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**Does removal of mammalian predators significantly
affect success of simulated nests in linear habitats?
Case study on American mink *Mustela vison***

&

**Predation on simulated duck nests in relation to nest
density and habitat type**

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Annotation

This thesis is made up of two studies dealing with predation of waterbird nests. In the first study, we determined whether removal of introduced predator *Mustela vison* affected nest survival of simulated duck nests in linear habitat. We found that short-time mink trapping could increase the nest survival of simulated nests. In the second study, we tested two hypothesis: 1) predation depends on density of waterfowl nests, 2) mammals are main predators in forest habitat and birds mainly depredate nests deployed in open land. We found no evidence of density-dependent predation on simulated waterfowl nests in both habitat types. Mammalian predators were considered as the most important cause of nest failure in our study, followed by birds. Predation pattern was changing during the season between June and July differently in forest and differently in open-field areas. Further, different predators depredated simulated nests in different habitat (forest, open) and treatment (high-density, solitaire nest) type.

Tato práce je psána ve formě 2 rukopisů. První z nich „Does removal of mammalian predators significantly affect success of simulated nests in linear habitats? Case study on American mink *Mustela vison*“ bude odeslán do časopisu *Folia Zoologica*. Druhý rukopis „Predation on simulated duck nests in relation to nest density and habitat type“ bude odeslán do časopisu *Journal of Zoology*.

Prohlašuji, že jsem tuto bakalářskou práci vypracovala samostatně pouze s použitím citované literatury.

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.....
Eliška Padyšáková

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Vám všem výše jmenovaným ještě jednou DĚKUJI.

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Úvodní komentář

Tato práce přináší výsledky dvou studií, jejichž společným jmenovatelem je predace hnízd vodních ptáků. V první z nich jsme zkoumali vliv odstranění introdukované šelmy, norka amerického *Mustela vison*, na hnízdní úspěšnost vodních ptáků hnízdících podél vodního toku (řeka Jihlava). V rámci druhé studie jsme testovali dvě hypotézy: a) predace je závislá na hustotě hnízd kořisti, b) savci jsou hlavními predátory v prostředí lesa, zatímco ptáci predují především v otevřené krajině. V obou studiích jsme k určování predátorů i k ověření hypotéz používali umělá kachní hnízda s jedním normálním a jedním voskovým vejcem.

První studie probíhala ve dvou etapách se 14-tidenní přestávkou, během které došlo na dvou sledovaných úsecích k odchyťování norka do živochytných sklopných pastí. Následné pozorování umělých hnízd ukázalo rozdíl mezi zásahovými úseky, na kterých byl norek odstraněn a kontrolními úseky, na kterých zůstalo společenství predátorů nezměněno. Značný nárůst v hnízdní úspěšnosti byl po odstranění norků patrný na zásahových úsecích, zatímco na kontrolních úsecích došlo k přesně opačnému efektu, slabému poklesu hnízdní úspěšnosti. Dle dosažených výsledků tedy usuzujeme, že i krátkodobé odstranění norků může zvýšit přežívání hnízd vodních ptáků.

Druhá studie byla rovněž rozdělena do dvou etap, abychom zaznamenali i případné změny v predčním tlaku během hnízdní sezóny. Umělá hnízda byla umístěná ve čtvercových plochách 10 x 10 m v pobřežních litorálech 48 rybníků Dačického mikroregionu. K testování hypotéz jsme sledovali jen osud hnízd umístěných uprostřed čtverce. U poloviny rybníků pak byla hustota hnízd navýšena na 5, abychom zjistili, zda vyšší hustota hnízd přitáhne i více predátorů. Zároveň byly rybníky rozděleny i podle prostředí, ve kterém se nachází (lesní nebo otevřená krajina). Následně jsme testovali jak průkaznosti jednotlivých efektů, tak i jejich interakce. Hlavními predátory v naší práci byli savci, mezi kterými dominovala divoká prasata. Nenašli jsme průkazný rozdíl v míře predace mezi jednotlivými typy studijních ploch s nízkou či vysokou hustotou umělých hnízd, tudíž nemůže potvrdit hypotézu, že predace je na hustotě hnízd závislá. Nicméně byla prokázána interakce mezi typem prostředí a časem, což ukazuje, že míra predace hnízd se měnila v průběhu sezóny jinak v lese a jinak v otevřené krajině. Značný nárůst hnízdní úspěšnosti v druhé etapě studie u hnízd umístěných u rybníků v otevřené krajině je zřejmě způsobený postupným vzrůstem a zhušťováním vegetace, která stále více zakrývala hnízda. Naše výsledky rovněž naznačují, že savci a ptáci se na predaci na

lokality s vysokou hustotou hnízd podílejí zhruba stejným dílem, kdežto solitérní hnízda jsou mnohem více napadána savci.

**Does removal of mammalian predators
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Abstract

Alien species of predators may influence the breeding success of waterfowl. Some previous studies tested whether predator removal may cause increase in breeding densities with contradictory conclusions. We examined the impact of introduced American mink removal on success of simulated nests in two treatments and two control transects in linear habitat along Jihlava river, Czech Republic, in 2005. The study was divided into two periods (June and July) with removal break. A total of 8 mink was removed from treatment transects. Whereas the nest survival in control transects slightly decreased from June to July, an opposite effect of season, i.e. increase in nest survival was apparent in treatment transects as a response to mink removal. We suggest that local reduction of mink populations could be short time effective tool for conservation of protected species

Key words: American mink, nest predation, simulated nests, predator removal, Czech Republic

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Introduction

Predation is often included in major causes of nesting failure of birds and may be considered to be one of the most important factors influencing the population densities and the composition of avian communities (Newton 1998, Nordström et al. 2002, 2003). Some studies have reported that mammals are more important as nest predators than birds (Bellebaum 2002, Pasitschniak-Arts and Messier 1995), although both mammalian and avian predators can be involved (Albrecht et al. 2006, Opermanis et al. 2001). Further, mammals might cause death or injury to an incubating female duck after predation attacks (Sargeant and Raveling 1992).

