på avledningsåkern. Vi räknade antal gäss på fält i området och använde oss av regressionsanalyser för att utvärdera sambandet mellan sannolikheten att grågässen besöker ett fält och fältegenskaper som gröda, avstånd till övernattningsplats och storlek. Enligt den högst rankade förklarandemodellen, var sannolikheten för förekomst av grågäss på fält högre på våren och i vall, medan sannolikheten minskade med avståndet till övernattningsplatsen. Våra resultat visar också att avledningsåkern generellt sett användes mer än andra fält i området under våren och sommaren. Avledningsåkern var dock mindre attraktiv i förhållande till andra grödor under hösten. Vi drar slutsatsen att det är viktigt att överväga variabler som påverkar gässens val av fält såsom årstid, gröda och avstånd till övernattningsplatser för att förstå gässens beteende och på så sätt kunna anlägga effektiva avledningsåkrar.

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Online supplementary material

Supplementary material available in the online version includes Fig. S1 and Table S1.

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Factors affecting apparent survival and resighting probability of wintering mallards *Anas platyrhynchos*: A case study from a small town in north-eastern Poland

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Survival of adults is a key demographic parameter affecting avian population dynamics. In urban areas, *e.g.*, city parks, birds stay in winter in large numbers where they have access to a multitude of food sources due to human activities, which is one of the key factors that attract birds into the cities. Our study estimates apparent survival of mallard ducks *Anas platyrhynchos* between non-breeding seasons in a small town in the coldest region in north-eastern Poland between 2005 and 2017. We found lower survival estimates for females (juveniles: 0.54; adults: 0.59) than males (juveniles: 0.76; adults: 0.72) and probabilities of resighting individuals in the next non-breeding season were higher if the bird was resighted in the study area during the prior breeding period. Thus, we conclude that sedentary mallards from the local urban population have relatively high survival, which may be explained by lower pressure from raptors, lack of hunting and higher winter temperatures in the urban site. Additionally, winter temperature was negatively related to resighting probability in the next non-breeding season. Resighting probability was time-dependent with a bimodal pattern with maximal estimates of 0.48 in 2007/2008 and 0.98 in 2013/2014, 0.98 in 2014/2015, 1.00 in 2015/2016. These results are most likely related to volunteers' activity that increased due to organized official competition with special awards during those seasons. Considering the fact that the type of ring (metal or plastic coloured) significantly influenced the probabilities of resighting of individuals, it is recommended that apparent survival studies on birds be conducted using colour rings. Moreover, we encourage to collect more capture-mark-recapture data to enable accurate estimations of duck survival, which not the least is a prerequisite for successful management and conservation efforts.

1. Introduction

Survival of adults is a key demographic parameter affecting avian population dynamics (Sæther & Bakke 2000, Flint *et al.* 2006, Tack *et al.* 2017). For waterbirds that spend winter in temperate climate zones, risks and challenges are associated with increased mortality due to harsh weather and limited access to food resources (Fredrickson 1969, Suter & van Eerden 1992). However, in urban areas, where birds stay in winter in large numbers, they have access to a multitude of food sources due to human activities, which is one of the key factors that attract birds into cities (Avilova & Eremkin 2001, Galbraith *et al.* 2015, Coogan *et al.* 2018). These cities are characterized by higher average winter temperatures resulting in more snow-free spaces and ice-free waters, and low avian predation pressure when comparing to rural areas (Luniak 2004). Additionally, urban areas provide refuges for waterbirds, *e.g.*, ducks Anatidae, because birds spending winter in these places are not exposed to hunting pressure (Figley & VanDruff 1982). Although higher survival in populations from urban areas has been found in different bird species (*e.g.*, Hõrak & Lebreton 1998, Anderies *et al.* 2007, Varner *et al.* 2014), some factors may negatively affect survival of birds staying in the cities. Domestic predators, such as cats *Felis catus* or dogs *Canis lupus* familiaris, are often abundant in urban environments, which can have profound effects on birds (Loss *et al.* 2013). Large glass surfaces and vehicle traffic can cause collision mortality (Hager *et al.* 2008). Moreover, staying in urban environments may have negative impacts on waterbirds due to facilitated pathogen transmission when they are congregating in winter in large numbers and high densities (Wobeser & Kost 1992, Meissner *et al.* 2015a, Murray *et al.* 2016, Kleyheeg *et al.* 2017). Dependency on anthropogenic foods may contribute to health risks such as nutritional imbalance, which may lead to metabolic disorders (Kreeger & Waiser 1984, Zsivanovits *et al.* 2006) or affect subsequent reproduction (Plummer *et al.* 2013, Ruffino *et al.* 2014). Studies conducted on duck survival so far have provided inconclusive results (*e.g.*, Soutiere 1989, Giudice 2003, Gunnarsson *et al.* 2008, Söderquist *et al.* 2021), potentially because those were based on birds of different encounter histories (resightings or dead recoveries), age (pulli, juveniles or adults) and origin (wild or raised in captivity). To our knowledge only one study compared apparent survival of a duck species, *i.e.*, mottled duck Anas fulvigula in urban and non-urban areas using capture-mark-recapture analyses (*e.g.*, Cormack-Jolly-Seber models) (Varner *et al.* 2014), which is the best way to achieve reliable estimates of survival rates (Clobert *et al.* 1987, Lukas *et al.* 2004). Other estimates of annual survival rates of urban dabbling duck species (*i.e.*, Heusmann 1981) were calculated using other methods and we believe resulted in underestimations (for a similar discussion, see also Gunnarsson *et al.* 2008).

The mallard *Anas platyrhynchos* is the most abundant and widely distributed dabbling duck species which shows a strong tendency for synurbization and is well adapted to urban environments (Figley & VanDruff 1982, Engel *et al.* 1988). Furthermore, this species is found in very large numbers during winter in many cities of the Northern Hemisphere (*e.g.*, Heusmann & Burrell 1984, Schonert 1991, Meissner *et al.* 2015b, Avilova 2016, Berliner Ornithologische Arbeitgemeinschaft 2019). The species include migratory populations (Figley & VanDruff 1982, Engel *et al.* 1988), but many mallards breeding in urbanized areas are sedentary (Heusmann 1981, Figley & Van Druff 1982, Heusmann & Burrell 1984, Luniak 2004, Zárybnický & Klvaňa 2008). In contrast to urban mallards the apparent survival of ducks in wild populations has previously been described (*e.g.*, Bergan & Smith 1993, Lake *et al.* 2006, Lancaster 2013, McDougall & Amundson 2017). They have also adapted to close association with humans and permit people to approach to very short distances to feed these birds bread or scraps of food, thus reducing their escape distance in urbanized areas (Figley & VanDruff 1982, Avilova & Eremkin 2001, Luniak 2004). Studies on urban populations of dabbling ducks provide an excellent opportunity to assess and estimate apparent survival, because these species reveal strong wintering site fidelity (Heusmann 1981, Guillemain *et al.* 2008). This makes resightings of ringed ducks much easier to obtain without catching them, compared to when data are gathered in waterbodies outside urban areas where ducks normally are more dispersed.

