

Mink predation in great crested grebe colonies: random robbery or a well-planned hunt?

Authors: Brzeziński, Marcin, Chibowski, Piotr, and Zalewski, Andrzej

Source: Journal of Vertebrate Biology, 71(22056)

Published By: Institute of Vertebrate Biology, Czech Academy of Sciences

URL: <https://doi.org/10.25225/jvb.22056>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Mink predation in great crested grebe colonies: random robbery or a well-planned hunt?

Marcin BRZEZIŃSKI^{1*}, Piotr CHIBOWSKI¹ and Andrzej ZALEWSKI²

¹ Faculty of Biology, University of Warsaw, Warszawa, Poland; e-mail: mr.brzezins2@uw.edu.pl, p.chibowski2@uw.edu.pl

² Mammal Research Institute, Polish Academy of Sciences, Białowieża, Poland; e-mail: zalewski@ibs.bialowieza.pl

► Received 9 September 2022; Accepted 14 October 2022; Published online 7 November 2022

Abstract. The study aimed to recognize whether the activity of a semi-aquatic invasive carnivore – the American mink *Neovison vison* – is related to the distribution of waterbird colonies. For this reason, we monitored mink occurrence in lake reedbeds and the fate of artificial nests imitating those of the great crested grebe *Podiceps cristatus*. The location of artificial nests in the grebe colony increased the probability of their survival compared to those placed outside the grebe colony. During the study, mink activity increased over time. In general, it was lower in colonies than outside of them, suggesting that the presence of natural nests does not increase the probability of mink occurrence in lake reedbeds. However, mink activity was negatively correlated with the distance from the lake shoreline and differed spatially according to the presence or absence of natural grebe nests. In grebe colonies, the probability of mink occurrence at greater distances from the lake shoreline was higher than outside, which can be explained by optimizing swimming effort while searching for prey. In conclusion, mink activity in colonies was lower than in areas with no waterbird nests, and nest location in a colony decreased predation risk by mink.

Key words: *Podiceps cristatus*, coloniality, artificial nests, *Neovison vison*, invasive species

Introduction

Predation is the crucial factor that limits productivity, drives the distribution and abundance of birds, and has evolutionary consequences (Newton 1993). Predators affect bird populations by depredating broods, hunting fledglings and adults (Chalfoun et al. 2002, Smith et al. 2010) or by non-lethal effects (Cresswell 2008). During their long evolutionary co-existence with predators, birds developed numerous strategies to avoid and reduce predation (Lima & Dill 1990, Lima 2009). Spatial and temporal niche segregation, anti-predator behaviour, camouflage etc., are adaptations under constant and permanent screening by natural selection and mitigate the

predators' impact. Different nest spacing patterns may, in part, represent adaptations to various predation pressures, and predation rates may depend on nest spatial distribution (Picman 1988, Sládeček et al. 2014, Pöysä et al. 2019, Šálek et al. 2022). However, according to the naive prey hypothesis (Salo et al. 2007), these adaptations are usually ineffective in confrontation with introduced non-native predators.

Over recent decades, numerous species of invasive predators have colonized novel habitats and extended their geographical range in many regions of the world, thus impacting native birds and other animals (Doherty et al. 2016). One of the most successful invasive carnivores introduced to

* Corresponding Author

Europe is the American mink *Neovison vison*. It is an opportunistic predator that hunts various prey types depending on their availability. Birds are important prey of mink (review in Jędrzejewska et al. 2001), and mink predation on adults and their broods results in a decrease in breeding success (e.g. Niemczynowicz et al. 2017). As such, it is considered the leading cause of decline of local populations of several waterbird species (Nordström et al. 2002, 2003, Banks et al. 2008, Peris et al. 2009). In addition to the harmful direct effects caused by predation, mink can affect waterbird populations indirectly by disturbing adults and juveniles in nesting sites (Burness & Morris 1993, Oro et al. 1999). However, mink predation and disturbance can also trigger changes in the distribution of nesting sites and the nesting behaviour of waterbirds (Andersson 1992, Kilpi 1995, Landgren 1996, Craik 1997, Hario 2002, Barros et al. 2016). The reduction of mink impact and increased probability of nest survival can be achieved by nesting in colonies instead of solitarily, nesting close to human settlements, and locating colonies in places inaccessible to mink (Nordström & Korpimäki 2004, Schuttler et al. 2009, Brzeziński et al. 2012, Barros et al. 2016).

In the Masurian Lake District in north-eastern Poland, mink established a wild population in the mid-1980s (Brzeziński et al. 2019). Since then, their impact has led to considerable changes in nesting site selection of some waterbirds, including the great crested grebe *Podiceps cristatus* (Brzeziński et al. 2012). This species is a facultative colonial breeder (Goc 1986); it can switch from solitary to colonial nesting, and predation pressure may affect the choice of nesting strategy. Breeding success in great crested grebe can vary considerably (review in Vogrin 2002) and is usually higher for nests located in colonies than for single nests (Goc 1986, Moskal & Marszałek 1986, Sachs et al. 2007). Such differences were also recorded in the Masurian Lake District; brood losses in colonies were lower than those recorded in grebes breeding solitarily, and an observed switch in behaviour towards colonial nesting probably followed from their higher breeding success in colonies (Brzeziński et al. 2012). However, the nesting success of great crested grebes breeding in colonies varies spatio-temporally, and the probability of nest survival in a colony decreases with nest distance to the shoreline and increases with nest aggregation and time of egg laying (Brzeziński et al. 2018). Therefore, although colonial breeding is generally an effective defence against predation, and grebe colonies are established

in hard-to-reach areas such as vast reedbeds in shallow bays, they are not entirely safe from mink (Brzeziński 2008).

