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Dynamics of rodent abundance and ground-nest predation risks in forest habitats of Central Europe: no evidence for the alternative prey hypothesis

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Abstract. Birds' nesting success may vary significantly between years. Ample evidence exists that this variation is caused by temporal fluctuations in rodent populations, as rodents are important components in the diets of nest predators. The alternative prey hypothesis supposes that generalist predators switch to alternative prey (bird nests) when their main prey (rodents) is lacking, thus causing increased nest predation. According to the shared predation hypothesis, by contrast, predator density is enhanced at rodent population peaks and results in simultaneous increase in main and alternative prey predation. To evaluate these hypotheses, nest predation rate dynamics were examined using artificial nests ($n = 560$) and rodent abundance (2240 traps) during four breeding seasons in Central European (the Czech Republic) secondary forests. Although rodent abundance increased at the population peak by almost seven times compared to the baseline and nest predation rate also showed significant inter-year variation, the data support neither the alternative prey nor shared predation hypotheses. In rich ecosystems with complex trophic levels, predators can use many resources as alternative prey. Therefore, bird nest predation risk does not increase or decrease in periods of low rodent abundance.

Key words: edge effect, generalist predators, shared predation hypothesis, prey distribution

Introduction

Nest predation is one of the main factors limiting the reproductive success of birds (Ricklefs 1969, Wegge & Storaas 1990, Martin 1995, Kauhala & Helle 2002). This source of mortality may exhibit significant inter-year variation (Summers 1986), although causes of these temporal fluctuations are poorly understood. It has been proposed that between-year variation in the nest predation rates is causally associated with temporal fluctuations in abundance of small mammals (i.e. voles, *Microtus* spp. and lemmings, *Lemmus* spp.; Bêty et al. 2001, Ackerman 2002), which constitute an important dietary component of many nest predator species. For instance, small mammals (including rodents) may comprise up to 70 % of food sources for some mammalian mesopredators, such as foxes, martens and weasels (Jędrzejewska & Jędrzejewski 1998, Martinoli et al. 2001, Panzacchi et al. 2008). Nevertheless, the effects on nest predation from the interplay of fluctuations in small rodents, foraging strategies and demographic responses of predators are

rather complex. One particular possible explanation, the so-called “shared predation hypothesis” (Norrdahl & Korpimäki 2000, Reif et al. 2004), assumes that predators increase in abundance when rodent density is peaking (Bêty et al. 2002) due to their increased survival and/or reproductive output (Tannerfeldt & Angerbjörn 1998) and because of migration to areas of high prey density (Korpimäki 1994). Consequently, the increase in predator abundance leads to a higher predation rate not only on the main prey (such as small rodents, i.e. those inducing the numerical response) but also on secondary prey (Norrdahl & Korpimäki 2000, Reif et al. 2004). Although this scenario may logically apply also for bird clutches, only a few studies report positive relationships between nest predation rates and rodent density (Table 1). Increases in predator abundance due to migration are expected to have immediate effect on predation risks for secondary prey. However, predation increases on secondary prey are likely to be delayed in comparison to the rodent peak if shared predation is induced via higher survival

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Table 1. Studies directed to testing the alternative prey hypothesis (APH). Studies were searched using the Web of Science, Scopus, ScienceDirect and Springer Link databases with various combinations of several keywords: “alternative prey hypothesis”, “nest predation”, “rodent” or “lemming cycle”, “bird-lemming hypothesis”. A total 43 studies were found based on these parameters and evaluated. Studies not focused on nest success of ground-nesting birds and population fluctuations of small mammals (rodents, lagomorphs) were excluded. In addition, studies not providing data (or information as to the source of data) on small mammal abundance were not considered.