This study was designed to estimate apparent survival rates of mallards between non-breeding seasons in one small town in the coldest region in north-eastern Poland and identify factors affecting resighting probabilities in the next non-breeding season. Based on earlier studies, we expected that adult mallards would have higher survival estimates than juveniles, as older ducks are more experienced in avoiding threats, *e.g.*, predation (Johnson *et al.* 1992, Lake *et al.* 2006, Gunnarsson *et al.* 2012). Additionally, we expected males to have higher survival estimates than females, because female ducks experience greater mortality during breeding season than males (Johnson *et al.* 1992, Devries *et al.* 2003, Brasher *et al.* 2006, Lake *et al.* 2006). Moreover, sedentary mallards from a local urban population were expected to have higher probability of being resighted in the next non-breeding season, compared to birds not observed during the breeding season, because urban habitats reveal lower pressure from avian raptors, lack of hunting and abundant anthropogenic food resources (see above).

2. Materials and methods

2.1. Study area

The mallards were captured in the city park in the small town of Ełk in north-eastern Poland (53.8176 N, 22.3516 E) with a population of about 61,782 inhabitants (GUS 2021) (Fig. 1). The study area is surrounded by several lakes while the Ełk River flows through its centre. This is the coldest region in northern Poland with the lowest average temperatures in January (–4.8ºC in the period 1966–1995, Stopa-Boryczka & Boryczka 2006).

2.2. Field study

In total, 160 mallards were caught in the study area between 2005 and 2016. Individuals were baited with pieces of bread that led them to enter into loop-traps made of fishing monofilament line (diameter 0.35 or 0.40 mm) placed on the ground, which were then pulled and tightened

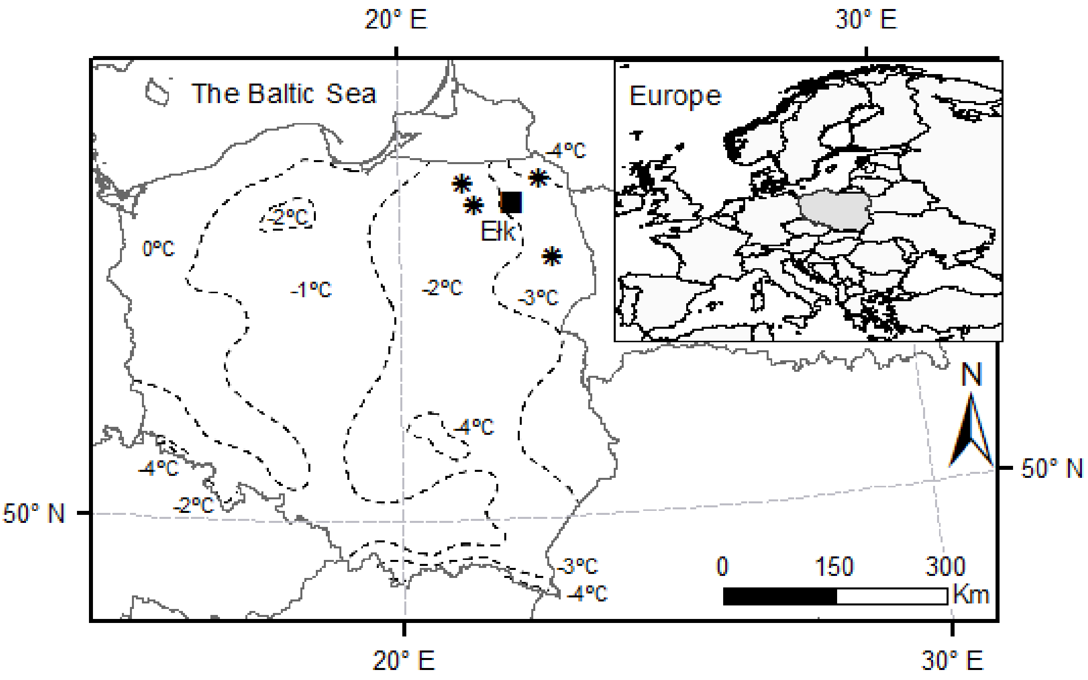

Fig. 1. Data were collected in the city of Ełk. January isotherms (Lorenc 2005) are shown as broken lines. The nearest meteorological stations are marked with asterisks.

on the bird's leg for successful capture (Meissner & Fischer 2017). Birds were aged and sexed according to plumage characteristics (Bauer & Glutz von Blotzheim 1968, Boyd *et al.* 1977) and four sex-age groups were distinguished: juvenile female (N=55), juvenile male (N=44), adult female (N=29) and adult male (N=32). We defined juveniles as individuals in their first year of life, and adults as individuals in their second year of life or older. Captured birds were marked with metal leg rings of oval shape with unique number sequences visible from one side. Between 2005 and 2009 additional colour plastic rings with engraved unique codes were added on the other leg. In total 100 mallards were marked with metal ring only and 60 birds with an additional plastic leg ring (Table 1). The inscription on both ring types was big enough to be read easily from a distance. Metal and plastic leg rings of marked individuals were identified with binoculars and/or from a picture made with a digital camera by sixteen volunteers (see Acknowledgements). A special project for volunteers was organized by Waterbird Research Group KULING to encourage observers to collect resightings of ringed mallards. In October mallards have completed pre-breeding (prealternate) moult, while in March egg laying has not yet started (Cramp & Simmons 1983, Engel *et al.* 1988). Thus, for further analyses all resightings recorded between 1st October and 31st March were classified as belonging to the non-breeding season. Multiple resightings of a given bird on the same day were treated as one record.

Table 1. The number of ringed (metal and/or plastic rings) and resighted mallards from 2005–2017.

	Ringed		Resighted	
Season	Metal	Plastic	Metal	Plastic
2005/2006	34	1		
2006/2007	4	28	1	19
2007/2008	8	5	8	21
2008/2009	13	18	8	26
2009/2010	3	8		17
2010/2011			1	13
2011/2012			1	5
2012/2013			2	8
2013/2014	8		4	9
2014/2015	10		14	6
2015/2016	20		29	2
2016/2017			25	1
Total	100	60	93	127

2.3. Statistical analyses

To identify factors affecting the probability of resighting of a given individual in the next non-breeding season after ringing, we used a generalized linear model (GLM) with binomial distribution and logit link-function (McCullagh & Nelder 1989). The binominal dependent variable (0 = not resighted, 1 = resighted) in the GLM analysis was related to type of ring (metal or plastic; the engraved plastic leg rings are easier to read than metal leg rings; Rock 1999, Meissner & Bzoma 2011), sex (male or female), age when ringing occurred (juvenile or adult) and presence (1) or absence (0) during breeding season in the study area, the number of seasons between 2005/2006 and 2015/2016 when a given individual was seen (to check if the probabilities of resighting of individuals were the same in each season), winter harshness in the season when individuals were ringed, winter harshness in the next season after ringing and the number of days an individual was resighted in the next non-breeding season after ringing (N days resighted). The latter variable was included because more days spent in the field in particular non-breeding seasons may have increased the probabilities of resighting birds in those years. Winter harshness was defined using the Hellmann index (Ijnsen 1988), which is the sum of all negative mean daily temperatures between 1st October and 31st March. We used the mean of daily average temperatures from the four nearest meteorological stations (Fig. 1, Białystok, Kętrzyn, Mikołajki and Suwałki; online database https://tutiempo.net). We used odds ratio (OR) to quantify the strength of the association between factors in the models and the probability of resighting of a given individual in the next non-breeding season. We performed GLM analyses in packages 'MASS' (Venables & Ripley 2002) and 'aod'

(Lesnoff & Lancelot 2012) in R (R Development Core Team 2020).