Searching modes of carnivores reflect their unique evolutionary adaptations to hunt a given prey (Jędrzejewska & Jędrzejewski 1998). Mink are primarily active along a narrow strip of the bank of waterbodies (Yamaguchi et al. 2003, Melero et al. 2008, Brzeziński et al. 2010), where they search for prey, both on land and in the water. It is held that surface swimming is a demanding process for mink (Dunstone 1993). Still, this semi-aquatic mustelid can swim relatively long distances away from the shoreline (Niemimaa 1995, Salo et al. 2008). Even in vast reedbeds and distant from the shoreline, waterbird colonies are thus accessible to mink. High concentrations of waterbirds attract predators (Rodgers 1987, Varela et al. 2007) and can be detected via auditory, olfactory and visual cues. Predators recognize patches with a high prey density and may learn to use such resources in response to their high profitability (Larivière & Messier 1998). If colonies attract predators, we may expect that mink would benefit from searching for food in areas where breeding birds and their broods are most numerous during the breeding season. Great crested grebe colonies are probably easily detected by mink, mainly due to the high vocal activity of these birds. Furthermore, grebe nests are relatively large platforms and can be easily spotted by mink if they are in large aggregations, regardless of their location in the reeds. On the other hand, swimming is energy-consuming. Therefore, according to optimal foraging theory, mink should optimize the trade-off between hunting costs and food intake and minimize swimming effort in reedbeds where the probability of finding prey is low.

This study aimed to answer whether mink activity in lake reedbeds in waterbird colonies is higher than in areas with no nests. We hypothesise that mink use cues from their potential prey, i.e. colonial breeding birds, and do not search for food randomly but increase their activity proportionally to the probability of finding and depredating waterbird nests. To answer this question, we monitored mink presence and the probability of survival of artificial nests placed in two great crested grebe colonies and two wide reedbeds with no grebe nests. We also analysed whether mink activity and artificial nest survival were affected by the distance to the lake shoreline and the exposure time.

Material and Methods

Study area

The study was conducted in 2018 in the Masurian Lake District (north-eastern Poland) at Lake Śniardwy, the largest lake in Poland (113.4 km²). The lake is eutrophic and up to 23.4 m deep; its littoral zone is overgrown mostly by reeds *Phragmites australis*. Four study plots were selected in total at the western and northern banks of the lake (Fig. 1). Two plots (B and C) were located in great crested grebe colonies, and the other two (A and D) were outside of the colonies. Grebe colonies were located in vast reedbeds that stretched over several hundred meters in two shallow bays. These colonies have been known to exist at these sites for many years. The number of breeding grebes in both colonies varies yearly; in colony B, the maximum number of breeding pairs recorded in the past was 330, and in colony C 450 pairs (M. Brzeziński, unpublished data). In 2018, the number of breeding pairs in the colonies was unknown, but the rough estimates were over 200 pairs in colony B, and 300 pairs in colony C. Study plots A and D were situated in reedbeds selected based on aerial images.

Mink monitoring

Monitoring of mink occurrence was carried out with 48 floating rafts (60 × 120 cm) distributed in study plots (12 rafts each). Rafts were floating wooden platforms with a clay plate in the middle that recorded mink footprints. This method effectively monitors this predator's abundance (Reynolds et al. 2004). Rafts were placed among the reeds and tethered to reed stems. The distribution of rafts in each plot was similar to that of artificial nests: three rafts were placed close to the shoreline (distance < 10 m), and nine rafts were placed at greater distances (Fig. 2). They were deployed on the 23rd (plots A and B) and 24th April (plots C and D), left until the 15th (plots A and B) and 16th June (plots C and D), and checked on the same days as for nests. Altogether there were eight raft checks. Mink visiting the rafts left tracks on the wet clay, and the clay was smoothed after each check; therefore, during each check, we recorded all tracks accumulated over a week. The distance between the two nearest rafts was about 50 m. In plot A, the furthest located raft was 131 m from the shoreline, in plot B 193 m, in plot C 259 m and plot D 206 m.