Source	Location	Main prey	Secondary prey	Predator	Latitude	Duration	APH*
Ackerman 2002	California	<i>Microtus californicus</i>	<i>Anas platyrhynchos</i>	<i>Mephitis mephitis</i>	38°14' N, 121°97' W	3 years	supported
Angelstam et al. 1984	Sweden	<i>Lepus timidus</i>	<i>Tetrao tetrix</i>	<i>Vulpes vulpes</i>	59°40' N, 15°25' E	5 years	supported
Béty et al. 2001	Canada	<i>Lemmus sibiricus</i> , <i>Dicrostonyx</i> <i>groenlandicus</i>	<i>Anser caerulescens</i> <i>atlanticus</i>	<i>Alopex lagopus</i> , <i>Larus hyperboreus</i> , <i>Stercorarius parasiticus</i> , <i>Corvus corax</i>	72° 53' N, 78°55' W	7 years	supported
Blomqvist et al. 2002	Sweden	<i>Lemmus sibiricus</i> , <i>Dicrostonyx torquatus</i>	<i>Calidris canutus</i> , <i>Calidris ferruginea</i>	<i>Alopex lagopus</i>	56°12' N, 16°24' E	50 years	supported
Brook et al. 2005	Canada	small mammals, <i>Lepus americanus</i>	<i>Aythya affinis</i> , <i>Anas platyrhynchos</i>	<i>Vulpes vulpes</i> , <i>Mustela vison</i> , <i>Corvus corax</i> , <i>Accipiter gentilis</i> , <i>Circus cyaneus</i> , <i>Bubo virginianus</i>	62°26' N, 114°23' W	10 years	supported
Haselmayer & Jamieson 2001	New Zealand	<i>Oryzotylagus cuniculus</i>	<i>Porphyrio porphyrio</i>	<i>Circus approximans</i> , <i>Mustela furo</i> , <i>Felis catus</i> , <i>Mustela erminea</i>	45°52' S, 170°30' E	5 years	supported
Iles et al. 2013	Canada	small mammals	<i>Somateria mollissima</i>	<i>Alopex lagopus</i> , <i>Larus smithsonianus</i>	58°43' N, 93°24' W	41 years	unsupported
Kostin & Mooij 1995	Russia	<i>Lemmus sibiricus</i> , <i>Dicrostonyx torquatus</i>	<i>Branta ruficollis</i>	<i>Alopex lagopus</i>	71°23' N, 90°14' E	7 years	supported
Lecomte et al. 2008	Canada	<i>Lemmus sibiricus</i> , <i>Dicrostonyx</i> <i>groenlandicus</i>	<i>Anser caerulescens</i> <i>atlanticus</i> and artificial nests	<i>Vulpes lagopus</i> , <i>Stercorarius parasiticus</i> , <i>Larus hyperboreus</i> , <i>Corvus corax</i>	72°53' N, 79°54' W	11 years	supported
Marcström et al. 1988	Sweden	<i>Clethrionomys glareolus</i> , <i>Sorex araneus</i> , <i>Microtus agrestis</i> , <i>M. oeconomus</i>	<i>Tetrao urogallus</i> , <i>Tetrao tetrix</i> , <i>Bonasa bonasia</i> , <i>Lagopus lagopus</i>	<i>Vulpes vulpes</i> , <i>Martes martes</i> , <i>Corvus cornix</i> , <i>C. corax</i> , <i>Garrulus glandarius</i>	66° N	9 years	supported

McKinnon et al. 2013	Canada	<i>Dicrostonyx groenlandicus</i> , <i>Lemmus trimucronatus</i>	<i>Chen caerulescens atlantica</i> and artificial nests	<i>Alopex lagopus</i> , <i>Larus hyperboreus</i> , <i>Stercorarius parasiticus</i> , <i>Corvus corax</i>	72°53' N, 78°55' W	3 years	supported
Nolet et al. 2013	Russia	<i>Lemmus sibiricus</i> , <i>Dicrostonyx torquatus</i>	<i>Branta bernicla bernicla</i>	<i>Alopex lagopus</i> , skuas and gulls	74°08' N, 86°44' E	48 years	supported
Perkins et al. 2007	Canada	<i>Lemmus</i> spp., <i>Dicrostonyx</i> spp.	<i>Arenaria interpres</i>	<i>Alopex lagopus</i> , <i>Stercorarius parasiticus</i>	64°01' N, 81°47' W	4 years	supported
Reiter & Andersen 2011	Canada	<i>Dicrostonyx richardsoni</i>	<i>Branta canadensis interior</i>	<i>Alopex lagopus</i>	58°34' N, 93°11' W	12 years	unsupported
Summers & Underhill 1987	Russia	<i>Lemmus sibiricus</i> , <i>Dicrostonyx torquatus</i>	<i>Branta bernicla</i> , <i>Calidris alba</i> , <i>C. ferruginea</i> , <i>Arenaria interpres</i>	<i>Vulpes vulpes</i> , <i>Martes martes</i> , <i>Mustela erminea</i> , <i>Meles meles</i>	72° N 96' E	18 years	supported
Syroechkovskiy et al. 1991	Russia	Lemmini	<i>Anser fabalis rossicus</i> , <i>Branta leucopsis</i> , <i>Anser albifrons</i> , <i>Cygnus columbianus bewickii</i>	<i>Alopex lagopus</i>	70°15' N, 58°47' E	3 years	supported
Šálek et al. 2004	Czech Republic	<i>Apodemus flavicollis</i> , <i>Clethrionomys glareolus</i> , <i>Microtus agrestis</i>	artificial nests	<i>Vulpes vulpes</i> , <i>Martes martes</i> , corvids	50°40' N, 13°36' E	2 years	supported
Underhill et al. 1989	Russia	<i>Lemmus sibiricus</i> , <i>Dicrostonyx torquatus</i>	<i>Calidris canutus</i>	<i>Alopex lagopus</i>	74°00' N, 98°00' E	19 years	supported
Wegge & Storaas 1990	Norway	<i>Apodemus sylvaticus</i> , <i>Clethrionomys glareolus</i> , <i>Microtus agrestis</i> , <i>Myopus schisticolor</i> , <i>Lepus timidus</i>	<i>Tetrao urogallus</i> , <i>Tetrao tetrix</i>	<i>Vulpes vulpes</i> , <i>Martes martes</i> , <i>Mustela erminea</i> , <i>Meles meles</i> , <i>Garrulus glandarius</i>	60°10' N, 12°30' E	8 years	supported
Wilson & Bromley 2001	Canada	<i>Dicrostonyx groenlandicus</i> , <i>Lemmus trimucronatus</i>	<i>Anser albifrons frontalis</i> , <i>Branta canadensis hutchinsii</i>	<i>Alopex lagopus</i> , <i>Larus hyperboreus</i> , <i>Stercorarius parasiticus</i>	68°21' N, 108°05' W	9 years	supported

APH* supported/unsupported, i.e. negative correlation/positive relationship between rodent abundance and nest predation.

rates and reproductive output in predators (Korpimäki et al. 1991).