Many previous experimental studies tried to estimate the impact of removal of a variety predators on breeding success of grassland birds (Dion et al. 1999), passerines (Nordström et al. 2003) or water bird communities (Nordström et al. 2002, Kauhala 2004, Meckstroth and Miles 2005). The spread of alien species of predators may cause much damage on native fauna, like population declines (Sidorovich and Macdonald 2001) or even local extinction (Newton 1998), since many native organisms lack mechanisms to confront the threats of the new predator.

The American mink *Mustela vison* SCHREBER 1777 is a medium-size mustelid species native in the North America. Mink was brought for fur farms in Europe in the 1920s. Nevertheless, many of them escaped and established free-living populations soon (Dunstone 1993, Bevanger and Henriksen 1995, Anděra and Hanzal 1996). Mink quickly started to spread all over Europe, including Czech republic where free-living individuals was detected in 1960s (Mazák 1964). As a mobile, generalist predator, mink had colonized variety of aquatic habitats, where it started to have notable impact on mammal (e.g. *Arvicola terrestris*), fish and water bird populations (Banks et al. 2004, Ferreras and Macdonald 1999, Craik 1997, Sidorovich and Macdonald 2001). There is not any extensive study about mink predation from Czech Republic. Heavy predation by mink on amphibians (Poledník and Poledníková 2005), grass snake *Natrix tessellata* (Kapler 1994), crayfish *Austropotamobius torrentium* (Fisher 2001) or waterfowl (Šálek et al. 2004) was observed in various regions.

Some experimental studies were implemented to see if it is possible to improve duck nest success by using trapping and removing to reduce and control the population size of predators. Kauhala (2004) found that the influence of predator removal on the breeding success of ducks in Finland varied in each part of the country and was also dependant upon

type of prey and predator. Nevertheless, Nordström et al. (2002) demonstrated that the breeding densities of some smaller species (shelduck, tufted duck , velvet scoter) drastically increased in mink removal areas whereas the populations of larger waterfowl species (mute swan, greylag goose, eider, goosander) did not show obvious increases in breeding densities after mink removal.

Main aim of this study was to assess whether mink removal have significant impact on duck breeding success on artificial nests in linear riverine habitats.

Methods

STUDY AREA

We conducted the study during the breeding season of 2005 in the middle part of Českomoravská vrchovina, Czech Republic (between 49°32' N, 15°42' E and 49°37' N, 15°74' E). This uphill rolling region at altitude 800 m.a.s.l. is dominated by agricultural land with gradual hills, vales and numerous woods and groves. This part of the country is the coldest one with mean annual temperatures 5 – 7 °C.

The main part of the study area is formed by the midstream portion of the Jihlava river stretch and cover 43 km of the river. River width varied between 5 and 15 m and river depth did not exceed 2 m. The fish communities in this part of the Jihlava river fall into trout and barbel fish zones (e.g. *Rutilus rutilus*, *Leuciscus leuciscus*, *Leuciscus cephalus*, *Gobio gobio*). The river banks are fringed with trees such as *Alnus glutinosa*, *Populus* sp., *Salix fragilis* and vegetation such as *Bidens* sp., *Chenopodium* sp., *Persicaria* sp., *Phalaris arundinacea*, *Phragmites australis*, *Urtica dioica*, *Rubus* sp. among many others. The adjacent landscape consist of mosaic of forests (24%), fields (55%), grasslands (9%) and variety of small extensive ponds. Main breeding watefowl species in the controlled area was *Anas platyrhynchos* and *Anas strepera* (pers. obs.).

EXPERIMENTAL DESIGN

We chose four 2.5-km study transects for the placement of simulated nests. The main criteria used for transects selection was their location in calm parts of the river valley out of villages and Jihlava town. Transects were positioned independently and did not overlap. The average distance between monitored transects was 11 km. Transects were placed within meadows of similar vegetative structure and composition. The river was fringed with meadows, spruce vegetation and cottagey settlements.

MINK REMOVAL

Feral mink was removed from 3.7. – 17.7.2005 from study transect no. 2 and 3. These transects are called treatment transects, whereas transects no.1 and 4 (without mink removal) are called control transects. Hinged box traps were used for mink capture since live-trapping is considered to be the most publicly acceptable, humane, and successful technique (Moore et al. 2000). A total of 12 traps were used per each transect. Wired box traps were set at ground level near the water in localities of presumable occurrence of mink. Fish were used as bait, and traps were checked once a day during the morning, the bait was changed every 3 days or according to the necessity (after hard rain).

SIMULATED NESTS

We used artificial nests containing chicken eggs to simulate waterfowl nests. We constructed waterfowl nests from dead vegetation found nearby by pressing the vegetation together to form a shallow cup. We shrewed each nest with duck feather to mimic animal scent. Each nest consisted of two domestic hen eggs, one of which was filled with wax. Wax-filled eggs were used for detecting and identifying predators from beak or teeth marks and chicken eggs served as a reward for predators (Albrecht et al. 2006). We wore rubber boots and gloves while manipulating with nests and eggs to reduce human scent.