To estimate probabilities of apparent survival (ϕ) corrected for the resighting probability (p) from live resighting data we used the Cormack-Jolly-Seber mark-recapture method (Cormack 1964, Jolly 1965, Seber 1965) using MARK 9.0 software (White & Burnham 1999). In the analyses we have only considered birds marked with metal leg rings, because only this type of ring was used in all seasons. We included sex-age groups (g) in our models of ϕ and p because both age and sex are known to have an impact on survival of mallards (Johnson *et al.* 1992, Smith & Reynolds 1992, Lake *et al.* 2006, Gunnarsson *et al.* 2012). A global model was defined to include as many parameters as possible (only two-way interactions were considered), but with accurately estimated parameters only. Bootstrap goodness-of-fit testing (GOF test) of 1000 simulations were done to examine the fit of the starting global model with the data. A variance inflation factor $\hat{c}$ was calculated as the observed deviance of the global model divided by the mean expected variance from the results of bootstrap simulations to quantify the amount of overdispersion, that is, the sampling variance exceeding the theoretical model-based variance (Burnham & Anderson 2002). Moderate amounts of overdispersion are common in analyses of mark-recapture data and values of $\hat{c} = 1$ to 3 indicate that the global model is acceptable (Lebreton *et al.* 1992). Model fit was assessed with quasi-Akaike's Information Criterion (QAICc; Akaike 1973, Burnham & Anderson 2002). Model selection was based on the difference in QAICc values between models (ΔQAICc). By definition, the best fitted model had a ΔQAICc of zero, and other models were equally parsimonious if ΔQAICc, ≤ 2 (Burnham & Anderson 2002, Arnold 2010). Estimates of apparent survival and resighting were calculated using the model averaging procedure of Program MARK, where parameter estimates were weighted by the Akaike weight of the model from which they were derived. To investigate whether birds from different sex-age groups were resighted at a different frequency, we calculated an indicator of ring resightings (IRR) for each individual marked only with metal rings. This indicator was obtained by dividing a total number of resightings of a particular bird in each non-breeding season by the total number of volunteer visits in the field in the same non-breeding seasons, each of which represents the probability of resighting of a given individual. Kruskal-Wallis test was used to verify differences between IRR among the sex-age groups. These analyses were performed using Statistica 13.1 (Dell Inc. 2016).

3. Results

In total, 39 (39% of ringed) of the mallards ringed with metal ring only were resighted as compared to 34 (57%) for those birds ringed with additional plastic rings.

3.1. Factors affecting probability of resighting in the next non-breeding season

We found that the ring type significantly influenced the probabilities of resighting in the next non-breeding seasons (Wald Statistic=5.3, p=0.022; Table 2). Individuals with plastic rings were three times as likely to be resighted in the next season (OR=3.06; Table 2). As we anticipated, greater winter harshness during the non-breeding season following when birds were ringed negatively affected the probability of resighting of an individual in the next non-breeding season (Wald Statistic=5.8, p=0.016; Table 2). Resighting probability in the next non-breeding season was four times higher if the bird was observed to be present in the study area during the most recent breeding season (Wald Statistic=5.6, p=0.017; OR=4.01; Table 2). None of the other variables in the analyses was significantly related to resighting probability (Table 2).

3.2. Apparent survival

Neither sex nor age was found to affect probability of resighting of an individual in the next non-breeding season (Table 2). Likewise, neither sex nor age had a significant influence on IRR among individuals marked with metal rings (Kruskal-Wallis test, $H_{3,47}=0.43$, p=0.94). Hence, we assumed that the probability of resighting

Table 2. Effects of selected factors on the probability of resighting of a given individual in the next non-breeding season after ringing according to the GLM model. For descriptions of variables, see method section.

Explanatory variable	Coefficient estimate	SE	Z	P	Odds Ratio (OR)
Intercept	0.276	1.03	0.27	0.789	1.32 (0.18–10.21)
Type of ring	1.118	0.49	2.29	0.022	3.06 (1.20–8.20)
Age	0.190	0.39	0.49	0.624	1.21 (0.56–2.59)
Sex	0.215	0.37	0.58	0.565	1.24 (0.59–2.59)
Number of seasons a bird was resighted	0.132	0.09	1.41	0.160	1.14 (0.95–1.28)
Winter harshness during first season	–0.028	0.01	–2.41	0.016	0.97 (0.95–0.99)
Winter harshness during subsequent season	–0.016	0.01	–1.39	0.163	0.98 (0.96–1.01)
Number of resighting days	0.0003	0.01	0.03	0.973	1.00 (0.98–1.02)
Presence during breeding season	1.390	0.59	2.38	0.018	4.01 (1.35–13.91)

of a given individual from all sex-age groups was similar. The structure of the global model ϕ (.) *p* (*t*) seems accurate based on the GOF test (GOF test <0.01, $\hat{c}=1.79 \pm 0.11$). The overall best model for survival is the one with no effects φ (.) for this parameter (Table 3, model no 1). However, the model ϕ (*g*) *p* (*t*), *i.e.*, with a group effect for survival probability, was equally parsimonious (ΔAICc=0.26). The second model for survival included sex-aged groups. The survival estimates were lower for females than males (young females: 0.54 ± 0.08 and adult females: 0.59 ± 0.11; young males: 0.76 ± 0.05 and adult males: 0.72 ± 0.08).

Resighting probabilities were time-dependent (Table 3) and estimates fluctuated during the study (Fig. 2). Resighting probabilities showed a bimodal pattern with the maximal estimates 0.48 in 2007/2008 and 0.98 in 2013/2014, 0.98 in 2014/2015, 1.00 in 2015/2016. The minimum resighting estimate was <0.001 in 2008/2009 (Fig. 2).

Table 3. Cormack-Jolly-Seber candidate models with apparent survival (ϕ) and resighting probability (*p*) for mallards ringed in Ełk between 2005 and 2016 (N=100). No. 1 = the null model, where (.) is mean constant, (*t*) is time dependent, and (*g*) is age and sex groups. ΔAICc = difference between AICc of the current model and the minimum AICc value; w_i = normalized Akaike weight; K = number of parameters.

