

Nest predators of woodland open-nesting songbirds in central Europe

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I used time-lapse videotaping to identify predators of open songbird nests in fragmented deciduous woodland (nine plots, 2–10 ha each) in the Czech Republic from 2002 to 2006. I documented 22 species of predators at 171 nests of 13 species (mainly Blackcap *Sylvia atricapilla*, Song Thrush *Turdus philomelos*, Common Blackbird *Turdus merula*, Yellowhammer *Emberiza citrinella* and Chaffinch *Fringilla coelebs*). The main predators were Pine Marten *Martes martes* (37% of 178 predation events), Jay *Garrulus glandarius* (29%), Buzzard *Buteo buteo* (7%) and Great Spotted Woodpecker *Dendrocopos major* (7%); mammals accounted for 48% of total predation. At least 3% of nests were depredated by multiple predators. In spite of their local abundance, Hooded Crows *Corvus cornix* did not present a serious threat for shrub nesting songbirds (< 1% of total predation). No predation by mice was recorded, suggesting that their importance has been overestimated in artificial nest studies. The proportional species composition of predators depended on which species occupied the monitored nest and location (study plot), but not on the year or the time of season. Corvids and raptors accounted for a relatively larger percentage of total predation of small ('warblers') and large ('thrushes') prey species, respectively, whereas carnivores were important predators of all prey species. Active nests of thrushes were only rarely robbed by Jays (< 4% of 52 events), presumably due to parental nest defence. Predation by woodpeckers was spatially clumped, probably due to individual foraging specialization. Predation by the other major predators was documented on most/all study plots.

Keywords: nest defence, nest predation, nest success, passerines, video.

To understand any predator-prey system, the predators should not be treated as abstract sources of risk (Lima 2002). Despite the general conviction that nesting losses in birds are caused primarily by predators, there is little definitive evidence of the nest predator's identity in different geographical areas, habitats and prey species. This is because various indirect methods of predator identification were shown to be unreliable and potentially biased (tracks left at depredated nests, Williams & Wood 2002; artificial nests, Thompson & Burhans 2004). At present, the only unambiguous evidence of predator identities comes from video monitoring of active nests. Yet, unlike the other methods,

videotaping is labour intensive and relatively expensive, which poses limits on the scale of field studies and the resulting sample sizes (Weidinger 2008a).

Most studies conducted to date have focused on a single prey species, and have assumed that the results can be extrapolated to species with similar nesting habits (Schaefer 2004). Even results of the few multi-species studies are based on pooled species data (Pietz & Granfors 2000, Renfrew & Ribic 2003, Thompson & Burhans 2003), possibly because of insufficient sample sizes for individual prey species. Consequently, the relative vulnerability of different co-occurring bird species to various nest predators remains largely unknown. In addition, many studies have not been spatially replicated and have tended to cover an area of similar size as the home-ranges of local predators. This

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means that multiple predation events by a particular predator species may have resulted from repeated sampling of the same individuals (Sanders & Maloney 2002, Thompson & Burhans 2004). If so, then the data are pseudoreplicated and may not represent typical behaviour of the species. Moreover, because of the spatial variation in predator communities, results from a single site/habitat may not be representative of other sites/habitats (Renfrew & Ribic 2003, Thompson & Burhans 2003, Thompson 2007). Finally, the current knowledge of nest predators is strongly geographically biased, as most video studies have been conducted in North America (Weidinger 2008a); only one single-species study on songbirds, yielding a reasonable sample of videotaped predation events, has been published from Europe (Schaefer 2004). Because predator-prey systems are locally specific, conclusions from one area may not be directly applicable to other biogeographical regions (Thompson 2007). Consequently, proper interpretation of factors influencing avian nest success and population trends (Thomson *et al.* 1998), as well as targeted predator control to mitigate nest predation (Stoate & Szczyr 2001), are hampered by the lack of quantitative information on who the dominant nest predators are in specific habitats and regions of Europe.

Here I present results of a 5-year video study of open-nesting songbirds breeding in fragmented woodland habitats representing a typical agricultural landscape of central Europe. Compared to most previous studies the present study is based on a relatively large sample of predation events, simultaneous monitoring of several co-occurring prey species and spatial replication. My goals were: (1) to describe qualitative and quantitative composition of nest predators, and (2) to evaluate the effects of study plot, year, time of season and prey species on the recorded predator composition. The study presents the first data of this kind from Europe for songbirds.