Nests were deployed on the ground at 100-m intervals along the river to minimize the probability of nearby nests being discovered by an intensively searching predator. Nests were located to vegetation on river banks in vicinity flow. Twenty-five nests were deployed per one transect, for a total of 100 nests per each period. Simulated nests were visited every 5 days for a total of 15 days. Depredated nests were removed from transects. A nest was considered depredated when at least one egg was missing or destroyed or if marks of predator were left on the wax eggs. The experiment was divided into two periods during June and July 2005 to mimic the nesting waterfowl season. The 14-day break between the two periods was used for mink remotion.

PREDATOR IDENTIFICATION

Egg remains, appearance of the nest and mainly beak and teeth marks left in the wax eggs allowed us to categorized predators as avian or mammalian. Tooth imprints of mammalian predators were determined by comparison to skull dentice from mammalian collection of Faculty of Biological Sciences, University of South Bohemia. Bill marks attributable to avian predators (mostly corvids) were not assigned to species. We followed Craik (1995) to diagnose mink predation; nests were little damaged, canine imprints were typically 1-2 mm wide and, if paired, ≈ 10 mm apart on the shell. Nests predated by rodents were excluded from the analysis because rodents were not considered as relevant predators of waterfowl nests. Predator identity remained unknown when plastic eggs had disappeared or the wax egg was either untouched.

STATISTICAL ANALYSIS

We used generalized linear mixed effect model approach (GLMM) to evaluate the effect of mink removal on nest survival (Mayfield 1961, 1975). In the analysis, the treatment (mink removed vs not removed) and period (June and July) were categorical predictors, and transect identity was treated as random effect. We specifically evaluated the significance of interaction term between treatment and period, since this would indicate the importance of mink removal in June on nest survival. We expected binomial distribution of dependent variable (nest survival, Aebisher, 1999). Best models were chosen using backward elimination of non-significant terms. The significance of particular term adjusted for the effects of other terms was based on the change in deviance between the full and reduced models, distributed as χ^2 (overdispersion ~ 1) with degrees of freedom equal to the difference in the degrees of freedom between the models with and without the term in question. Analyses were performed using R 2.4.0 statistical package.

Results

A total of 200 simulated nests with eggs were arranged in two periods, 52 (26%) of all the simulated nests were depredated mainly by mammals (20%) followed by avians (4%). Nevertheless, we were not able to distinguish between mammalian and avian predators in most predation events (40%). Mink depredated 6 nests (60% of the nests destroyed by mammals) within 15 days of exposure in June (before mink removal) and none nest in July (after mink removal). However the amount of determined nests was only minor.

In total 8 American mink individuals were removed during two-week-long trapping period.

Total nest survival was 74%. There was a slight seasonal increase in nest survival from 66% in June to 81% in July (effect of season: $\chi^2 = 3.20$, $p=0.07$, slope = 1.78 ± 0.55). Nest survival in transects with mink removal was similar to those with mink retained (effect of treatment: $\chi^2 = 0.11$, $p=0.76$, slope = 0.69 ± 0.39). However, there was a significant treatment:date interaction ($\chi^2 = 11.44$, $p=0.001$, slope = -2.17 ± 0.69) indicating opposite effect of season in transects with July mink removal and those with mink retained.. Whereas the nest predation in control transects slightly increased from June to July, an opposite effect of season, i.e. decrease in nest predation was apparent in treatment transects (Fig. 1).

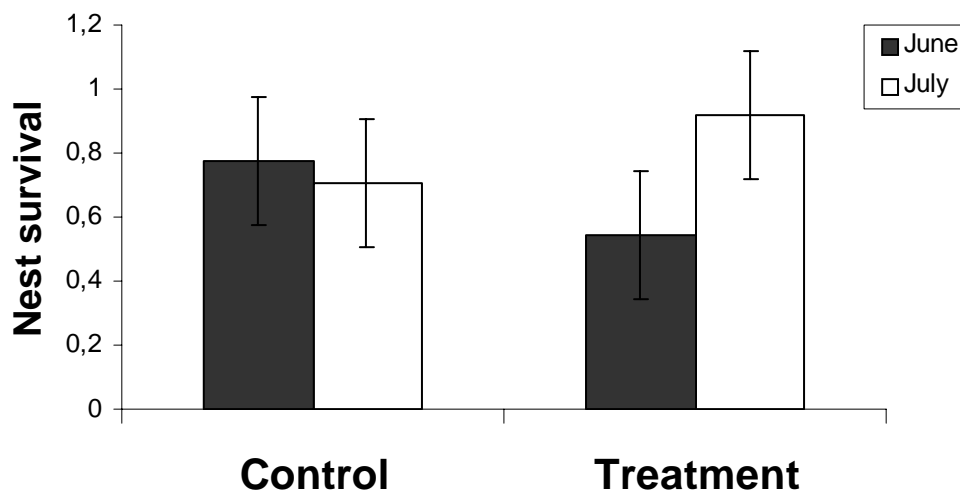


Figure 1. Survival of simulated nests in two transect types in June and July, Czech Republic, 2005.

Discussion

There still exist strong disagreement among authors that found clear experimental documentation that trapping and removing can effectively reduce nest predation (Rohwer et al. 1997, Kauhala 2004, Nordström et al. 2002) and authors that argued that even long-term predator removal did not enhance breeding numbers of target birds (Côté and Sutherland 1997, Meckstroth and Miles 2005).

We were able to detect a significant effect of short time mink removal on nest success of simulated nests placed in linear riparian habitats. We observed better nest success in transects after mink removal, whereas nest success remained similar in transects with mink present (Fig. 1).