No.	Model	ΔAICc	w_i	K
1.	ϕ (.) *p*(*t*)	0.00	0.53	13
2.	ϕ (*g*) *p*(*t*)	0.26	0.47	16
3.	ϕ (*t*) *p*(*t*)	21.80	<0.01	23
4.	ϕ (.) *p*(.)	59.59	<0.01	2

4. Discussion

Our results of apparent survival rates are in line with what has been reported from mallards in USA (*e.g.*, Nichols *et al.* 1987, Giudice 2003), Sweden (Gunnarsson *et al.* 2012, Söderquist *et al.* 2021) and Finland (Gunnarsson *et al.* 2008). Similar survival rates to our results were also obtained in Sweden based on farmed mallards, which were ringed before release to wild (0.64 in females and 0.71 in males; Söderquist *et al.* 2021). Other study results based on survival rates of mallards came from two private farms which breed in captivity and released into the wild in the USA showed lower survival rates than ours (0.27, 0.47 and 0.55 for females, and 0.29 and 0.35 for males; Soutiere 1989). It is important to keep in mind that these studies, unlike ours, were based on data of birds shot or "found dead" which are harder to get than resighting data, or on pulli and juveniles which both have lower survival than older

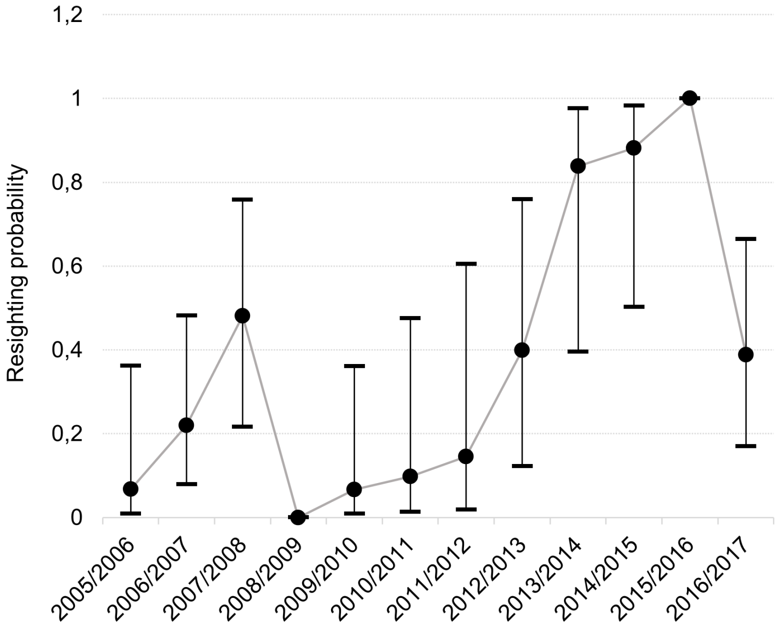

Fig. 2. Resighting probabilities (estimates ± SE) of mallards in non-breeding seasons from 2005/2006 to 2016/2017.

birds (*e.g.*, Soutiere 1989). Moreover, hunting effort and predator pressure negatively affects annual survival rates of rural mallards (Figley & VanDruff 1982, Smith & Reynolds 1992, Luniak 2004, Gunnarsson *et al.* 2008, 2012, McDougall & Amundson 2017) whereas there is no hunting pressure in cities. Many raptor species are poorly pre-adapted to survive in the urban landscape and avoid cities (Luniak 2004), but domestic cat and dog predation are important anthropogenic causes of bird mortality (Erickson *et al.* 2005). However, animal control law enforcement efforts tend to be more strictly enforced for dogs than for cats (Dauphine & Cooper 2009) and free-ranging dog populations are normally effectively controlled, while cats are a major threat to birds (Erickson *et al.* 2005, Loss *et al.* 2013).

Our data showed only differences between sex groups in estimates of survival rates, however, sex and age were not observed to affect probability of resighting of an individual in the next non-breeding season. Similar results were reported for mallards (Gunnarsson *et al.* 2008, 2012, Söderquist *et al.* 2021), as well as for other dabbling ducks (Nicolai *et al.* 2005, Varner *et al.* 2014). Males of dabbling ducks do not assist with egg incubation or brood rearing (Afton & Paulus 1992), thus their energy effort and predation risk are lower than for females (Sargeant *et al.* 1984). Hence, duck females experience greater mortality during breeding than males, as they are more vulnerable to predation during nesting and chick care (Devries *et al.* 2003, Brasher *et al.* 2006). This means that the survival of females to the next winter is lower than for males.

The age effect on survival was not found to be significant in our study. Additionally, we found that neither sex nor age had a significant influence on the IRR value among individuals. Hence, volunteers identified the ring number of each individual regardless of the sex and age of mallards. Other studies on recovery rates of dabbling ducks, including mallards, have reported higher values for juvenile than for adults (*e.g.*, Giudice 2003, Gunnarsson *et al.* 2008, McDougall & Amundson 2017). Older birds are more experienced in avoiding threats, *e.g.*, predation (Gunnarsson *et al.* 2012) and hunting (Fox *et al.* 2015). Likewise, in a Swedish study on mallards, there were no clear effects on annual survival related to duck age (Gunnarsson *et al.* 2012). Juvenile mallards have the same structural body size as adults but have a lower body mass and have smaller nutrient reserves in their first winter (Reinecke *et al.* 1982, Olsen & Cox 2003), which may negatively affect their survival (Davis *et al.* 2011). However, discrepancies between our results and other studies are possibly due to site-specific impacts or sample size. Our research took place in an urban area which provides a refuge for mallards characterized by an abundance of anthropogenic food resources (Luniak 2004), which in part my explain similar resighting probabilities in our study. Artificial food such as bread is easily digestible and provides a readily available food source (Sears 1989, Polańska & Meissner 2008) and a regular food supply may lead to similar nutrient reserves in juveniles and adults. However, the increased amount of food available for wintering mallards did not eliminate the negative impact of the harshness of winter on probability of resighting in the next non-breeding season. Harsh weather can negatively affect individuals' body condition, which influences overwinter survival of mallards (Bergan & Smith 1993), and other duck species (Conroy *et al.* 1989, Haramis *et al.* 1986). Furthermore, winter temperatures may contribute indirectly to survival of mallards in the subsequent season because waterbirds shorten their migration distance or become sedentary in mild winters (Gunnarsson *et al.* 2012, Jordan *et al.* 2019), thus allowing allocating more resources to body condition instead of spending energy on migration (Bergan & Smith 1993).

Survival estimates of mallard were not time-dependent in our study, *i.e.*, they do not depend on particular non-breeding seasons. Similar results were shown in studies of mallards ringed in USA, Finland, and Sweden (Bergan & Smith 1993, Gunnarsson *et al.* 2008, 2012). Studies that have shown time-dependence on bird survival may be reflected by a long-term climate change (*e.g.*, Barbraud & Weimerskirch 2001, Jenouvrier *et al.* 2005), as these studies were based on data from many decades, in contrast to our study that lasted only 12 years. However, we have shown that resighting probability was time dependent. That resighting estimates were higher in some years compared to others are most likely related to volunteers' activity that increased in some seasons due to organized official competition among observers with special awards. The extremely low probability of resighting in 2008/2009 may have been caused by limited activity of volunteers in the study area.

As expected, we found that the probability of resighting individuals in the next non-breeding season was higher if the bird was resighted in the study area during the local breeding period. Mallards breeding in urbanized areas are often sedentary (Håland *et al.* 1980, Heusmann 1981, Zárybnický & Klvaňa 2008). The sedentary mallards from local urban populations would have a better chance for survival because urban habitats have lower pressure from raptors, lack of hunting and higher winter temperatures (Luniak 2004, Varner *et al.* 2014). Annual survival of mottled ducks and survival probabilities of songbirds were also higher in urban than wild or rural settings (Hõrak & Lebreton 1998, Varner *et al.* 2014).