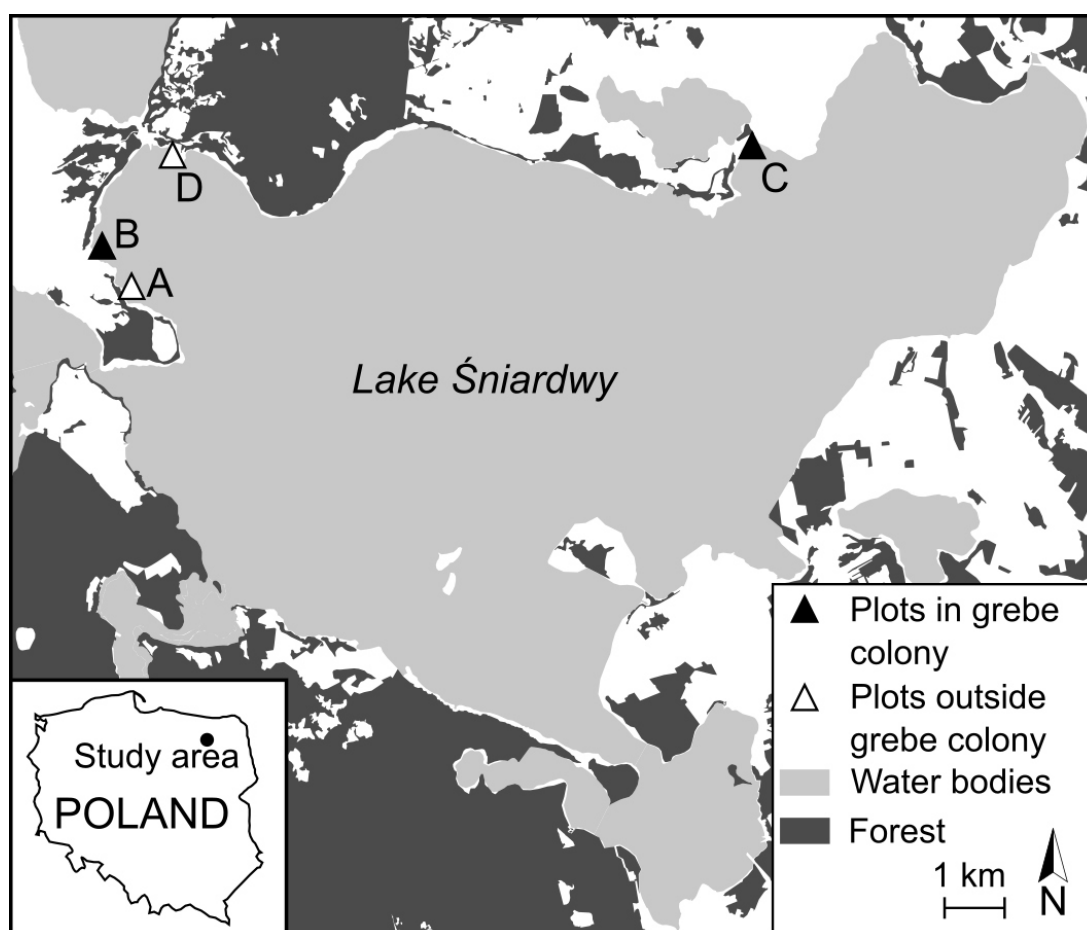


Fig. 1. Study area in Mazurian Lakeland, north-eastern Poland.

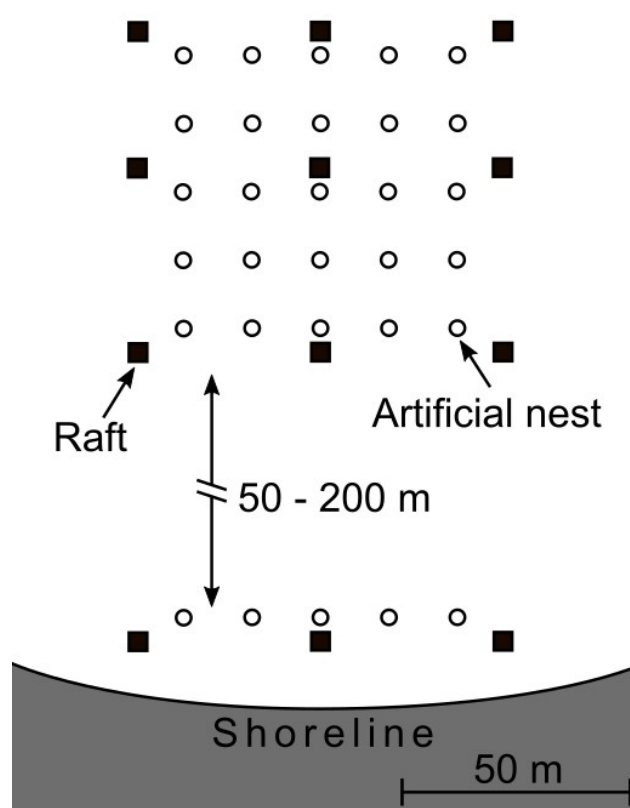


Fig. 2. Diagram of artificial nest and raft distribution in a study site.

To estimate factors affecting mink distribution, we used a generalised linear model with a binomial distribution with the day of the study (breeding season), distance from the lake shoreline and artificial nest location in or outside the grebe colony (two-level factor), and two-way interaction between them, as covariates. As the first day of the breeding season (which in our study lasted from the beginning of May to mid-June), we used the date on which the first set (40%) of artificial nests was established. To analyse the probability of mink occurrence, we used the lme4 package implemented in R (R Core Team 2021). When the data supported multiple models, we selected among them using AIC (Akaike's information criterion) values for the fit of each model. We chose as the best-performing models those within 2 ΔAIC units of the most parsimonious model. To illustrate the direction of variable influence, we predicted mink probability of occurrence for variables included in the top model.

Artificial nest monitoring

In each plot, we placed 30 artificial nests resembling those of the great crested grebe. Artificial nests were floating wooden platforms (45 × 45 cm) covered with aquatic vegetation. We placed three chicken eggs in each nest and covered them slightly with plants, as grebes do when they abandon the nest. Nests were

placed in six lines (five nests per line) parallel to the lake shoreline (Fig. 2). The precise position of each artificial nest was mapped using GPS. We then calculated the distance from the nests to the lake shoreline. At each plot, one line was placed close to the shoreline (< 10 m) and five other lines at a greater distance, determined by the location of grebe colonies (plots B and C) or the location of the selected reedbeds (plots A and D). Therefore, the distance between the artificial nests and the lake shoreline differed among the plots. In plot A, the furthest located nest was 131 m from the shoreline, in plot B 197 m, in plot C 254 m and in plot D 200 m. The distance between two neighbouring artificial nests equalled about 10-15 m and was similar in all plots. Artificial nests were placed for four weeks, which is the great crested grebe's incubation period (27 days; Goc 1986). However, not all nests were placed simultaneously in the plots; 40% of nests were placed on 30th April (plots A and B) and 1st May (plots C and D), 40% on 7th and 8th May, and 20% on 13th and 14th May (the same proportion in each line). This pattern resembled the dynamics of egg laying by great crested grebes observed in the previous year (Brzeziński et al. 2018). After two weeks, the eggs (if not depredated) were exchanged for new ones (to refresh them). Nests were visited at 6-7 day intervals. They were considered depredated if all eggs were missing or broken. Following a predation event, nests were not supplied with new eggs.