This can indicate that mink was the only serious predator in given area, although we directly identified only 6 nests depredated by mink (see Results). But there is a big threat that compensatory predation by other species appears if smaller plots of land are used (Rohwer et al. 1997). Furthermore, local removal of target predator may release free place, which conspecific or interspecific competitors may quickly complete (Henke and Bryant 1999). Thus, limiting removal to only one species of predator, even if that species is major nest predator, usually not improve total nest success (Norrdahl and Korpimäki 1995). Kauhala (2004) have not found in his experiment the desired effect on breeding success of birds after removing only one predator like the introduced raccoon dog *Nyctereutes procyonoides* in Finland. We think that this might be also the case in our study, but we just started the second period of nests experiment right after the mink removal, so the remaining predators did not have the needed time to replace mink.

Waterfowl researchers who have seen substantial improvements in nest success after predator removal (Rohwer et al. 1997, Kauhala 2004, Nordström et al. 2002) concur that determinantal point to predator density reduction is the using of large treatment areas and keeping area predator-free with effective game-keeping. In this way a drastical increase in breeding densities of some smaller species may arise, but there was observed no improvement in breeding numbers of the populations of larger waterfowl species (Nordström et al. 2002). In later study, Nordström et al. (2003) found that mink removal increased the breeding densities of many birds species (e.g. seabirds, waders and passerines) living in archipelagos with many small islands. Kauhala (2004) observed the breeding success of ducks in Finland after removal of medium-sized predators like raccoon dog, red fox, pine marten and American

mink. Positive effect of marten and fox removal on predator numbers and the breeding densities of waterfowl was found in most parts of Finland.

In contrast, even long-term predator removal did not have the desiderative effect. Meckstroth and Miles (2005) admitted that removal areas had higher nest densities, but lower hatching success than reference sites. Sidorovich (1993) warned that when the population density decreases, the reproductive rate escalates. Consequently, nor a single strong one-season-long trapping pressure cannot considerably reduce predator density in given area.

Nevertheless, it is still not clear whether introduce of alien species of predators may have a negative impact on the breeding success or behavior of water birds. Direct relationship seems to exist between duck nest failure and presence of introduced species (Ferrerias and Macdonald 1999, Nordström and Korpimäki 2004), although few researchers (Bartoszewicz and Zalewski 2003, Kauhala 2004) did not found negative impact of some introduced predators on the breeding densities. Ferrerias and Macdonald (1999) have reported that mink presence significantly affected the density of breeding coots and the number of chicks hatched per pair of coots. Nordström and Korpimäki (2004) found that the presence of mink affected the distribution of species richness and abundance in birds. Colonies of birds had retreated to more isolated islands, which are not visited by mink as often as less isolated ones.

Artificial nest predation may not always correspond to the actual rate of predation on natural nests (Loiselle and Hoppes 1983). Some earlier studies concur that the artificial nests suffered significantly lower predation rates than real nests (Martin 1987, Dion et al. 1999, 2000), but in our study we did not measure the natural nest predation rate, therefore we are not assessing this factor. We used artificial nests for identifying nest predators (Bayne et al. 1997) and investigation of relative treatment effect (Dion et al. 2000, Martin 1987).

Trapping seems to be the most widespread and successful method for mink eradication (Bonesi et al. 2007). We suggest that short-time mink trapping could increase nest survival of simulated nest. Bonesi et al. (2007) demonstrated that to keep mink at endurable densities, at least 3 month mink removal is necessary every year. Important is not only total trapping effort in target areas but also mink eradication in peripheral areas to prevent individual immigrants from neighbour non-controlled populations. Local reduction of mink populations could be short time effective tool for conservation of protected species, but long term eradication management is needed.

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Predation on simulated duck nests in relation to nest density and habitat type

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Abstract

We tested whether predation rate depends on nest density (density-dependent predation), and mammals are main predators in forest, whereas birds predominate as predators in open-field areas. We used simulated nests for identifying nest predators, and for investigation of relative treatment effect (low vs. high-density patches). Nests were deployed in open area or forest by 48 ponds in Czech Republic, in June and July 2005-2006. There was only a little variance between nest survival of solitary nests and nests placed in high-density plots (NS = 63% and 60%, respectively). We found no evidence of density-dependent predation on simulated waterfowl nests in both habitat types. Mammalian predators were considered as the most important cause of nest failure in our study, followed by birds. Nevertheless, there was a significant habitat type:predator type interaction, indicating that mammalian predators preferred simulated nests deployed in forest, conversely, we detected little difference in frequency of predation between birds and mammals in open-field areas.

Key words: density-dependent predation, simulated nests, Czech Republic, nest predators, nest success

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Introduction

Nest predation belongs to the most important factor affecting the populations of many waterfowl species (Klett et al. 1988, Ricklefs 1969, Martin 1995). By this fact many strategies and adaptations were created to decrease nest failures: nest habitat change (Nordström and Korpimäki 2004), reduction of clutch size (Julliard et al. 1997), concealment of nests (Scheick and Hannon 1993) or spacing nest away from nesting neighbors (Martin 1988).

Habitat fragmentation, local habitat condition or high food availability could be one of the recent reasons for duck nesting in higher density patches. Waterfowl may feel constrained to nest in higher densities in small patches caused by dispersion of agriculture land replacing natural grassland (Kantrud 1993, Larivière and Messier 1998, Pasitschniak-Arts and Messier 1995). Thereafter these high concentrations of nests serve to predators as profitable storage of easily accessible resources. Thus, populations of birds nesting in high densities are exposed to higher nest predation (Nams 1997). Density-dependent predation is linked with the area restricted predator search (Larivière and Messier 1998) or numerical response of predator community to aggregated nesting patches (Holt 1977).