The alternative, mutually exclusive scenario to shared predation is the “alternative prey hypothesis” (Angelstam et al. 1984). This indicates that increased main prey abundance results in decreased predations on such secondary prey as bird clutches due to the switching of predator foraging strategies (Wilson & Bromley 2001, Bêty et al. 2002, Korpimäki et al. 2005). Many mammalian mesopredators are primarily dependent on small mammals such as voles and lemmings (Ims & Fuglei 2005). If their main prey becomes scarce, they increase the breadth of their diet by using a limited amount of secondary prey (Bêty et al. 2001) and/or exploit habitats that would be suboptimal during rodent peaks (Norrdahl & Korpimäki 2005, Lecomte et al. 2008) in accordance with the predictions of the optimal foraging theory (MacArthur & Pianka 1966). The alternative prey hypothesis has mostly been tested in boreal and arctic ecosystems that are typified by low species diversity and low food web complexity consisting of 2-3 levels (Summers & Underhill 1987, Lecomte et al. 2008). However, the evidence for the alternative prey hypothesis seems rather weak at lower latitudes, which differ from boreal/arctic ecosystems in having greater prey diversity, more complex trophic cascades and, possibly, a less clear prey profitability hierarchy. The small number of pertinent studies as well as drawbacks associated with their experimental designs do not allow making any general assessment as to the validity of the alternative prey hypothesis at low latitudes. For example, only two studies have aimed at testing the alternative prey hypothesis in non-arctic/non-boreal parts of Europe (Saniga 2002, Šálek et al. 2004). Unfortunately, Saniga (2002) did not sufficiently assess main prey density and Šálek et al. (2004) examined changes in predation rate and rodent density during only two consecutive nesting periods and did not directly test the association between rodent densities and predation risk.

The aim of this study was to test the alternative prey and shared predation hypotheses based upon longitudinal data on temporal fluctuations in artificial ground-nest predation and rodent abundance in secondary forest habitats (forest edge and forest interior) in Central Europe (the Czech Republic). Although fluctuations in rodent numbers do not commonly occur in regular cycles within Central Europe, rodent populations nevertheless exhibit irregular yet pronounced spatial and temporal variation in this region (Tkadlec & Stenseth 2001). At the same time, previous research has

shown that both nest predation rates and mammalian predator activity fluctuate considerably between consecutive breeding seasons (Svobodová et al. 2011, Svobodová et al. 2012). The obtained data allowed for testing the main predictions of both the alternative prey hypothesis and the shared predation hypothesis. Whereas the alternative prey hypothesis predicts a negative relationship between nest predation rates and small rodent abundances, the shared predation hypothesis predicts a positive association between nest predation rates and rodent counts. Furthermore, since predators may increase their reproductive success in the year subsequent to the rodent peak, a positive relationship between predation rate and rodent abundance in the subsequent year would support the shared predation hypothesis with a one-year delay in predator response. To achieve greater robustness in the conclusion, assessment of both temporal variations in nest predation risk and small rodent abundance was undertaken in two dominant habitat types: forest edges and forest interiors.

Material and Methods

The study area was located in South Bohemia (the Czech Republic) in the Písecké Mountains region (49°11'-49°18' 14°09'-14°22', 350 m a.s.l., 60.3 km²), which is formed by a complex of production forest stands (45 % of the study area) surrounded by farmland. Coniferous and deciduous growths are typically dominated by spruce (*Picea abies*), pine (*Pinus sylvestris*) and beech (*Fagus sylvatica*). Mixed growths bordering the forest complex are mostly composed of such broadleaved species as oaks (*Quercus* spp.) and limes (*Tilia* spp.) along with coniferous trees from production stands. Since the forest growths are intensively cultivated, they are frequently interrupted by clearcuts, plantations and road networks. The surrounding farmland (53 % of the study area) consists mainly of hay meadows, pastures and cultivated fields that are regularly partitioned by woodlots and a network of narrow (i.e. > 10 m wide) linear strips of uncultivated vegetation (2 % of the study area; see Šálek et al. 2009 for more details), such as growths along drainage channels, windbreaks and roads.

Habitat types where the monitoring of nest predation and rodent densities took place were classified into two categories: 1) forest edges, and 2) forest interiors (places where the distance from the nearest forest edge = 100 m). Forest edges were usually fringed with oaks, limes, such trees from coniferous stands as spruces and pines, poplars (*Populus* spp.) and birches

(*Betula pendula*). The shrub layer was usually dense, consisting mainly of shrubs and saplings of canopy trees (hazels, *Corylus avellana* and blackthorns, *Prunus spinosa*). This habitat type was also characterized by dense and highly diversified herbaceous vegetation originating mainly from nearby meadows. The boundary between forest and adjacent habitats was sharp and clearly distinguishable. The tree canopies of forest interiors were typically dominated by conifers (spruces and pines) while broadleaved tree species such as oaks, birches and beeches formed occasional admixtures. Shrub and herbal undergrowth was very sparsely developed (Svobodová et al. 2012). Previous research had determined there to be a relatively broad community of potential nest predators inhabiting the study area (Svobodová et al. 2011, 2012). Carnivores include red fox (*Vulpes vulpes*), martens, Eurasian badger (*Meles meles*), and smaller carnivores from the family of mustelids (Mustelidae, *Mustela nivalis* and *M. erminea*). Avian nest predators present include carrion crow (*Corvus corone*), Eurasian magpie (*Pica pica*) and Eurasian jay (*Garrulus glandarius*). In addition, wild boar (*Sus scrofa*) has been shown to contribute markedly to predation on artificial ground clutches in the study area.