Nesting success calculation

We estimated daily survival rates (DSR) for nests using the nest survival module in the program MARK 6.0 (White & Burnham 1999) via the RMark package (Laake & Rexstad 2014) in R 4.0.3 (R Core Team 2021). This module uses a generalised linear model with a logit-link function and binomial errors to estimate daily nest survival probability with various combinations of covariates. We estimated model coefficients and log-likelihoods using maximum-likelihood estimation. We tested the influence of nest location (in and outside the grebe colony), nest distribution (distance from the lake shoreline), and nest age (the first date we used for when the nest was established) on DSR. We included these parameters as covariates and computed model support using AIC with a correction for small sample size (AIC_c). We evaluated the strength of the evidence for each model using normalised weights, w_i (Burnham & Anderson 2002). We selected the model with the smallest ΔAIC_c as the best among all compared models; however, models within an ΔAIC_c of 2.00 were considered equally supported (Burnham &

Table 1. Model-averaged parameter estimates, standard errors (SE), and 2.5-97.5% confidence for each variable carried over into the final model set, explaining the probability of mink occurrence in the study plot with artificial nests.

Parameter	Estimate	SE	2.5 %	97.5 %	z value	P (> z)
Intercept	7.58e-01	4.771e-01	-0.1413	1.6734	1.584	0.113
Shore_dist	-2.17e-02	4.244e-03	-0.0297	-0.0139	5.099	3e-07***
Colony	-1.72e+00	5.721e-01	-2.7782	-0.6696	3.000	0.003**
Day_season	1.10e-02	1.199e-02	-0.0082	0.0365	0.913	0.361
Shore_dist × Colony	1.47e-02	4.694e-03	0.0062	0.0236	3.121	0.002**
Colony × Day_season	2.97e-03	1.018e-02	-0.0224	0.0466	0.291	0.771
Shore_dist × Day_season	4.85e-06	5.981e-05	-0.0002	0.0003	0.081	0.936

Colony artificial nests in or outside grebe colony, *Day_season* number of days since the first set of artificial nests was established, *Shore_dist* artificial nest distance from the lake shoreline.

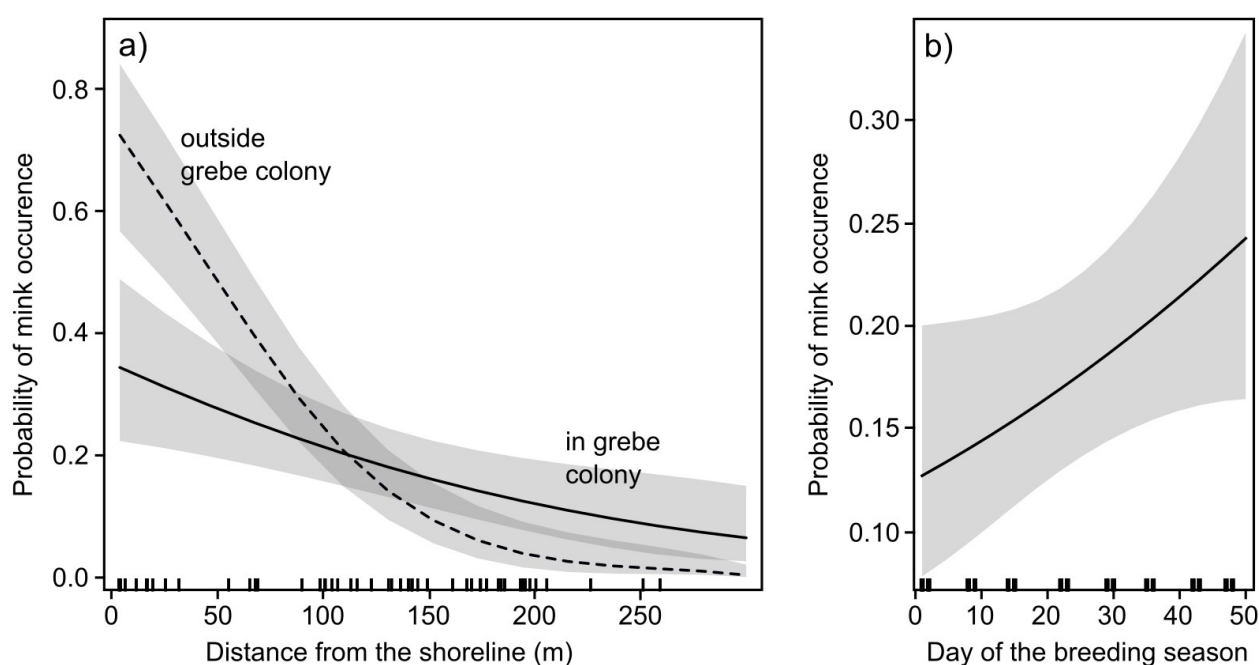


Fig. 3. Probability of mink occurrence on the raft.

Anderson 2002). We reported results from two top models but acknowledging model uncertainty, we calculated model-averaged estimates of the DSR model set (Burnham & Anderson 2002).