METHODS

Study area and field methods

The study took place in the Czech Republic (49°54'N, 16°02'E, 240–350 m asl) from 2002 to 2006. The study area is characterized by a mosaic of arable land, with villages and remnants of deciduous woodland (woodlots and riparian strips; < 5%

of total area). I collected data from nine plots (each 2–10 ha) located in distinct habitat patches (nearest-neighbour distance 1.4–3.7 km) within an area of *c.* 50 km². Tree vegetation on study plots is dominated by: *Fraxinus excelsior*, *Populus nigra*, *Alnus glutinosa*, *Quercus petraea* and *Salix* spp., with the dense undergrowth consisting mainly of: *Sambucus nigra*, *Padus avium*, *Prunus spinosa* and *Urtica dioica*.

Included in this study were 13 species of open-nesting songbirds whose nests were found most often (Table S1). Distribution of videotaping effort among species was roughly proportional to the number of nests found. I tried to distribute video cameras with respect to calendar date and nest age as equally as possible, given the number of nests available at a particular time. Videotaping started in 2002 (two video sets) and continued to 2006 (nine sets). For details of the field protocol and video equipment see Weidinger (2006). Repeated nest visits in this study system did not reduce survival of the monitored nests (Weidinger 2008b).

Data analysis

The present analysis was intended as exploratory; I avoided formal hypothesis testing. Because the data on predator species composition are categorical in nature, I present the data by simple cross-tabulation (Tables S1 & S2). The unit of analysis was the predation event, defined as a record of one predator species depredating one nest; repeated visits of the same predator species to the same nest were omitted. If a nest was sequentially depredated by several predator species, I counted one predation event for each species. Although the final (complete) predation events could be detected in all cases, it is likely that a small proportion of previous (partial) predation events at the same nests remained undetected. The distribution of the total number of predation events among different predator species and explanatory categorical variables was unbalanced. Hence, the data were grouped for subsequent analyses.

The response variable was predator species or predator group with two (mammals, birds), three (martens, Jay, other) or four (carnivores, corvids, raptors and owls, other) levels. I tried to determine predators to the lowest taxonomic level possible. Although species identification was not always possible (Pine/Stone Marten *Martes* spp. and Weasel/Stoat *Mustela* spp.), this had no effect on

classification of predators in groups. The continuous explanatory variable was the Julian date of the predation event (linear or full quadratic effect). Categorical explanatory variables were study plot (nine study plots pooled in seven groups), year (5 years, the first 2 years pooled), stage of the depredated nest (two levels: eggs, nestling) and species of the depredated nest (two or three levels). The prey species were categorized as 'large' (body-weight > 70 g; Song Thrush *Turdus philomelos*, Common Blackbird *Turdus merula*, Jay *Garrulus glandarius*) or 'small' (< 30 g; all other species; see Table S1). The reasoning follows that large species are potentially capable of more efficient nest defence than small species (Weidinger 2002) and/or their eggs/nestlings may present difficult prey for small predators. To further assess variation within the small species group, I classified the two ecologically similar *Sylvia* warblers (Blackcap *Sylvia atricapilla*, Garden Warbler *Sylvia borin*) as a separate group; classification of species into more groups was not possible due to limited sample size.

I used multinomial logistic regression (PROC LOGISTIC, SAS Institute 2004) to model predator composition. For each response variable (predator species or predator group with two, three or four levels) I fitted a set of univariate non-nested models. I did not consider models with multiple explanatory variables because such data would contain many empty cells (no events for most combinations of categorical variables). I adopted an information-theoretic approach (Burnham & Anderson 2002) to rank models according to the Akaike's information criteria (AIC) relative to the best supported model (the model with the lowest AIC). The relative support for the various models within a set can be interpreted as the relative importance of different explanatory variables of predator composition.