Artificial nests were constructed by digging small depressions in the ground and then lining these with small amounts of dry plant material. Each nest was baited with two brown chicken eggs (Yahner & Mahan 1996) to ensure against predation by small predators such as rodents (Picman 1988, Haskell 1995, DeGraaf & Maier 1996). One egg in the nest was filled with a mixture of beeswax and vegetable oil for the purpose of predator identification (Pasitschniak-Arts & Messier 1995). Each wax egg was anchored in the nest hole by a string and nail in order to prevent predators from carrying it away (Summers et al. 2004, Suvorov et al. 2012). In an earlier experiment conducted in exactly the same area, no differences had been found in predation between nests baited with quail versus chicken eggs (Svobodová et al. 2012), thus suggesting that artificial nest design has a low effect on experimental outcomes. Hence, we argue that the artificial nests used in this study may be representative for a heterogeneous group of ground nesting birds (e.g. Eurasian woodcock *Scolopax rusticola*, yellowhammer *Emberiza citrinella*, tree pipit *Anthus trivialis*) occurring in the Central European landscape.

Inter-year variation in the rate of nest predation was studied using artificial nests during breeding periods from 2006 to 2009. In 2006, 200 artificial nests were

installed. In the subsequent years, 120 nests were placed. Further, to evaluate the edge effect hypothesis, half of the artificial nests were placed at the forest edge (i.e. 5 m from the forest border into the forest interior) and half within the forest interior (100 m distant from the forest edge). The distance between two adjacent nests was > 300 m in 2006. During subsequent years, however, nest pairs (i.e. one edge nest and one interior nest) were placed in closer proximity (hereafter together referred to as a “location”). The distance between nests within individual pairs was > 100 m and the distance between pairs, similarly as in 2006, was > 300 m, in order to minimize the effect of spatial pseudoreplication (e.g. Gehring & Swihart 2003). While that variation in study design resulted in lower nest density during 2006 compared with the other seasons, it nevertheless can be assumed that this fact had minimal effect on the results of the experiment. Nests were always placed in the same locations during late April of each year. They were checked after 14 days of exposure, which is equal to the main nesting and incubation period of most bird species in the study area (Hudec & Štastný 2005). A nest was considered depredated when at least one of the two installed eggs was damaged, removed from the nest bowl or missing. Nest predators were identified according to beak or tooth marks left on the wax eggs (Nour et al. 1993) and were assigned to four categories: carnivore (red foxes, martens, small mustelids), bird, wild boar and unidentified predator (see Svobodová et al. 2012 for further details).

Rodent capture took place during the same period as did the artificial nest experiment. Common snap traps baited with wicks dipped in grease and flour were used (Heroldová et al. 2008). The traps were laid in lines of 35 traps each with the traps 5 m apart. The total length of each line was thus about 175 m. As were the artificial nests, the lines of traps were placed in the two habitat types: 1) forest interior and 2) forest edge at the same eight locations every year (64 lines with 2240 traps in total). To eliminate the potential effect of spatial pseudoreplication, the spatial distribution of capture lines followed the same rules as in the case of the artificial nest experiment (see above). Since snap traps were used whose efficiency can be affected by capture from the previous day, the traps were exposed in each location only for 24 hours.

Nest fate (survived/depredated, i.e. 0/1) after 14 days of nest exposure was included as a binary response variable into a general linear mixed effect model (GLMM, binomial distribution, logit link function) to evaluate variation underlying nest predation probability. Habitat type (i.e. forest edge or forest

interior) and year were included as categorical explanatory variables and location was included as a random effect.

The number of captured rodents vs. the number of empty traps in a given line (consisting of 35 traps) was included as a binomial response variable in the GLMM (binomial distribution of error, logit link function). As with the model above, habitat type, year and the interaction between these variables were fitted as fixed effects and the location was included as a random effect.

The best minimal adequate model (i.e. that model with the greatest parsimony and having all variables significant) was achieved by backward elimination of non-significant effects. The significance of a particular explanatory variable was calculated by the change in deviance (assuming a χ^2 distribution) between the model containing that variable and the reduced model (i.e. using likelihood-ratio tests; Crawley 2002). All analyses were performed in R 2.12.1 software (R Development Core team 2008). GLMMs were fitted using the lmer function implemented in the lme4 R package (Bates et al. 2012). The significance of between-year differences in rodent abundance and nest predation risk was assessed by Tukey's HSD test using the multcomp package (Hothorn et al. 2008).