Results

Mink activity

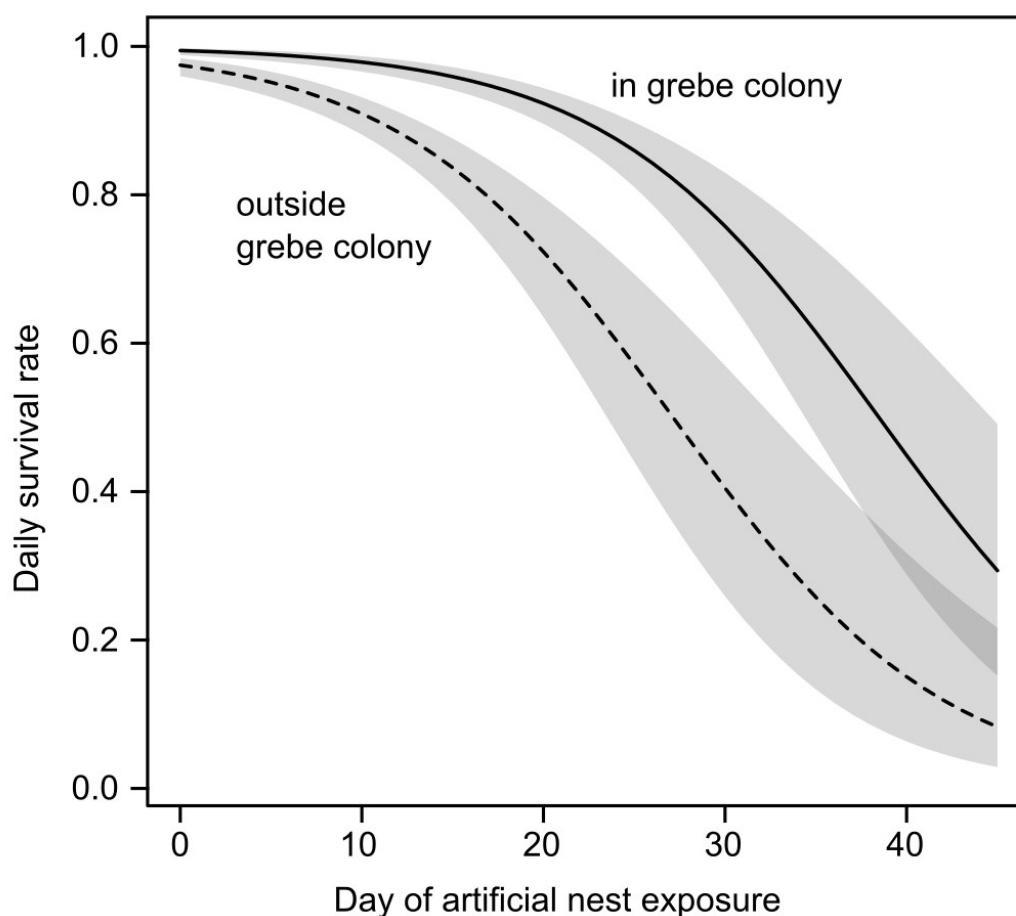
Out of 384 raft checks (12 rafts checked eight times in four plots), the presence of mink tracks was recorded 88 times (22.9%), and mink tracks were detected on 33 rafts (68.8%). The probability of mink occurrence on the rafts varied between study plots. Model selection provided support for three models of the probability of mink occurrence (Table 1). The top model included the day of the breeding season and the interaction

between the distance from the lake shoreline and raft location in or outside the grebe colony. The two next best models were only 1.41 and 1.59 AIC_c units worse than the top model. The second model included only the interaction between the distance from the lake shoreline and raft location in or outside the grebe colony. The third included all variables of the top model and the interaction between the day of the breeding season and raft location in or outside the grebe colony. The probability of mink occurrence on the raft increased consecutively over the study period from 0.127 (CI = 0.078-0.200) on the first day to 0.243 (CI = 0.164-0.343) on the 50th day (Fig. 3b). It also varied as a function of the distance from the lake shoreline and interaction with raft location in the grebe colony (Fig. 3a). Outside the grebe colony, the probability of mink

Table 2. Daily survival models of artificial nests at Lake Śniardwy.

Model	<i>K</i>	AIC _c	ΔAIC _c	<i>w_i</i>	Deviance
Colony + Nest_age	3	279.17	0.00	0.732	273.15
Shore_dist + Colony + Nest_age	4	281.18	2.01	0.268	273.15
Shore_dist + Nest_age	3	310.93	31.76	0.00	304.91
Nest_age	2	315.03	35.86	0.00	311.02
Colony	2	354.22	75.04	0.00	350.21
Shore_dist + Colony	3	356.20	77.03	0.00	350.18
Null	1	360.95	81.78	0.00	358.95
Shore_dist	2	361.15	81.98	0.00	357.14

Models are ranked by differences in Akaike's Information Criterion for small sample size (ΔAIC_c) values. Covariates are as follows: *Colony* artificial nests in or outside grebe colony, *Nest_age* duration of artificial nest exposure in days, *Shore_dist* artificial nest distance from the lake shoreline, *K* number of parameters, *w_i* Akaike weight.

**Fig. 4.** Daily survival rates (DSR) of artificial nests.

occurrence close to the shoreline was higher (0.741, CI = 0.581-0.855) than in the grebe colony (0.350, CI = 0.226-0.499). The probability of mink occurrence decreased with distance to the shoreline; however, with an increasing distance from the shoreline, mink activity was greater in grebe colonies compared to sites with no grebe nests. In the grebe colony, the probability of

mink occurrence 250 m from the shoreline was 0.089 (CI = 0.045-0.169), whereas outside the colony, it was 0.012 (CI = 0.003-0.043). In general, across the distance from the shoreline, the average probability of mink occurrence was lower in the grebe colony (0.179) than outside the colony (0.212; averaged for every 10 m from the shoreline).



Daily survival of artificial nests

Predation pressure on artificial nests was high: during the four-week-long exposure, all nests were depredated in plots A, C and D, and 76.7% in plot B. Model selection provided support for two models for artificial nest survival rate ($\Delta AIC_c \leq 2.00$; Table 2). All competing top models included the artificial nest location in or outside the grebe colony and nest age, and one of them additionally included artificial nest distance from the lake shoreline. The DSR of nests averaged across the full model set decreased over the following days, and it was affected positively by the presence of natural grebe nests (Fig. 4). In the grebe colony, the DSR of artificial nests decreased over the following days from 0.9943 (CI = 0.9882–0.9973) on the first day to 0.2935 (CI = 0.1518–0.4911) on the 46th day, whereas outside of grebe colony it decreased from 0.9747 (CI = 0.9599–0.99841) to 0.0829 (CI = 0.0287–0.2167), respectively (Fig. 4).