The type of ring influenced the probabilities of resighting in the next non-breeding seasons. This is as expected, because other studies have shown that colour plastic rings can be easily read in the field and adding them to the normal metal leg ring greatly increases the resighting rates (Rock 1999, Meissner & Bzoma 2011).

Our study revealed that estimates of apparent survival of mallards between non-breeding seasons in a small town in the coldest region in north-eastern Poland were similar to what has previously been reported from Europe and other countries of the world, and that the estimates were independent of sex and age of individuals. The probability of resighting individuals in the next non-breeding season was higher if the bird was resighted in the study area during the preceding breeding period. That sedentary mallards from local urban populations have a relatively high resighting probabilities may be promoted by low predation, lack of hunting and higher winter temperatures as compared to rural birds. In addition, as we anticipated, greater winter harshness during the non-breeding season following when birds were ringed negatively affected the probability of resighting of an individual in the next non-breeding season. Considering the fact that the type of ring (metal or plastic coloured) significantly influenced the probabilities of resighting of individuals, it is recommended that apparent survival studies on birds should be conducted using colour rings. Moreover, we encourage to further capture-mark-recapture data collections to enable accurate estimations of duck survival, which not the least is a prerequisite for successful management and conservation efforts.

Faktorer som påverkar överlevnad och återfångst hos övervintrande gräsänder (*Anas platyrhynchos*) – en case studie i en liten stad i nordöstra Polen

Vuxna individers överlevnad är en av de centralaste demografiska parametrarna i studier av fåglars populationsdynamik. I stadsmiljöer, såsom parker, övervintrar ett stort antal fåglar eftersom de har tillgång till olika födoresurser på grund av människans aktiviteter. I vår studie analyserar vi överlevnaden hos ringmärkta gräsänder *Anas platyrhynchos* baserat på individobservationer utanför häckningsperioden i en liten stad i nordöstra Polen mellan 2005 och 2017. Våra resultat visar att överlevnaden hos honor (juveniler: 0.54; vuxna: 0.59) är lägre än hos hanar (juveniler: 0.76; vuxna: 0.72) och att sannolikheten för återfynd av en individ är högre om den observerats under den föregående häckningsperioden. Vår slutsats är att platstrogna gräsänder i urbana populationer har relativt hög överlevnad, vilket kan bero på lägre predationstryck från rovfåglar, frånvaro av jakt och högre vintertemperaturer. Vi fann även att vinterns temperatur negativt påverkade sannolikheten för återfynd. Under studien varierade sannolikheten för återfynd mellan åren med två toppar, först med värdet 0.48 under perioden 2007/2008 och sedan med värden 0.98-1.00 under perioden från 2013/2014 till 2015/2016. Denna årliga variation i sannolikheten för återfynd påverkades troligtvis av högre insats i form av officiella tävlingar i observering av änder under toppåren. Eftersom vi fann att typen av ring som användes (metall eller plast) påverkade sannolikheten för återfynd rekommenderar vi att framtida motsvarande studier använder sig av färgringar. Vi uppmuntrar att samla in mera märknings-återfångst data för att möjliggöra trovärdiga uppskattningar av änders överlevnad, vilket är en nödvändighet för framgång inom naturskydd och hållbar förvaltning.

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Ultraviolet film reduces bird–glass collision risk

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It is estimated that millions of birds globally die due to collisions with glass surfaces. In order to reduce this mortality, it is essential to provide an objective assessment of the effectiveness of bird-friendly preventive methods. Several types of opaque films and stickers are available nowadays and can be highly effective in protecting birds from fatal collisions. However, by being visible to the human eye, they can affect the users' quality of view from within protected spaces. Products that take advantage of the birds' ability to see ultraviolet light seem to offset these impediments. This study determines if UV-reflective BirdShades film prevents birds from collisions with glass in natural environmental conditions. We monitored eight glass bus stops, where we had previously recorded high numbers of birds collisions. On four of them, we applied UV film, and the other four bus stops were used as control. A generalized additive mixed model showed a significant interaction between time (before vs. after) and film UV treatment (control vs. treated). Before the treatment, the number of collisions tended to be higher at treated bus shelters than control. However, this significantly changed after the treatment, suggesting that UV film reduces bird glass collision rate over 5-fold. Our study is the first worldwide that tested UV film on glass shelters and supports a conclusion that the UV film efficiently reduces the risk of bird collision.

1. Introduction

With millions of birds killed each year by collisions with glass, the issue is considered a major cause of bird mortality worldwide (Machtans & Thogmartin 2014, Loss *et al.* 2014). Birds often strike transparent panes while attempting to reach the habitat seen on the other side of the glass (Klem 2009). Collisions also occur when birds mistakenly fly towards reflected images, a common condition with some glass types and lighting conditions. Birds die flying into windows of different shapes and sizes, throughout the day and seasons of the year and during all-weather circumstances. Thus, the fatal strikes may occur wherever birds and glass coexist (Klem 2009, Klem 2014, Żmihorski *et al.* 2021).

Recently, more attention is being paid to finding and using methods that effectively prevent birds from deadly strikes (Klem 2009, Klem & Saenger 2013, Sheppard 2019, Ribeiro & Piratelli 2020). Numerous tests of the surface treatments indicate that opaque vertical stripes of particular widths and separations, as well as some arrangements of opaque dots and other shapes and patterns that do not leave too much open space on the windows (matching “the hand rule”), are effective in reducing bird collisions (Klem 2009, Klem & Saenger 2013, Rössler *et al.* 2015, Ribeiro & Piratelli 2020). However, various types of opaque patterns on glass can be problematic due to the purpose of the building, the architectural vision of the designer, and the preferences of the building users. Therefore, there is a challenge to create designs for glass that will be as unobtrusive to human vision as possible, while effectively preventing birds from fatal collisions.

Products taking birds’ ultraviolet (UV) vision into account certainly meet such expectations (Aidala *et al.* 2012, Swaddle *et al.* 2020). The spectrum of birds’ vision extends into the ultraviolet, thus UV markings that reflect differentially in the UV are visible to birds but mostly invisible for humans (Hart 2001, Lind *et al.* 2013). Spectral sensitivity of birds extends into the UV portion of the spectrum 300–400 nm. However, this sensitivity is not typical in all bird species. Instead, it is a property for passerines, parrots, gulls and terns, and ostriches (Hart 2001). The species commonly reported to collide with glass are for example White-throated Sparrow (*Zonotrichia albicollis*), Dark-eyed Junco (*Junco hyemalis*), American Robin (*Turdus migratorius*) and Swainson’s Thrush (*Catharus ustulatus*) (Basilio *et al.* 2020). Some bird species (notably raptors) have intraocular filters that prevent UV light from forming the retinal image. UV may form part of the image in other non-passerines species, but it is not detected by the photoreceptors (Ödeen *et al.* 2011). Moreover, UV reflective markings on glass surfaces are only visible to birds if there is sufficient UV light falling on the glass (for example during daylight when UV light is the strongest) and the markings have high reflectivity in the UV (Ödeen *et al.* 2011, Håstad & Ödeen 2014). BirdShades (BirdShades Innovations GmbH, Erzherzog-Johann Straße 9, Austria, www.birdshades.com) has produced a window film reflective in the ultraviolet wavelength spectrum of light which has a striping pattern faintly visible to humans. The effectiveness of the reflective UV film by BirdShades was investigated by Swaddle *et al.* (2020) who showed in tunnel tests that it reduced the likelihood of collisions of two passerine species (zebra finch, *Taeniopygia guttata* and brown-headed cowbird, *Molothrus ater*) with windows during daylight by 75–90%. Also, they showed that both species slow their flight by approximately 25% when approaching windows treated with the BirdShades film, thereby reducing the force of collisions if they were to happen.