To test for the existence of association between rodent densities and predation risk, subsequent analysis was restricted to nests that surrounded the lines of traps (max. distance from lines = 900 m, total n = 247). A different maximum distance cut-off was tested as well (max. distance = 400 m, n = 127), but this analysis provided identical results. The proportion of predated nests in a given location and in a given year was considered to be a response variable and the numbers of captured rodents (log transformed) to be an explanatory variable in the GLMM (binomial distribution of error, logit link function). Sampling sites and years were considered random intercepts and the relationship between predation risk and numbers of captured rodents at individual sites and in individual years to be random slopes. The same approach was

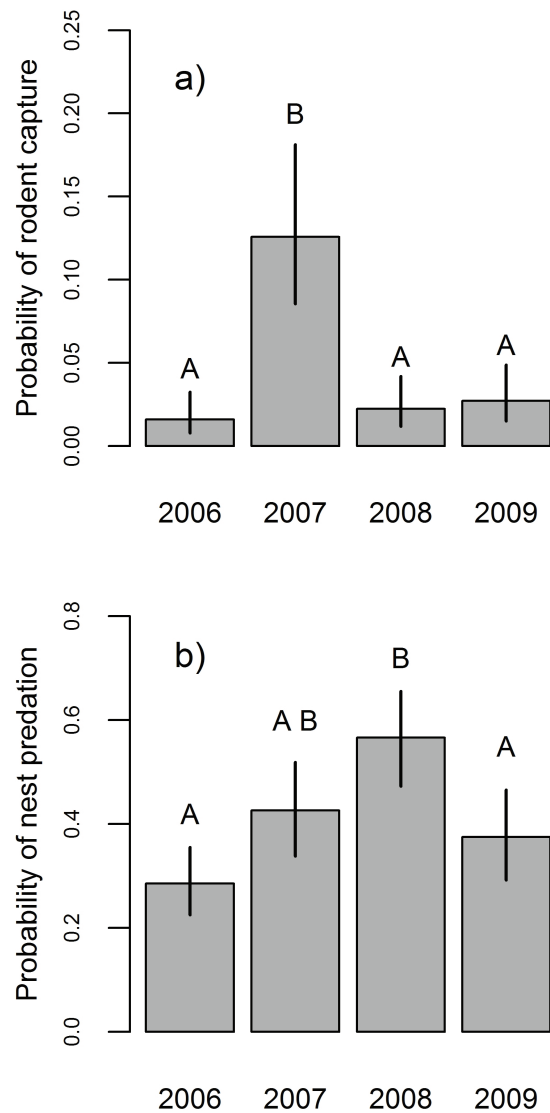


Fig. 1. Mean probability (\pm 95 % confidence intervals) of a) rodent capture per trap, and b) nest predation risk in secondary forests of South Bohemia (2006-2009) based on the prediction of a general linear mixed effect model. Different letters above bars indicate significant differences in rodent capture probability and nest predation risk between corresponding years based on Tukey's HSD test (α = 0.05).

applied to test the hypothesis that rodent densities in a given location predict predation rates during the subsequent year (i.e. the explanatory variable was number of captured rodents in the previous year).

Table 2. Occurrence of predation on experimental nests in South Bohemia (2006-2009). A total of 537 nests were randomly distributed within two forest habitat types. Predator categories were identified according to markings on wax-filled eggs.

	Forest interior				Forest edge				Total
	2006	2007	2008	2009	2006	2007	2008	2009	
Carnivores	8	6	3	4	22	8	4	2	57
Birds	2	1	0	0	4	0	1	2	10
Wild boar	3	0	2	4	1	1	4	0	15
Unidentified	9	15	25	13	5	18	25	20	130