RESULTS

Species composition of predators

I videotaped 175 predation events at 168 nests by 22 species of predators. I directly observed three additional events at three nests (Tables S1 & S2). The primary predators were martens (collectively 37%, 66/178), with the Pine Marten responsible for more predation events and depredated nests in more study plots than the Stone Marten. Although I was unable to identify 73% (48/66) of marten

records to species, other evidence from the same study plots (images from still cameras at artificial nests, direct observation, type of habitat) suggests that perhaps all those records were also Pine Martens. If so, then the four most dominant predators (Pine Marten, Jay, Buzzard *Buteo buteo* and Great Spotted Woodpecker *Dendrocopos major*) accounted for 81% (144/178) of total predation events (Tables 1 & 2). Mammals made up 48% (85/178) of total predation events. At least 3% (6/175) of nests were preyed upon by two or more predator species.

Variation in predator composition

The most important explanatory variable of predator composition in a sample of video records was the study plot (Table 3). There was a strong positive correlation between the total number of records for a given predator species and the number of study plots where the species was recorded (Spearman $r = 0.90$, $n = 20$). Three of the four dominant predators (Pine Marten, Jay and Buzzard) were recorded on most study plots. The second best explanatory variable was species category of the monitored nest (Table 3). Nests of small species were robbed by all predator species/groups, irrespective of nesting stage, whereas the active nests of larger species (thrushes) were only rarely depredated by Jays (Table 1). Predators did not differ appreciably between nests of *Sylvia* warblers and nests of other similarly sized species (Table 3). The least important of the examined explanatory variables were the year and date (Table 3). Cross-tabulation of predators by month (Table S2) suggests that the proportion of corvid/avian predation decreases throughout the nesting season, but this trend was not detectable with date treated as continuous explanatory variable (Table 3).

DISCUSSION

Species composition of predators

Identification of Pine Marten and Jay as the two major nest predators was not unexpected: they are traditionally listed among the suspected nest predators in woodland habitats (Angelstam 1986, Jedrzejewska & Jedrzejewski 1998), though the available video evidence suggests predominance of Jay predation (Schaefer 2004, Stevens *et al.* 2008).

Table 1. Percentage contributions (with number of events in parentheses) of various categories of predators to the total predation of open songbird nests. Depredated nests are categorized by prey species and nest content as deserted nests with eggs (DE), active nests with eggs (E), and active nests with nestlings (N).

Predator	Large prey species ^a				Small prey species ^b			
	DE	E	N	Pooled	DE	E	N	Pooled
Dominant species ^c								
Pine/Stone Marten	18 (2)	55 (12)	57 (17)	49 (31)	33 (1)	23 (7)	33 (27)	30 (35)
Jay	64 (7)	5 (1)	3 (1)	14 (9)	67 (2)	48 (15)	32 (26)	37 (43)
Buzzard	–	5 (1)	30 (9)	16 (10)	–	–	4 (3)	3 (3)
Great Spotted Woodpecker	9 (1)	5 (1)	–	3 (2)	–	16 (5)	7 (6)	10 (11)
Dominant groups ^d								
Carnivores	18 (2)	59 (13)	60 (18)	52 (33)	33 (1)	29 (9)	44 (36)	40 (46)
Corvids	64 (7)	27 (6)	3 (1)	22 (14)	67 (2)	48 (15)	32 (26)	37 (43)
Raptors and owls	–	9 (2)	37 (11)	21 (13)	–	3 (1)	7 (6)	6 (7)
Classes								
Mammals	27 (3)	59 (13)	60 (18)	54 (34)	33 (1)	32 (10)	49 (40)	44 (51)
Birds	73 (8)	41 (9)	40 (12)	46 (29)	67 (2)	68 (21)	51 (41)	56 (64)
Total predation	100 (11)	100 (22)	100 (30)	100 (63)	100 (3)	100 (31)	100 (81)	100 (115)

^aBlackbird, Song Thrush and Jay.

^bAll other prey species (Table S1).

^cFor complete list of predator species (Tables S1 and S2).

^dCarnivores: Pine/Stone Marten, Weasel/Stoat, Domestic Cat, Badger, Mink, Polecat, Fox; Corvids: Jay, Magpie, Hooded Crow; Raptors and owls: Buzzard, Sparrowhawk, Tawny Owl, Goshawk, Honey Buzzard, Long-eared Owl.

Table 2. Percentage contributions (with number of events in parentheses) of various categories of predators to the total predation of open songbird nests as documented by video in different studies and areas.