A UV film that reflects shorter wavelengths of light (spectrum 300–400 nm) should be visible to many birds, both passerines and non-passerines (Goldsmith & Butler 2005, Aidala *et al.* 2012, Lind *et al.* 2013). To the human eye, the BirdShades film appears highly translucent and the ultraviolet stripes are visible only in certain lighting conditions (when looking right at the glass surface then the stripes are invisible, but with a lot of sunlight and looking at different angles, a slight pattern of stripes is visible). However, additional research is still needed (*e.g.*, under various conditions, with different methods) to test the effectiveness of such products in preventing bird collisions.

This study aimed to determine if ultraviolet film efficiently prevents birds from collisions with glass in natural environmental conditions (at different times of day, birds might perceive the glass surface differently and that can affect the risk of collisions). Therefore, this study goes further than Swaddle *et al.* (2020) by testing the product’s effectiveness in a real-world setting with free-living birds and random mix of species. Here, we used our former bird–glass collision data from glass bus shelters (Zyśk-Gorczyńska *et al.* 2020, 2021a) located in Poland, and experimentally placed the UV film on some of them. This allowed us to separate random temporal variation in collision risk from the treatment effect in before-after control-impact study design.

2. Material and methods

In 2017 and 2018, we monitored 85 glass bus shelters in the Lower Silesia Province (in South-West Poland) as a part of a larger study focused on bird–glass collisions (Zyśk-Gorczyńska *et al.* 2020, 2021a, b). Among these 85 locations, we selected eight glass bus shelters for which we found a particularly high number of bird collisions in 2017 and 2018. We divided the eight shelters into treatment and control groups (four shelter per group; Fig. 1). We assigned them according to the collision number. In general, the treatment group was composed of shelters with the highest number of bird collisions. On the bus shelters in the treatment group we applied BirdShades UV film. The entire exterior surface of the back glass panels was covered by the film expanded from a roll (30 cm wide) in May 2021 (Fig. 2). BirdShades film is reflective in the near UVA range between 300 and 400 nm, which means it is visible to passerines birds species and is mostly transparent to the human eye. The film was received from the company, which allowed us to perform an experimental evaluation of its effectiveness and publish results. The lateral panels were left uncovered as we aimed to see if collisions would occur on bus shelters if only the back panels were covered with the film (*i.e.*, one-sided UV film). Moreover, part of the reason we did not cover the lateral panels was the expense of the treatment film. The four remaining shelters were not protected from bird collisions and served as control group. The surroundings of the two groups were similar. They were located in a similarly urbanized area with similar bird communities. Moreover, our previous study at these shelters indicated that bird abundances recorded were poor predictors of bird–glass collisions. Similarly, habitat composition near bus shelters hardly predicted variation in bird–glass collision risk (see Zyśk-Gorczyńska *et al.* 2021a).

We monitored all eight shelters in 2017 and 2018 (130 visits in total; Zyśk-Gorczyńska *et al.* 2020) and again in 2021. We only included monitoring in the spring-summer season (May to August) for analyses as during these months in 2017 and 2018 we found the highest number of collisions (see Zyśk-Gorczyńska *et al.* 2020). During this period in each year, each bus shelter was visited every *ca.* 1–2 weeks (173 visits in total). The total number of visits and the time of visits were the same for all of the bus shelters. During each visit, all glass surfaces of each bus shelter were carefully checked for traces of bird–glass collisions, *i.e.*, feathers or bird contours, which were then removed after each visit to prevent examining them again during subsequent visits. All traces that could not be unequivocally

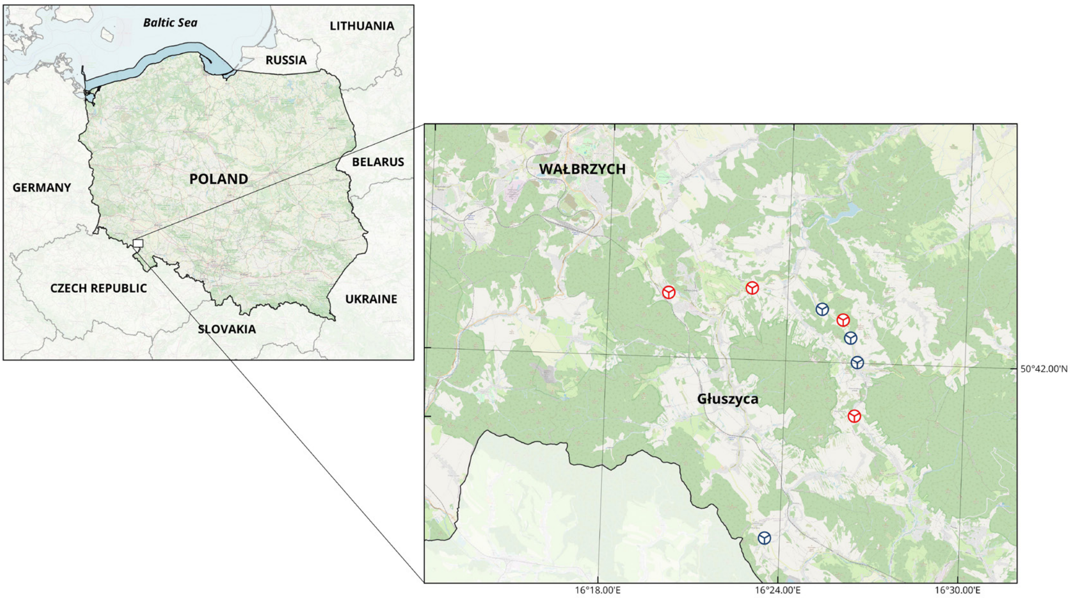

Fig.1. Study area with monitored bus shelter locations (red markers indicate bus shelters treated with UV reflective film and blue markers indicate control bus shelters). Source: Open Street Map.

Fig. 2. (A) The UV film was applied on the outer side of the bus stop glass panels. (B) An exemplary bus stop covered with BirdShades UV film (it is mostly invisible for human eyes).

classified as results of bird collisions (*e.g.*, smudges), were ignored. Moreover, we searched for bird carcasses within 3-meter radius from the bus shelter during each visit. As an effect, we obtained the number of collisions separately for each bus shelter and visits for the periods before and after treatment.