Discussion

We have shown that the probability of mink occurrence on the rafts placed in lake reedbeds increased over the waterbird breeding season. Sites outside of grebe colonies were visited more often by mink near the shoreline but less often at a longer distance than sites in colonies. However, the probability of mink occurrence in the grebe colony 100–250 m from the shoreline was relatively low. This finding is in accordance with results for artificial nest DSR, which was higher inside grebe colonies than outside. This result suggests that reedbeds with natural nest aggregations are a safer place to breed compared to those with no nests and that predation by mink (and other predators) is more limited.

The probability of mink occurrence in reedbeds was strongly related to the distance from the lake shoreline. This result confirms that long-distance swimming can be energy-consuming for mink and unrewarding if food resources are limited. Interestingly, the probability of mink occurrence in relation to the distance from shoreline changed differently in and outside grebe colonies. In grebe colonies, mink swam long distances more often than outside colonies, probably due to the higher food abundance; the presence of grebe and artificial nests. During the breeding season, predators can increase their activity in bird colonies, which host abundant and predictable prey (Wittenberger & Hunt 1985). However, in spring, reedbeds offer diverse prey such as fish, crayfish, amphibians and water beetles, which

can be easier to hunt in shallow waters close to the lake shoreline than grebes or their broods in a distant colony. Therefore, in areas where waterbirds are not abundant, mink optimize their hunting efforts and are primarily active close to the bank, where they can find prey other than waterbird broods.

The risk of nest predation can be increased by contact and mate calls between adult birds (Mougeot & Bretagnolle 2000, Krams 2001). Adult grebes communicate in colonies by calls, and these sounds can be heard from hundreds of meters. Therefore, the high vocal activity of grebes in breeding colonies is undoubtedly easily detected by predators, including mink. Our study could not verify whether grebe vocalization facilitates the detection of a colony and attracts mink to the nests; it showed that mink activity in colonies was not higher than outside of them. We explain this, among others, by mink territorial spacing pattern. According to former estimates, mink densities in the study area could be as high as one individual/1 km of lake shoreline (Brzeziński et al. 2012); therefore, about 2–3 mink individuals could be active at each study plot. However, although individual mink distribution in the study area was unknown, we expect that mink individuals were distributed there linearly with overlapping but separated home ranges, typical for the mink spacing pattern (Yamaguchi & Macdonald 2003, Melero et al. 2008). Individuals whose home ranges encompass waterbird colonies may have access to the nests, but individuals occupying shoreline sections distant from colonies probably do not penetrate them, as their diet in spring does not comprise waterbirds and their broods (Brzeziński 2008). The territorial distribution of mink individuals can explain mink tracks recorded in all studied sections of the lake shoreline, both in and outside waterbird colonies, though that is not to say mink activity is distributed evenly.

Our results show that the DSR of the artificial nests was higher in the grebe colony than outside. Several colonial waterbirds have evolved communal defence (even against the mink; Nordström et al. 2004), but not grebes. Therefore, the observed difference in DSR in and outside the colony could be related to the “dilution effect”; within the colony, artificial nests were spatially mixed with natural nests, the density of nests was higher and the probability of nest depredation was lower. This situation is in accordance with the prediction that grebes aggregate into colonies to reduce predation pressure (Brzeziński et al. 2012).



In our study, the DSR of artificial nests was much lower than the DSR of natural nests in a grebe colony studied at Śniardwy Lake previously (see Brzeziński et al. 2018). Similar results were obtained, for example, in an experiment conducted in Cape Horn Biosphere Reserve (Chile), where artificial nests were exposed to mink predation and had significantly lower survival rates (with only 0.4% surviving) than natural nests (Schuttler et al. 2009). Artificial nests differ from natural nests in a number of important aspects that may influence predation rates – the former are usually easier to find, and predation rates are higher than in the latter (King et al. 1999, Mezquida & Marone 2003, Burke et al. 2004). There are at least two possible explanations for differences between natural and artificial nest DSR in our study area: the temporal presence of adult grebes at natural nests (mainly at night) and better concealment of natural nests and eggs in the nest. Eggs in natural nests were better covered than in artificial nests because plant material was supplied by the adult birds, whereas in artificial nests, it was replaced by us at one-week intervals between consecutive checks; it was usually dry and did not cover the eggs as well as fresh plant material. Despite all these obstacles, the depredation of artificial nests can be used as a relative index of spatial and temporal variation in nest predation risk (Roos 2002), and our study focused on relative comparisons, not on transforming survival rates of artificial nests into natural ones.

The share of nests depredated by mink and other potential predators (marsh harrier *Circus aeruginosus*, hooded crow *Corvus corone*) in a given study site was challenging to evaluate because eggshell remains were rarely explicitly indicative of a predator species. Undoubtedly mink was not the only species depredating nests, and the two mentioned bird species were responsible for some of the nest losses. However, in the previous study conducted at Lake Śniardwy, the DSR of grebe broods was related to the probability of mink occurrence, suggesting that nest losses in the colony resulted mainly from mink predation (Brzeziński et al. 2018).

Conclusions

In conclusion, this study shows that during the breeding season, mink activity in great crested grebe aggregations is not higher than elsewhere in lake reedbeds, as we hypothesized. However, the answer to whether mink predation in grebe colonies is random robbery or a well-planned hunt is not unequivocal. In general, mink activity in reedbeds during the breeding season increased over time, suggesting that mink could have learned where food resources (grebe eggs in natural nests and chicken eggs in artificial nests) were available, adapted their hunting efforts to the increasing prey availability and progressively increased activity in these areas. Mink activity decreased with distance to the shoreline, but in colonies, mink were more active at longer distances from the shoreline in comparison with sites outside colonies. Therefore, mink increased their activity proportionally to the probability of finding and depredating grebe nests. On the other hand, the daily survival rate of artificial nests, spatially mixed with natural nests, was higher inside grebe colonies than outside, and this finding supports the proposition that colonial breeding can reduce predation.