Nest predators might be able to recognize high density patches and can alter they spacing-use pattern (Larivière and Messier 1998). Larivière and Messier (2001) showed that striped skunks (*Mephitis mephitis*) exposed to high density patches significantly reduce their home range sizes and activity pattern. Locally, nest predators could increase searching within restricted area after finding clutch site which might lead to the nearest neighbour effect regardless of the overall nesting density in habitat patches.

Nest predation can also depend on the interactive effect of habitat and predator type. Some predation studies reported that mammals are more important (Bellebaum 2002, Pasitschniak-Arts and Messier 1995), although both mammalian and avian predators can be involved (Opermanis et al. 2001, Poledník and Poledníková 2005). Further, mammals often caused death or injury of the incubating female duck after predation attacks (Sargeant and Raveling 1992), unlike many avian predators. Mammals particularly use their olfactory scent to find a food resource (Nams 1997), so they are able to depredate nests in denser vegetation or in forest (Dion et al. 2000, Bayne et al. 1997). On the other hand, birds primarily detect nests in open areas with shorter vegetation (Dion et al. 2000) or in idle pasture (Pasitschniak-Arts and Messier 1995) as they rely on vision for detecting nests.

Herein, we assume that: i) high density of nest might attract more predators to the restricted area (density-dependent predation) and ii) mammals are primary predators in forest habitats whereas birds mainly predate in open areas.

Methods

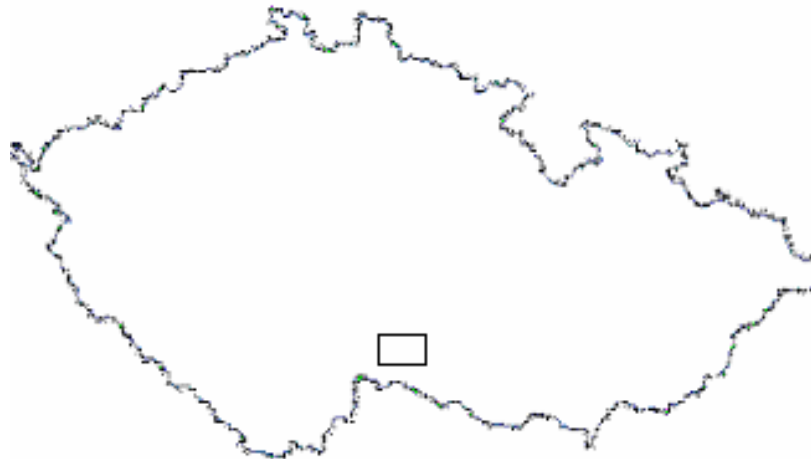
STUDY AREA

Our study area was situated in the Dačicko microregion (Dačice 49°3′ N, 15°26′ E), which forms part of the largest and the least populous district of the Czech Republic (Map 1). This region has gently rolling topography (with altitudes ranging from 400 to 700 m.a.s.l.) and is characterised by intensively cultivated agricultural land (47%) with high share of forest (20%).

Numerous various ponds occur throughout the area (about 100 ponds/100 km²). Ponds range in size from 0.01 to 10 ha (on average 1.3 ha) and their depth does not exceed 2 m. Most of the ponds is managed for commercial fish production (most common breeding species are *Cyprinus carpio* and *Tinca tinca*).

The climate is terrestrial with mild summers (mean temperatures 11 – 14°C) and cold winters (mean temperatures -1 – 1 °C). Mean annual rainfall is 600 – 750 mm.

The main predators in the study area are American mink (*Mustela vison*), martens (*Martes foina*, *Martes martes*), red fox (*Vulpes vulpes*), wild boar (*Sus scrofa*), polecat (*Putorius putorius*) and corvids (*Pica pica*, *Garrulus glandarius*, *Corvus corone*).



Map 1. Location of study area in the Dačicko microregion in Czech Republic, central Europe.

DESIGN OF THE NEST EXPERIMENT

We chose 48 ponds surrounded either with open land or forest to examine the effect of different types of adjacent habitats on predation patterns. The distance to the nearest monitored neighbour ponds were minimally 300 meters. Within each site we selected one 10 x 10 m plot for the placement of simulated nests. All plots were located in areas of similar vegetative structure and composition in suitable nest locations.

SIMULATED NESTS

Simulated nests containing chicken eggs were used to emulate waterfowl nests (Larivière and Messier 1998). Simulated waterfowl nests were constructed from local natural vegetation by pressing the vegetation together to form a shallow cup (Jobin and Picman 1997). Each nest was lined with duck feathers to represent animal scent (Guyn and Clark 1997). Each nest was placed on the ground in vegetation in such a way to simulate the location of natural nests. Two chicken eggs were inserted in each nest: fresh egg was freely placed in the cup while wax-filled egg was fixed to the ground by a string. Wax-filled eggs were used to help us detect and identify predators from beak or teeth imprints (Dion et al. 2000). Fresh eggs served as a reward for predators. We were wearing rubber boots and gloves while manipulating with nests and eggs to reduce human scent (Dion et al. 1999).

For testing density dependent predation 2 patterns of quadrates (10 x 10 m) were formed. High density patch was composed of 5 nests, whereas low density quadrates included only one nest. We compared predation rate at foreordained nests placed in the middle of the quadrates (*target nests*), ad hoc we mounted number of nests to 5 in high density patches (i.e. 24 ponds with low density of 1 nest within quadrat and 24 ponds with high density of 5 nests within quadrat, respectively). To minimize the difference in amount of human scent, the pathway was walked in the areas of low density in the same way as in the areas of high density.