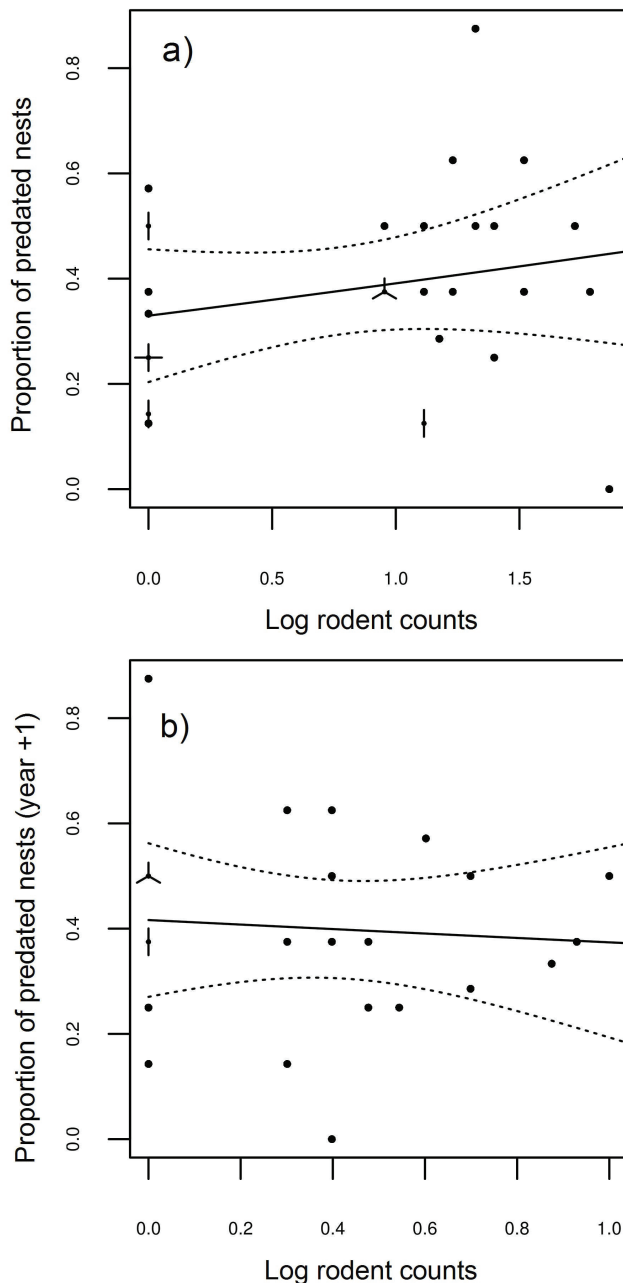


Fig. 2. Relationship between proportion of nests predated in a given location (eight locations were sampled each year) during 14-day exposure and a) small rodent abundance (log transformed counts), and b) small rodent abundance during the previous year. Predictions are based on the general linear mixed effect model. Dashed lines correspond to 95 % confidence intervals. Individual observations are represented by either black dots or by converging segments in the case of more than one combination of predation rates and small rodent abundance.

Results

Nest predation on artificial nests significantly differed among years ($\chi^2 = 23.23$, $\Delta df = 3$, $P < 0.001$) in the study area. The lowest rate was recorded in 2006 (28.6 %, $n = 189$, Fig. 1a). Nest predation increased over the next two years (2007: 42.6 %, $n = 115$; 2008: 56.6 %, $n = 113$), while it decreased again during the final year

of observation (37.5 %, $n = 120$). Tukey's HSD test showed significant differences in nest predation risk only between 2006 and 2008 and between 2008 and 2009 ($P < 0.001$ and $P = 0.019$, respectively, Fig. 1a). A marginally non-significant difference in predation rates was found between 2006 and 2007 ($P = 0.060$). No significant or temporally consistent difference was found in the probability of nest predation between the forest edge (mean predation rates across all years = 44 %) and the forest interior (mean predation = 38 %, $\chi^2 = 2.22$, $\Delta df = 1$, $P = 0.14$). The interaction between habitat type and year was also not significant ($\chi^2 = 0.45$, $\Delta df = 3$, $P = 0.91$). The most common predators on artificial nests (by percentage of identified predators) were unidentified carnivores (37 %), wild boars (18

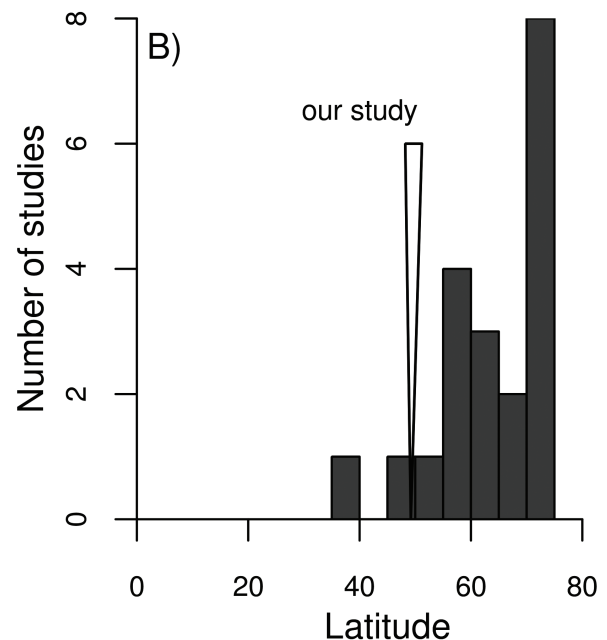
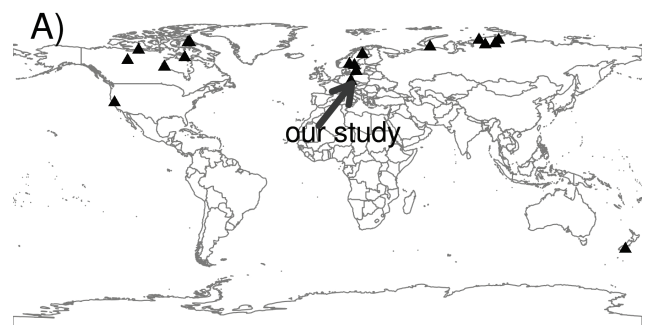


Fig. 3. Geographic distribution of studies on the alternative prey hypothesis (included in Table 1) A) visualised on a world map, and B) plotted as a histogram against the latitude (absolute values) of corresponding sampling locations.

%), small mustelids (17 %), red foxes (16 %) and birds (12 %). However, a large number of predators were not identified at all (Table 2).