2.1. Statistical analysis

We analyzed bird–glass collision data with a generalized additive mixed model (GAMM) with the logarithmic link and Poisson error distribution implemented in the "mgcv" package (Wood 2017) in R (R Core Team 2021). In the GAMM, we included each visit at each bus shelter as a single data record (n=173) and the number of collisions as a response variable. We applied a before-after-control-impact (BACI) design by considering the interaction of the two explanatory variables: time (before vs after applying UV film, *i.e.*, 2017 and 2018 vs. 2021) and treatment (UV film applied vs. no UV film applied, the latter used as a control). We assumed that a significant interaction term in the GAMM indicates the effect of the UV film on bird–glass collision risk (Chavelier *et al.* 2019). Moreover, in the model, we included month as a categorical factor (May–August) as well as random bus shelter ID and year ID effects, to account for possible temporal and spatial data dependency. Random effects were fitted with the help of ridge penalty splines (Wood 2017). Additionally, we compared number of collisions inside vs. outside of bus shelters with the help of Chi-square test.

3. Results

We recorded 91 bird–glass collisions on the eight bus shelters during the three-year study, ranging from 0 to 6 per bus shelter and visit. In 2017 and 2018 (*i.e.*, before treatment), we recorded 58 collisions, including 15 in control bus shelters and 43 in treatment bus shelters. In 2021 (*i.e.*, after treatment), we found 33 evidences of bird collisions (feathers, bird contours, or carcasses), 24 collisions in control bus shelters, and 9 collisions in treatment bus shelters (covered with UV film). Before the treatment (*i.e.*, in 2017 and 2018) number of collisions tended to be marginally higher at treated (covered UV film afterward) bus shelters as compared to control bus shelters (p=0.113), but this changed after the treatment: in 2021 the number of collisions was lower (p=0.050) at treated bus shelters as compared to control bus shelters (Fig. 3, Supplementary Table S1) and interaction between time and treatment was significant (p<0.001). The effect

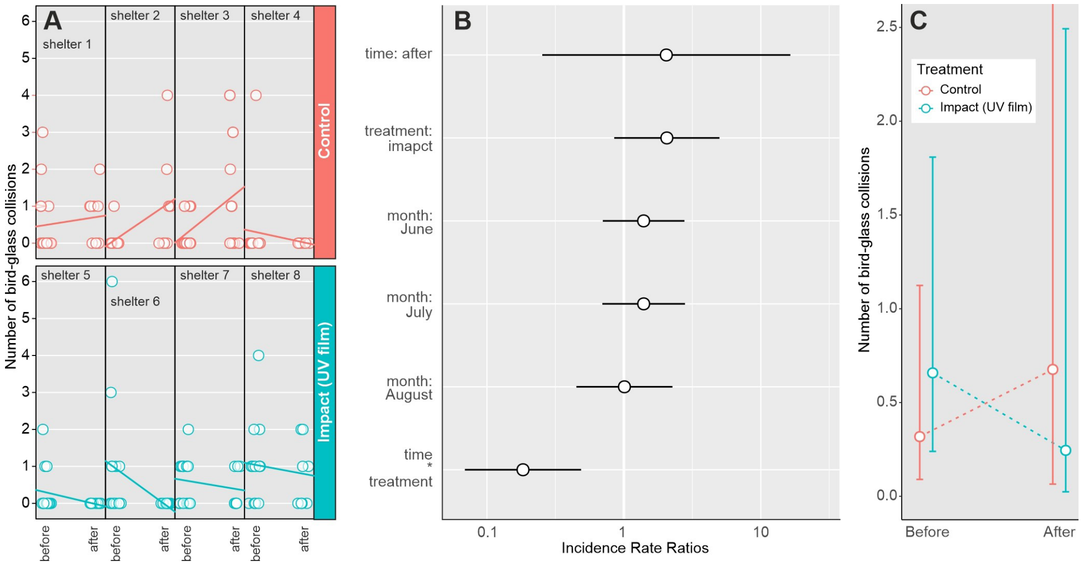

Fig. 3. (A) Raw observations together with regression lines of bird–glass collisions before and after treatment (with point jittering to reduce overplotting) at controlled and treated bus shelters, (B) parameter estimates of GAMM model analyzing bird–glass collisions in relation to time and treatments, and (C) number of bird–glass collisions (accompanied by 95% confidence intervals) predicted by the GAMM for glass bus shelters with different treatments, before and after applying UV film on the glass. At shelters covered with UV film, the number of collisions dropped by *ca.* 5-times compared to control shelters. See Supplementary materials for full parameter estimates of the GAMM.

size of interaction was estimated at 0.175 (95% CI: 0.066–0.463), indicating that the predicted number of collisions after UV film was applied was reduced in treatment group of shelters 5.71-times (95% CI: 2.15–15.13) as compared to control shelters. No significant effect of month was confirmed.

Among 91 recorded collisions, 46 were recorded at the outer while 45 at the inner side of the glass bus shelters. The proportion of the number of collisions between outer and inner sides did not differ from 1:1 (Chi-square test, p=0.071 for "before" period, and p=0.103 for "after" period) at control bus shelters. For impact bus shelters the share of collisions at inner and outer sides was similar for "before" period (p=0.170) but significantly differed from1:1 for "after" period (p=0.020) in which only one collision was recorded at outer (*i.e.*, UV film-covered) side, while six were recorded at inner, non-covered side and two of the collisions occurred on the lateral panels which were also not protected with UV film (Fig. 4).

4. Discussion

We showed that the use of UV BirdShades film can prove effective to reduce bird collisions with glass. We found a significant decrease in the number of collisions after UV film application (reduced in the treatment group of shelters 5.71-times as compared to control shelters) which generally confirms former findings concerning the effectiveness of the BirdShades UV film in preventing collisions in flight tunnel tests (Swaddle *et al.* 2020). Several studies showed that some birds species perceive UV wavelengths from approximately 300–400 nm (Bennett & Cuthill 1994, Hunt *et al.* 1998, Klem 2009, Swaddle *et al.* 2020). Klem (2009) described a solution that uses ultraviolet (UV) signals in the form of adjacent and contrasting UV-reflecting and UV-absorbing elements, while Klem & Saenger (2013) found external films with UV-reflecting components of 20–40% over 300–400 nm to effectively prevent bird-window collisions. Importantly and unlike some experimental studies performed in a flight tunnel, we confirmed the effectiveness of the UV

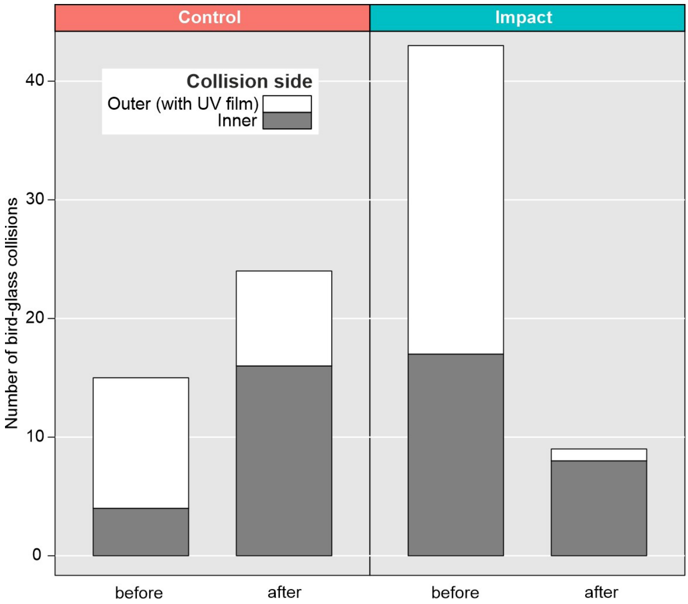

Fig. 4. Location of 91 bird–glass collisions (outer vs. inner side of a bus-shelter) recorded at four control and four impact bus-shelters before (2017 and 2018) and after (2021) treatment. After applying UV film at the outer side of four shelters, only one collision was recorded at outer side (*i.e.*, UV film-covered).

film in natural light conditions and on the actual objects located in the landscape: highly reflective glass panels of bus shelters formerly reported as an important source of bird–glass mortality (Zyśk-Gorczyńska *et al.* 2020).