Nests were placed in the 2 quadrate types on the same date and were checked at 5-day intervals, for a total period of 15 days. Depredated nests were removed from the sites. A nest was considered depredated when at least one egg was missing or destroyed or if marks of predator were left on the wax eggs (Dion et al. 1999, Larivière and Messier 1998). The experiment was divided into two periods during June and July 2005 with 14-day break to

mimic the nesting waterfowl season. The experiment was repeated in 2006 with the same methods.

PREDATOR IDENTIFICATION

Egg remains, appearance of the nest and mainly beak and teeth marks left in the wax eggs allowed us to categorized predators as avian or mammalian. Tooth imprints of mammalian predators were determined by comparison to skull dentice from mammalian collection of Faculty of Biological Sciences, University of South Bohemia. Bill marks attributable to avian predators (mostly corvids) were not assigned to species. Predated nest by rodents were excluded from the analysis because they were not considered as relevant predators of waterfowl nests. Predator identity remained unknown when the wax egg had disappeared or was either untouched.

STATISTICAL ANALYSIS

We used generalized linear mixed effect model approach (GLMM) to evaluate the effect of increased nest density on nest survival (Mayfield 1961, 1975). In the analysis, the temporal replicate (June, July), habitat type (forest, open) and treatment (high density, solitaire nest) were treated as categorical predictors, and each year-locality combination (96 in total) was treated as random effect. In addition, we performed the same analysis using target nest survival only as the dependent variable (for definition of target nests see above). We expected binomial distribution of dependent variable (nest survival, Aebisher, 1999). Best models were chosen using backward elimination of non-significant terms. The significance of particular term adjusted for the effects of other terms was based on the change in deviance between the full and reduced models, distributed as χ^2 (overdispersion ~ 1) with degrees of freedom equal to the difference in the degrees of freedom between the models with and without the term in question. Analyses were performed using R 2.4.0 statistical package.

Differences in the proportion of high-density patches where minimally 2 nests were depredated versus only 1 nest depredated (nearest neighbour effect) in one 5 day exposure interval was analysed for each predator type (mammal, bird) using difference test in Statistica

6.0 (StatSoft Inc. 2000). Using only depredated target simulated nests, we tested the effects of predator type (mammal, bird), treatment (high density, solitaire nest), habitat type (forest, open) and their interactions by log-linear analysis of frequency tables in Statistica 6.0 (StatSoft Inc. 2000). We performed all analysis using two-tailed tests. Proporcional graphs were done in Microsoft-Excel (Microsoft corporation 1985-2001).

Results

During both years, 576 simulated nests with eggs were installed at the 48 study areas. Only nests placed in the middle of the plots both with low and high density (n=192) were included in statistical analysis (target nests). Of those, 36% (n=69) of target nests were depredated, mainly by mammals (52%) followed by avians (29%) (effect of predator type: $\chi^2=10.87$, $df=2$, $p=0.004$, Table 2). We were not able to distinguish between mammalian and avian predators in 19% cases. Among identified mammal predators (n=36), wild boars *Sus scrofa* was most common (33%), followed by American mink *Mustela vison* (22%), polecats *Mustela putorius* (17%) and red foxes *Vulpes vulpes* (11%).

Total nest survival was 38%. There was only a little variance between nest survival of solitaire nests and nests placed in high-density plots (NS = 63% and 60%, respectively). We found no evidence of density-dependent predation on simulated waterfowl nests in both habitat types ($\chi^2=2.53$, $df=1$, $p=0.112$). Nevertheless, there was a significant temporal replicate effect ($\chi^2=10.4$, $df=1$, $p=0.001$), and habitat type:temporal replicate interaction ($\chi^2=6.609$, $df=1$, $p=0.01$) indicating that predation pattern was changing during the season between June and July differently in forest and differently in open-field areas (Table 1). Although initial nest predation rates were quite similar in both habitat types, an evident decrease in nest predation was observed in open-field areas from June to July, whereas an decrease in nest predation was not so apparent in forest habitat (Fig.1).

Table 1. Results of GLMM (binomial error, random effect: year-locality combination, 96 in total). Terms included in the minimal adequate model are indicated (MAM, Crawley 2002). MAM: $\chi^2=20.84$, $df=4$, $p=0.00034$.

Tested characteristics	<i>DF</i>	<i>Chi-square</i>	<i>p</i>
1	1	10.4	0.001
2	1	1.786	0.181
3	1	2.137	0.144
12	1	6.609	0.01
13	1	0.12	0.729
23	1	2.528	0.112
123	1	0.158	0.691

Tested characteristics: 1 – temporal replicate (June, July), 2 – habitat type (forest, open), 3 – treatment (high-density, solitaire nest); *DF* – degrees of freedom; *p* – probability. The effect of temporal replicate ($p < 0.05$) and interaction between temporal replicate and habitat type ($p < 0.05$) were significant.