In total, 117 individual rodents were trapped in 2240 traps. The most numerous species were the yellow-necked mouse (*Apodemus flavicollis*) and wood mouse (*Apodemus sylvaticus*). As in the case of nest predation, rodent numbers differed significantly among years ($\chi^2 = 91.562$, $\Delta df = 3$, $P < 0.001$). A pronounced peak of rodent numbers was recorded in 2007 (65.0 %, $n = 76$, while in the remaining years rodent numbers were on average about one-sixth those in the peak year ($P < 0.001$ in all cases, Fig. 1b). Rodent abundance did not differ significantly between forest edge and forest interior ($\chi^2 = 2.798$, $\Delta df = 1$, $P = 0.094$), though rodents nevertheless tended to be more abundant in general at forest edges compared to forest interiors. The interaction between habitat type and year was also not significant ($\chi^2 = 0.757$, $\Delta df = 3$, $P = 0.860$).

No association was found between the proportion of predated nests and rodent counts at the locations where rodent abundance was assessed (GLMM: slope \pm SE = 0.276 ± 0.286 , $\Delta df = 1$, $\chi^2 = 0.814$, $P = 0.367$, Fig. 2a). Similarly, rodent density in a given location did not predict nest predation in the following year (GLMM: slope \pm SE = 0.300 ± 0.563 , $\Delta df = 1$, $\chi^2 = 0.098$, $P = 0.755$, Fig. 2b).

Discussion

The data show that both rodent abundance and nest predation risk exhibit considerable temporal variation. The effect of habitat on predation risk and rodent abundance, however, is of relatively low importance. Many previous studies have implied that fluctuations in rodent abundance may cause marked effects on ecosystem functioning (e.g. Ims & Fuglei 2005), including nest predation risk (Ackerman 2002). In theory, both increases (Korpimäki & Norrdahl 1989) and decreases (Bêty et al. 2001) in nest predation rates might be expected when small rodent populations increase.

The alternative prey hypothesis, which predicts decreased nest predation risk during population peaks of small rodents, has received considerable support in many empirical studies. An extensive literature search (Table 1), turned up 20 studies which directly evaluated the alternative prey hypothesis and where small mammals (rodents, lagomorphs) and ground nests represented the main and the alternative prey, respectively. Most of these studies found support for the alternative prey hypothesis ($n = 18$). Nevertheless,

this nearly universal support for the alternative prey hypothesis might be artificially inflated by several factors. First, this set of studies exhibits a non-random geographical distribution (Fig. 3). While most data from testing the alternative prey hypothesis come from the Arctic (13 studies with latitude $> 60^\circ$) and the north temperate zone (five studies with latitudes between 60° and 40°), only one study has been performed in the tropics or subtropics. In addition, only one study comes from the Southern Hemisphere. The mean latitude of the studies on the alternative prey hypothesis was 65° , which suggests a clear bias toward higher latitudes. The existing literature on the alternative prey hypothesis might be affected by a severe publication bias as well. In other words, mentioning the alternative prey hypothesis in the context of a certain type of result might be a more or less opportunistic *ex post* decision to make an article more appealing to potential readers, even when those results were not *a priori* collected for the purpose of testing the alternative prey hypothesis. Moreover, similar data that do not exhibit a pattern corresponding to the alternative prey hypothesis might possibly be less likely to be published. Nevertheless, a more extensive and rigorous review of the literature on temporal fluctuations in nest success would be necessary to account for these concerns.

The present study was situated at a latitude lower than those of 90 % of those studies which have tested the alternative prey hypothesis (Table 2, Fig. 3). Based on field data collected in the study area, it was possible to reject the alternative prey hypothesis. Contrary to the prediction of the alternative prey hypothesis, nest predation risk did not decrease during the rodent population peak. The lack of evidence for the alternative prey hypothesis and the fact that the results contradict those of most previous studies may be caused by several factors. The main predators of the artificial nests, such as red fox and martens, are habitat generalists (Svobodová et al. 2012) and so they may also respond to rodent abundance from adjacent farmland. We do not believe, however, that unobserved variance in rodent density on farmland would have a substantial effect on artificial nest predation in the study area. Data from the previous experiment indicate that rodent abundances in forest and farmland are strongly correlated and, in addition, rodent abundances are substantially lower in surrounding meadows than in forest habitats (Svobodová et al. 2011, Ježková M. unpublished data). In particular, the diversity of nest predator and rodent species is likely to be greater in the study area compared to higher latitudes, where

the evidence for the alternative prey hypothesis is rather strong. At the same time, lower latitudes may also offer a greater diversity of alternative prey that is of comparable or even higher profitability compared to bird nests. Many carnivores preying on artificial nests in the study area are obviously not dependent solely on bird nests as secondary prey, because during nesting periods a significant part of their diet is composed of birds, reptiles, amphibious insects (Jędrzejewska & Jędrzejewski 1998, Lanszki et al. 2007) and the young of larger mammals (e.g. the European hare, *Lepus europaeus* and roe deer, *Capreolus capreolus*; Lindström 1994, Kjellander & Nordström 2003, Panzacchi et al. 2008). In addition, a large number of the artificial nests were preyed upon by wild boar and corvids, whose diet is not dependent on rodents (Schley & Roper 2003, Hoyo et al. 2009). Consequently, for these predators the rodent population dynamic is unlikely to modulate profitability of bird clutches. At the same time, it is also possible that the results were affected by the fact that the population increase of small rodents in the area (ca 6.5 times the population baseline) was less pronounced compared to that of other studies focused on the alternative prey hypothesis. For example, main prey density was more than 30 times higher than the minimum during its population boom in some cases (Wegge & Storaas 1990, Ackermann 2002). Consequently, the change in main prey abundance observed in the study, although seemingly dramatic, might have had a negligible effect on predators' foraging tactics. Finally, irregular fluctuation of rodent density, which is typical for lower latitudes, might have contributed to the weak response by predators and consequently to the low effect on nest predation rates. In particular, it can be hypothesized that regular rodent population cycling at high latitudes may induce greater selective pressure on predators' foraging flexibility. On the other hand, the fact that the alternative prey hypothesis has been supported by several studies performed in areas where regular population cycling does not occur (Ackerman 2002, Šálek et al. 2004) suggests that the importance of this effect is rather limited.