Acknowledgements

We would like to thank E. Bujko for his help during fieldwork and A. Fells for improving the English in the manuscript.

Author Contributions

M. Brzeziński and A. Zalewski designed the study and developed the methodology, M. Brzeziński conducted the fieldwork, A. Zalewski analysed the data and performed statistical analyses, P. Chibowski made figures. All authors discussed the results, wrote the text and contributed to the final manuscript.

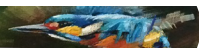
Data Availability Statement

The datasets used and/or analysed during the current study are available from the corresponding author upon reasonable request.

Literature

- Andersson A. 1992: Development of waterbird populations in the Bullerö archipelago of Stockholm after colonization by mink. *Ornis Svec.* 2: 107–118.
- Banks P.B., Nordström M., Ahola M. et al. 2008: Impacts of alien mink predation on island vertebrate communities of the Baltic Sea Archipelago: review of a long-term experimental study. *Boreal Environ. Res.* 13: 3–16.
- Barros Á., Romero R., Munilla I. et al. 2016: Behavioural plasticity in nest-site selection of a colonial seabird in response to an invasive carnivore. *Biol. Invasions* 18: 3149–3161.
- Brzeziński M. 2008: Food habits of the American mink *Mustela vison* in the Mazurian Lakeland, Northeastern Poland. *Mamm. Biol.* 73: 177–188.
- Brzeziński M., Chibowski P., Gornia J. et al. 2018: Spatio-temporal variation in nesting success of colonial waterbirds under the impact of a non-native invasive predator. *Oecologia* 188: 1037–1047.
- Brzeziński M., Marzec M. & Żmihorski M. 2010: Spatial distribution, activity, habitat selection of American mink (*Neovison vison*) and polecats (*Mustela putorius*) inhabiting the vicinity of eutrophic lakes in NE Poland. *Folia Zool.* 59: 182–190.
- Brzeziński M., Natorff M., Zalewski A. & Żmihorski M. 2012: Numerical and behavioural responses of waterfowl to the invasive American mink: a conservation paradox. *Biol. Conserv.* 147: 68–78.
- Brzeziński M., Żmihorski M., Zarzycka A. & Zalewski A. 2019: Expansion and population dynamics of a non-native invasive species: the 40-year history of American mink colonisation of Poland. *Biol. Invasions* 21: 531–545.
- Burke D.W., Elliott K., Moore L. et al. 2004: Patterns of nest predation on artificial and natural nests in forests. *Conserv. Biol.* 18: 381–388.
- Burness G.P. & Morris R.D. 1993: Direct and indirect consequences of mink presence in a common tern colony. *Condor* 95: 708–711.
- Burnham K.P. & Anderson D.R. 2002: Model selection and multimodel inference: a practical information–theoretic approach, 2nd ed. *Springer-Verlag, New York, USA*.
- Chalfoun A.D., Thompson III F.R. & Ratnaswamy M.J. 2002: Nest predators and fragmentation: a review and meta-analysis. *Conserv. Biol.* 16: 306–318.
- Craik C. 1997: Long-term effects of North American mink *Mustela vison* on seabirds in western Scotland. *Bird Study* 44: 303–309.
- Cresswell W. 2008: Non-lethal effects of predation in birds. *Ibis* 150: 3–17.
- Doherty T.S., Glen A.S., Nimmo D.G. et al. 2016: Invasive predators and global biodiversity loss. *Proc. Natl. Acad. Sci. U.S.A.* 113: 11261–11265.
- Dunstone N. 1993: The mink. T. & A. D. Poyser, London, UK.
- Goc M. 1986: Colonial versus territorial breeding of the great crested grebe *Podiceps cristatus* on Lake Družno. *Acta Ornithol.* 22: 95–145.
- Hario M. 2002: Mink predation on black guillemots at Soderskar in 1994–1999. *Suomen Riista* 48: 18–26.
- Jędrzejewska B. & Jędrzejewski W. 1998: Predation in vertebrate communities: the Białowieża Primeval Forest as a case study. *Springer-Verlag, Berlin Heidelberg, Germany*.
- Jędrzejewska B., Sidorovich V.E., Pikulik M.M. & Jędrzejewski W. 2001: Feeding habits of the otter and the American mink in Białowieża Primeval Forest (Poland) compared to other Eurasian populations. *Ecography* 24: 165–180.
- Kilpi M. 1995: Breeding success, predation and local dynamics of colonial common gulls *Larus canus*. *Ann. Zool. Fenn.* 32: 175–182.
- King D.I., DeGraaf R.M., Griffin C.R. & Maier T.J. 1999: Do predation rates on artificial nests accurately reflect predation rates on natural nests? *J. Field Ornithol.* 70: 257–262.
- Krams I. 2001: Communication in crested tits and the risk of predation. *Anim. Behav.* 61: 1065–1068.
- Laake J. & Rexstad E. 2014: RMark – an alternative approach to building linear models in MARK. In: Gooch E. & White G.C. (eds.), Program MARK: a gentle introduction. *Colorado State University, Fort Collins, USA*.
- Landgren T. 1996: Re-distribution of black-headed gull *Larus ridibundus* colonies in NE Vanen during 1985–95. *Ornis Svec.* 6: 45–56.
- Larivière S. & Messier F. 1998: Effect of density and nearest neighbours on simulated waterfowl nests: can predators recognize high-density nesting patches? *Oikos* 83: 12–20.
- Lima S.L. 2009: Predators and the breeding bird: behavioural and reproductive flexibility under the risk of predation. *Biol. Rev.* 84: 485–513.
- Lima S.L. & Dill L.M. 1990: Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* 68: 619–640.
- Melero Y., Palazon S., Revilla E. et al. 2008: Space use and habitat preferences of the invasive American mink (*Mustela vison*) in a Mediterranean area. *Eur. J. Wildl. Res.* 54: 609–617.
- Mezquida E.T. & Marone L. 2003: Are results of artificial nest experiments a valid indicator of