Typically of field studies, we were not able to fully control conditions and there may have been more bird strikes on the glass panels of both control and film-covered shelters than recorded by us. First, many dirt smudges were hard to clearly classify as traces of bird collisions (Zyśk-Gorczyńska *et al.* 2020, 2021a) and all these non-obvious traces were ignored. Thus, some of the indirect evidence of bird collisions may have been ignored. Second, some bird strikes on windows may not leave any traces of collisions (such as feathers, smudges, bird counters). Importantly, in our opinion, the presence of the UV film did not affect the detection of collision evidence. Smudges, dirt, and dust appeared on the glass panels as a result of the typical use of the bus stops by passengers. Therefore, we assume that if there was evidence of collision, *i.e.* feathers or bird contours, they would be visible on the glass during controls. Interestingly, the number of detected bird collisions at not treated shelters increased in 2021 compared to 2017 and 2018. Several reasons can be mentioned to explain this trend. The number of bird collisions might depend on various factors, including the time of day, the land cover, or the presence of places attractive to birds for feeding, nesting, or shelters (Klem 2009). In the case of bus shelters, these factors may have changed over several months. Additionally, the degree of dirt on the glass panels/ the degree of glass visibility for birds, acts of vandalism (graffiti) and even human presence at a bus stop (and its surroundings, *e.g.*, sidewalk, bike routes) could have been additional variables affecting the number of bird collisions (Zyśk-Gorczyńska *et al.* 2020). Furthermore, the increase in the number of collisions at non-treated bus shelters in 2021 balances the potential error resulting from the non-random selection of shelters for the study (we assigned the bus shelters with the most collisions to the “treatment” and those with less collisions to the “control”). It appeared that the number of collisions recorded at shelters in control group increased in 2021, and, therefore, the division between control group and the treatment group (the stops with the highest number of bird strikes) might not have been that obvious anymore. Various factors may affect variation in number of bird collisions that can change also seasonally.

Unfortunately, glass causes refraction of light rays, including ultraviolet, which can decrease the visibility of this marking from the side where the film was not applied. Our findings conclude that some collisions occurred at glasses covered with UV film, but almost exclusively from side without the film. We suggest that if the use of the film is to be limited to the windows of buildings, then the film may prove to be effective (when the film covers problem/external surfaces where bird collisions appear). In the case of remaining glass objects, however, UV film should be applied at both sides of the glass, but this still needs to be empirically verified. Also, BirdShades film is not one of the easiest to apply. Although the film is supplied in rolls, two people, preferably with experience in this type of work, are needed for the application. In addition, despite strenuous efforts, air bubbles between the surface of the glass and the film may appear. In our opinion, the problem may be in the film's location on large glass surfaces (probably for smaller glass panels, certainly smaller than bus shelters panels, it would be easier to apply). This feature of the film should be improved if possible.

5. Conclusion

To prevent bird-window collisions, windows must be altered to be easily detected and avoided by birds. Using UV signals that birds see and humans do not is an elegant and practical solution. Our study showed that the BirdShades UV film reduces the risk of bird collisions in a natural setting with free-living birds and we conclude that such products could be largely effective in mitigating and preventing window collisions. UV-based films are usually more expensive than traditional glass stickers or other glass marking techniques, so to reduce the costs, one may consider leaving the outer part of the glass without the UV filter, as birds rarely hit parts of the glass close to its edge (Zyśk-Gorczyńska *et al.* 2021b). External UV films can be used to retrofit existing windows to render them bird-safe, and the use of sheet glass with UV coating (glazing) patterns in new and remodeled construction may provide a long-term solution to protect birds from the harmful effects of window strikes worldwide.

Undoubtedly, it is vital to test the effectiveness of the BirdShades film on windows in buildings where the light levels are most often lower inside a room than outside and this creates a high reflection of the adjacent habitat and sky that misleads birds that attempt to reach it.

Ultraviolettikalvo lasipinnoilla vähentää lintujen törmäysriskiä

Lasipintoihin törmääminen aiheuttaa arviolta miljoonien lintujen kuoleman vuosittain. Kuolleisuuden vähentämiseksi tarvitaan tietoa siitä, kuinka hyvin erilaiset törmäyksiä estävät menetelmät toimivat. Läpinäkymättömiä kalvoja ja tarroja käytetään nykyään paljon ja niiden oletetaan suojelevan lintuja törmäämiseltä. Tällaiset kalvot voivat toisaalta olla haitallisia ihmisen näkökulmasta, koska ne heikentävät lasipintojen läpinäkyvyyttä. Tuotteet, jotka hyödyntävät lintujen UV-valonäköä, voivat siksi olla käyttäkelpoisempia. Tässä tutkimuksessa selvitimme, estävätkö UV-valoa heijastavat BirdShades-kalvot lintuja törmäämästä linja-autokatosten lasipintoihin. Seurasimme kahdeksaa linja-autokatosta, joissa olimme aikaisemmin havainneet runsaasti lintujen törmäyksiä. Asensimme UV-kalvot neljään katokseen, ja toiset neljä katosta toimivat kontrolliryhmänä. Analyysimme (GAMM) mukaan ajan (ennen vs. jälkeen asennuksen) ja UV-kalvon asentamisen (kontrolli vs. UV-kalvollinen) välillä oli merkittävä yhteys. Ennen UV-kalvon asentamista törmäysten määrä oli suurempi UV-kalvollisissa linja-autokatoksissa kuin kontrollikatsoksissa. Tämä kuitenkin muuttui merkittävästi UV-kalvon asentamisen jälkeen. Tulos viittaa siihen, että UV-kalvo vähentää lintujen törmäyksiä yli viisinkertaisesti. Tutkimuksemme oli ensimmäinen, joka testasi UV-kalvoa linja-autokatoksissa. Tulokset tukevat johtopäätöstä siitä, että UV-kalvon lisääminen lasipinnoille vähentää tehokkaasti lintujen törmäysriskiä.

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Online supplementary material

Supplementary material available in the online version includes Table S1, the summary of generalized additive mixed model (GAMM) analysing number of bird–glass collisions in relation to time and bus-stop characteristics.

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