Some previous studies used relatively short-term monitoring of nest predation and rodent density fluctuation to test the alternative prey hypothesis. For example, the contributions of Šálek et al. (2004) and Ackerman (2002) are based on data just from two and three years, respectively. The data from the present study demonstrate that relatively long-term data covering the periods both before and after the rodent peak are necessary for testing the alternative prey

hypothesis. In particular, if the dataset had covered just the two breeding seasons in 2007 and 2008, it might have been erroneously found to support the alternative prey hypothesis, because, consistently with the predictions of this hypothesis, rodent abundance decreased and nest predation increased during these two years.

The opposite pattern of that predicted by the alternative prey hypothesis is expected under the "shared predation hypothesis". In particular, between-year differences in nest predation risk may correlate positively with small mammal density, due to an apparent competition-like effect (Holt 1977) induced by the numerical and dietary (functional) response of predators to the main prey (reviewed by Chalfoun et al. 2002). The shared predation hypothesis has been supported, however, mainly in the case of such predator specialists as weasels (*Mustela nivalis*) and stoats (*Mustela erminea*), for whose diets rodents comprise an important part (Jędrzejewski et al. 1995, Dupuy et al. 2009). It is nevertheless noteworthy that there also are studies providing support for the shared predation hypothesis in the case of generalist predators (Zalewski et al. 1995, O'Donoghue et al. 1997, Jędrzejewska & Jędrzejewski 1998). In any case, the present data do not support the "shared predator" scenario. We hypothesize that the rich Central European ecosystem probably hosts high densities of alternative prey which are of comparable or even higher profitability compared to bird nests. In addition, small rodents do not represent the main food sources in the area of this study for such important nest predators as wild boar and corvids (Schley & Roper 2003, Hoyo et al. 2009).

Many studies focused on nest predation have found nesting success to be decreased along the edges of various habitat types compared to within habitat interiors (e.g. Andrén 1992, Bayne & Hobson 1997, Malt & Lank 2007). Some predator species specifically exploit edge habitats because their main prey (rodents in the present study) is concentrated along these landscape structures (Ries & Sisk 2004, more in Koubová et al. 2011). The present study does not support the edge effect hypothesis, however, as the probability of nest predation and small rodent numbers did not differ substantially between forest interiors and forest edges. It is noteworthy in this regard that most studies supporting the edge effect on nesting success have been conducted in North America and Northwest Europe (reviewed in Batáry & Báldi 2004), which regions have different landscape compositions and predator communities compared

to Central European conditions. It can therefore be hypothesized that, corresponding to the absence of the alternative prey hypothesis in the study area, the existence of the edge effect on nest predation is less obvious in a region with rich predator communities such as Central Europe's intensively managed landscape (Svobodová et al. 2012).

It may be argued that these results are ambiguous, as artificial nests were used for monitoring nest predation risk. Several concerns associated with the use of artificial nests have previously been raised (Storaas 1988, Willebrand & Marcström 1988), as they do not wholly mimic several features of real nests, such as parental behaviour (Weidinger 2002, Kreisinger & Albrecht 2008), scent (Whelan et al. 1994), microhabitat features (Yahner & Piergallini 1998), nest density (Major & Kendal 1996) and the construction of real nests (Báldi 2000). All of these characteristics are, in fact, crucial determinants of nesting success. Although these concerns have some merit, these key features of real nests may vary between breeding seasons. Using artificial nest experiments thus enables researchers to hold these invariant. The use of artificial nests, therefore, provides a considerable methodical advantage for longitudinal studies, as it allows for decreasing potential bias associated with this source of variation. In addition, it is worthy of note that artificial nests had been used in three previous studies on the alternative

hypothesis and that all of them provided support for this hypothesis (Šálek et al. 2004, Lecomte et al. 2008, McKinnon et al. 2013). Therefore, despite well-known methodological drawbacks, artificial nests are still, to a certain extent, useful tools for analysing temporal variation of complexities in trophic cascades, including predator vs. main vs. alternative prey relationships.

In conclusion, high inter-year variation was found in nest predation and rodent density, but the data suggest no straightforward link between these findings. The data allow for rejecting both the alternative prey hypothesis and the shared predation hypothesis. It can be supposed that in rich ecosystems having complex trophic levels, predators can use many sources of alternative prey, and therefore predation risk for bird nests is not substantially related to small rodent abundance. Hence, the possible importance of rodent abundances in relation to nest predation risk must be considered cautiously and with a view to specific local conditions.

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