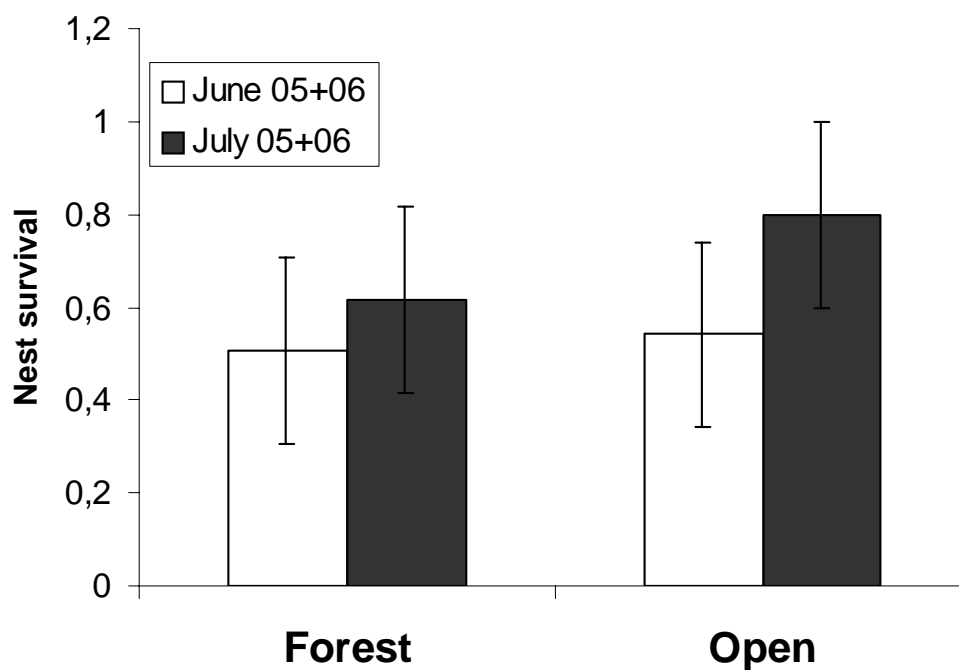


Figure 1. Survival of simulated waterfowl nests in two types of nesting habitat, Czech Republic, 2005-2006.

Nearest neighbour effect was observed only for nests depredated by mammals ($p=0,0031$). Once we tested the interactions between effects (Table 2), different predators depredated nests in different treatment ($\chi^2=10.49$, $df=2$, $p=0.005$) and habitat type ($\chi^2=9.48$, $df=2$, $p=0.009$). Both mammalian and avian predators plundered simulated nests similarly in high-density patches whereas solitaire nests were depredated mainly by mammals (Fig. 2). Mammalian predators also significantly preferred simulated nests deployed in forest, conversely, we detected little difference in frequency of predation between birds and mammals in open-field areas (Fig. 3).

Table 2. Results table of log-linear analysis of contingency tables (marginal association only) – individual significant test characteristics and their interactions.

Tested characteristics	DF	Chi-square	p
1	1	0.013	0.908
2	1	0.334	0.564
3	2	10.873	0.004
12	1	0.126	0.723
13	2	10.486	0.005
23	2	9.477	0.009

Tested characteristics: 1 - treatment (high-density, solitaire nest), 2 – habitat type (forest, open), 3 - predator type (mammal, bird); DF – degrees of freedom; p – probability. The effect of predator type ($p < 0.01$), interaction between treatment and predator type ($p < 0.01$) and interaction between habitat type and predator type ($p < 0.01$) were significant.

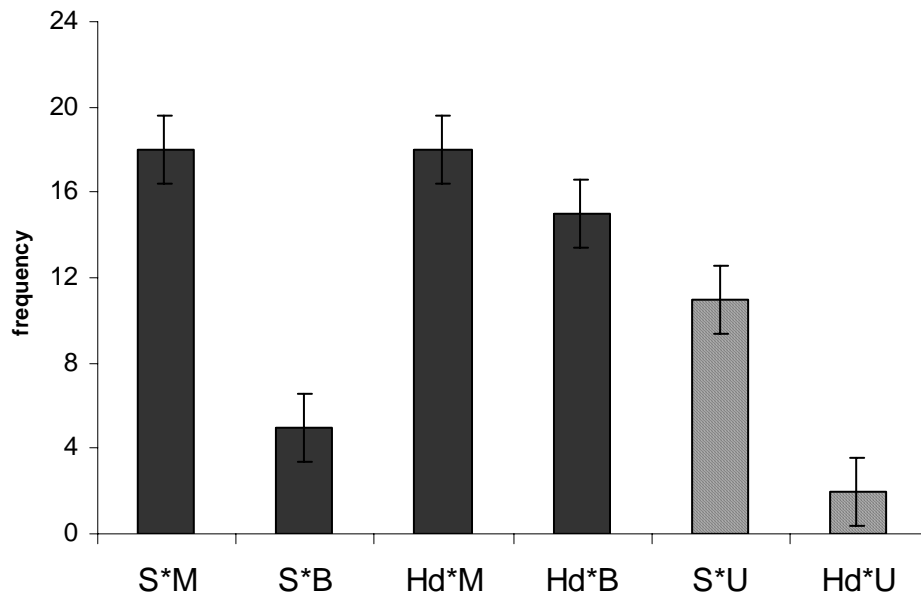


Figure 2. Frequency of predation events according to interaction of treatment and predator type. Treatment: S – solitaire nest, Hd – high-density; predator type: M – mammal, B – bird, U – unknown.