- success of natural nests? *Wilson Bull.* 115: 270–276.
- Moskal J. & Marszałek J. 1986: Effect of habitat and nest distribution on the breeding success of the great crested grebe *Podiceps cristatus* on Lake Żarnowieckie. *Acta Ornithol.* 22: 147–158.
- Mougeot F. & Bretagnolle F. 2000: Predation as a cost of sexual communication in nocturnal seabirds: an experimental approach using acoustic signals. *Anim. Behav.* 60: 647–656.
- Newton I. 1993: Predation and limitation of bird numbers. In: Power D.M. (ed.), *Current ornithology. Curr. Ornithol. vol. 11, Springer, Boston, USA: 143–198.*
- Niemimaa J. 1995: Activity patterns and home ranges of the American mink *Mustela vison* in the Finnish outer archipelago. *Ann. Zool. Fenn.* 32: 117–121.
- Niemczynowicz A., Świętochowski P., Brzeziński M. & Zalewski A. 2017: Non-native predator control increases the nesting success of birds: American mink preying on wader nests. *Biol. Conserv.* 212: 86–95.
- Nordström M., Högmänder J., Laine J. et al. 2003: Effects of feral mink removal on seabirds, waders and passerines on small islands in the Baltic Sea. *Biol. Conserv.* 109: 359–368.
- Nordström M., Högmänder J., Nummelin J. et al. 2002: Variable responses of waterfowl breeding populations to long-term removal of introduced American mink. *Ecography* 25: 385–394.
- Nordström M. & Korpimäki E. 2004: Effects of island isolation and feral mink removal on bird communities on small islands in the Baltic Sea. *J. Anim. Ecol.* 73: 424–433.
- Nordström M., Laine J., Ahola M. & Korpimäki E. 2004: Reduced nest defence intensity and improved breeding success in terns as responses to removal of non-native American mink. *Behav. Ecol. Sociobiol.* 55: 454–460.
- Oro D., Pradel R. & Lebreton J.D. 1999: The effects of nest predation and food availability on life history traits in Audouin's gull. *Oecologia* 118: 438–445.
- Peris S., Sanguinett J. & Pescador M. 2009: Have Patagonian waterfowl been affected by the introduction of the American mink *Mustela vison*? *Oryx* 43: 648–654.
- Picman J. 1988: Experimental study of predation on eggs of ground-nesting birds: effects of habitat and nest distribution. *Condor* 90: 124–131.
- Pöysä H., Lammi E., Pöysä S. & Väänänen V.-M. 2019: Collapse of a protector species drives secondary endangerment in waterbird communities. *Biol. Conserv.* 230: 75–81.
- R Core Team 2021: R: a language and environment for statistical computing. *R Foundation for Statistical Computing, Vienna, Austria.*
- Reynolds J.C., Short M.J. & Leigh R.J. 2004: Development of population control strategies for mink *Mustela vison*, using floating rafts as monitors and trap sites. *Biol. Conserv.* 120: 533–543.
- Rodgers J.A., Jr. 1987: On the antipredator advantages of coloniality: a word of caution. *Wilson Bull.* 99: 269–271.
- Roos S. 2002: Functional response, seasonal decline and landscape differences in nest predation risk. *Oecologia* 133: 608–615.
- Sachs J.L., Hughes C.R., Nuechterlein G.L. & Buitron D. 2007: Evolution of coloniality in birds: a test of hypotheses with the red-necked grebe (*Podiceps grisegena*). *Auk* 124: 628–642.
- Salo P., Korpimäki E., Banks P.B. et al. 2007: Alien predators are more dangerous than native predators to prey populations. *Proc. R. Soc. Lond. B* 274: 1237–1243.
- Salo P., Nordström M., Thomson R.L. & Korpimäki E. 2008: Risk induced by a native top predator reduces alien mink movements. *J. Anim. Ecol.* 77: 1092–1098.
- Schuttler E., Klenke R., McGehee S. et al. 2009: Vulnerability of ground-nesting waterbirds to predation by invasive American mink in the Cape Horn Biosphere Reserve, Chile. *Biol. Conserv.* 142: 1450–1460.
- Sládeček M., Kubelka V., Mlíkovský J. & Šálek M. 2014: Coping with nest predation risk in a species-rich bird community inhabiting a Siberian wetland. *Folia Zool.* 63: 256–268.
- Smith R.K., Pullin A.S., Stewart G.B. & Sutherland W.J. 2010: Effectiveness of predator removal for enhancing bird populations. *Conserv. Biol.* 24: 820–829.
- Šálek M., Sládeček M., Kubelka V. et al. 2022: Beyond habitat: effects of conspecific and heterospecific aggregation on the spatial structure of a wetland nesting bird community. *J. Avian Biol.* 2022: e02928.
- Varela S.A.M., Danchin E. & Wagner R.H. 2007: Does predation select for or against avian coloniality? A comparative analysis. *J. Evol. Biol.* 20: 1490–1503.
- Vogrin M. 2002: Breeding success of great crested grebe *Podiceps cristatus* on fishponds. *Ornis Svec.* 12: 203–210.
- White G.C. & Burnham K.P. 1999: Program MARK: survival estimation from populations of marked animals. *Bird Study* 46 (Suppl. 1): S120–S139.



- Wittenberger J.F. & Hunt G.L. 1985: The adaptive significance of coloniality in birds. *Avian Biol.* 8: 1–78.
- Yamaguchi N. & Macdonald D.W. 2003: The burden of co-occupancy: intraspecific resource competition and spacing patterns in American mink, *Mustela vison*. *J. Mammal.* 84: 1342–1355.
- Yamaguchi N., Rushton S. & Macdonald D.W. 2003: Habitat preferences of feral American mink in the Upper Thames. *J. Mammal.* 84: 1356–1373.