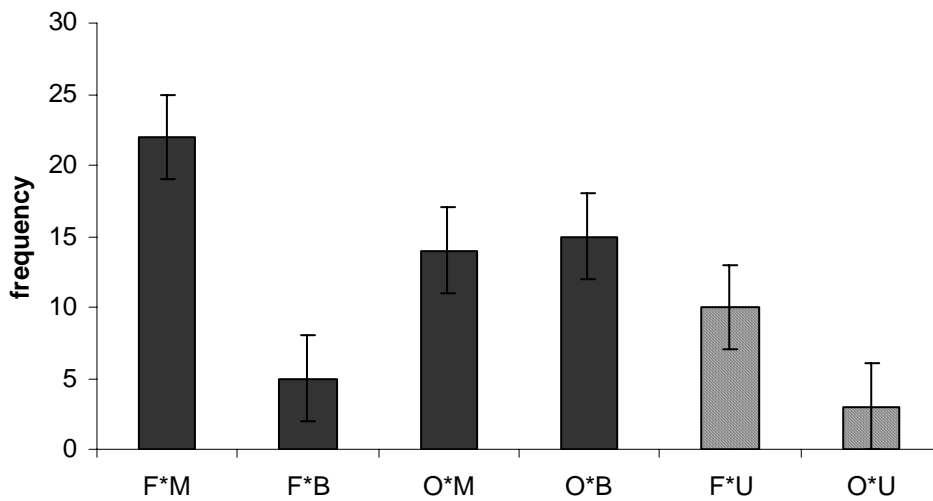


Figure 3. Frequency of predation events according to interaction habitat type and predator type. Habitat type: F – forest, O – open area; predator type: M – mammal, B – bird, U – unknown.

Discussion

Based on nest survival, we observed little difference between the two density types (63% vs. 60% for nests in low and high density plots, respectively). Nests placed within high density patches have higher probability of being found than a nest being placed alone in the area of the same size. For example, when a predator searching for food item crosses the area with high nest density, it has a five-time higher chance to meet the nest. Furthermore, the five-times more intensive parental activity (for predators relying on vision) (Roper and Goldstein 1997) and animal odor (for scent-oriented predators) at real nests may attract more predators (Nams 1997). This might lead to higher predation rate in higher prey-density areas. Although some researchers maintain that predation is density dependent (Larivière and Messier 1998, Nams 1997, Esler and Grand 1993, Elmberg et al. 2005), our results correspond to surveys (Ackerman et al. 2004, Duebbert and Lokemoen 1976) that show no relationship between predation rate and nest density among patches.

The decisive difference between predation events caused by mammals and birds was observed only on solitary nests, whereas nests deployed in high-density patches suffered similar attacks by both types of predators (Fig. 2). Importance of density and so nearest neighbour effect might depend on type of nest predator or also distance between deployed nests (Tuda 1993). With decreasing distance between nests, predation risk might increase. Larivière and Messier (1998) demonstrated that probability of neighbour nest depredation was frequent in high and intermediate density in contrast with rate in low density patches. We presume that our project design (5 nests within 10 sq. meters in high density blocks) might be attractive for predators exhibit area-restricted searching. Our results confirm that cluster of nests might effect area restricted searching by mammalian predators. Hoi and Winkler (1994) revealed that predation of neighbour nest close by increased in aggregated clutches. Furthermore, depredated nests could offer olfactory and visual cues (i.e., broken eggshells, exposed yolk), which may cause nearest neighbor effects by attracting different predators of the same or different species (Wada 1994).

Predators were presented with the ability to recognize high-density nesting patches (Larivière and Messier 1998) and the formation of long-term search images (Nams 1997). These characteristics allow them to use high-density patches as profitable food resources, even though mammalian predators depredate nests opportunistically (Larivière and Messier 1997a). Furthermore, Larivière and Messier (1998) found that density effect in simulated as

well as in natural nests occurred in the late nesting season, but no significant effect was recorded in the early nesting season. This can indicate that predators needed some time to recognize high nest density patches and form search image, which then led to increase in patch use over the next few days. But our result (significant temporal replicate effect) differs with this conclusion since we observed apparent decrease in nest predation from June to July (Fig. 1). Although artificial nest predation may not always correspond to the actual rate of predation on natural nests (Loiselle and Hoppes 1983), the results of studies testing density dependence with both nest types (Ackerman et al. 2004, Butler and Rotella 1998, Wilson et al. 1998, Buler and Hamilton 2000) indicate that simulated nests can be used for finding comparable patterns of nest predation.

Our data show significant interaction between temporal replicate and habitat type (Table 1). Rapid increase in nest survival in open-field areas in July may be caused by changes in vegetative characteristics during season. Taller vegetation may result in lower predation rates when main predators are birds (Hill 1984). Moreover, high and dense cover could impede in foraging exploring of small mustelid species and may lead to higher exploitation of vegetation sparse patches or habitat edges. Actually, Šálek et al. (in prep.) revealed that mustelid predators use significantly more frequently habitat edges than littoral zone or uniform grassland habitats.

We found mammalian predators to be the most important cause of nest failure in our study. Birds can equal mammals in predation rate in open-field areas, since type of predator interacted with habitat type (see Results). Birds significantly preferred open areas with shorter or less dense vegetation cover because avians rely on visual cues while foraging for prey item (Sullivan and Dinsmore 1990). Pasitschniak-Arts and Messier (1995) identified mammals as the major predators in the three of four habitat types as delayed hay, dense nesting cover and rights-of-way, contrast to idle pasture where avian predation was higher. Similar to our results, mammals were with birds comparable predators of simulated nests placed in open-field areas, but they depredated unequivocally more nests in forest habitat. Bayne et al. (1997) showed mammals as the major predators on artificial nests in numerous forest types. Differences in predation rates among habitat types caused by mammals may be imputed to diversity of local predator community. The only mammalian predator, polecat *Putorius putorius*, preferred open areas for detecting nests. In contrast, wild boars as the major mammalian predators in our study, with one exception caused nest failure in forest habitats. Similarly, other main predators as red foxes and American minks predominantly depredated nests in forest.

Finally, our findings provide no evidence for density dependent predation on simulated waterfowl nest. In contrast to avian predators, mammals exposed to aggregated nest cluster showed trend to area restricted searching. For detail understanding if high nest density patches may lead to functional (area restricted searching) or numerical (attraction of more predators) response of predators more research is needed.

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