Predator ^a	This study ^b		Europe ^c		North America ^d
	A	B	C	D	
Dominant species					
Pine/Stone Marten	37 (66)	31 (17)	14 (7)	–	–
Jay	29 (52)	40 (22)	57 (28)	60 (12)	–
Buzzard	7 (13)	4 (2)	–	5 (1)	–
Great Spotted Woodpecker	7 (13)	13 (7)	–	10 (2)	–
Dominant groups					
Carnivores	44 (79)	35 (19)	27 (13)	15 (3)	7 (1)
Corvids	32 (57)	40 (22)	61 (30)	65 (13)	14 (3)
Raptors and owls	11 (20)	9 (5)	2 (1)	10 (2)	6 (1)
Classes					
Mammals	48 (85)	36 (20)	35 (17)	15 (3)	38 (5)
Birds	52 (93)	64 (35)	65 (32)	85 (17)	33 (7)
Total predation	100 (178)	100 (55)	100 (49)	100 (20)	100 (17)
Total predator species	22	10	12	6	6

^aSee Table 1.

^bThis study: A, all prey species (total sample of records); B, Blackcap.

^cEurope: C, Blackcap (Schaefer 2004); D, Spotted Flycatcher *Muscicapa striata* (Stevens *et al.* 2008).

^dNorth America: medians calculated from 12 case studies conducted in woodland habitats (Farnsworth & Simons 2000, Liebezeit & George 2002, Williams & Wood 2002, Stake & Cimprich 2003, Thompson & Burhans 2003 (only the forest habitat), Peterson *et al.* 2004, Stake *et al.* 2004, Small 2005, King & DeGraaf 2006, Franzreb 2007, Marzluff *et al.* 2007, Reidy 2007).

Although the Stone Marten is at least equally abundant as the Pine Marten in my study area (based on hunting statistics), the Pine Marten was

clearly a more important nest predator in woodland habitats. Interestingly, only the Stone Marten was videotaped at nests in a similar study, patches

Table 3. Three sets of multinomial logistic regression models explaining composition of songbird nest predators (categorical response variable with two, three or four levels). Categorical explanatory variables were study plot (seven levels), year (four levels), depredated species with two (large, small) or three (large, *Sylvia* warblers, other small) levels and nesting stage (eggs, nestling); continuous explanatory variable was Julian date (linear or full quadratic effect). Alternative univariate models are ranked from best to worst based on Akaike's information criteria (AIC = $-2LL + 2K$). Shown is the number of model parameters (K), $-2 \times \log$ -likelihood ($-2LL$) and difference in AIC from the best model (ΔAIC).

Model	K	-2LL	ΔAIC
Three predator groups (martens, Jay, other) ^a			
= i + study plot (7)	14	336.7	0.0
= i + prey species (2)	4	374.8	18.1
= i + prey species (3)	6	374.8	22.1
= i (intercept)	2	387.2	26.5
= i + nesting stage (2)	4	384.0	27.3
= i + date	4	385.8	29.1
= i + year (4)	8	379.0	30.3
= i + date + date ²	6	383.1	30.4
Four predator groups (carnivores, corvids, raptors and owls, other) ^a			
= i + study plot (7)	21	386.4	0.0
= i + prey species (2)	6	417.0	0.6
= i + nesting stage (2)	6	421.6	5.3
= i + prey species (3)	9	416.1	5.7
= i (intercept)	3	433.4	11.0
= i + date	6	430.4	14.1
= i + year (4)	12	419.2	14.9
= i + date + date ²	9	428.3	18.0
Two predator groups (mammals, birds)			
= i + study plot (7)	7	226.5	0.0
= i + year (4)	4	237.9	5.4
= i + nesting stage (2)	2	242.7	6.2
= i (intercept)	1	244.9	6.4
= i + prey species (2)	2	243.3	6.8
= i + date	2	244.0	7.6
= i + prey species (3)	3	242.7	8.2
= i + date + date ²	3	243.9	9.4

The traditional likelihood ratio χ^2 test for an effect of, for example, prey species (2) on predator composition (four groups) can be obtained as: $\chi^2 = 433.4 - 417.0 = 16.4$, $df = 6 - 3 = 3$, $P < 0.001$.

^aSee Table 1 for group definition and Table S1 for complete list of predator species.

of secondary deciduous woodland in southern Germany (Schaefer 2004), suggesting that the relative importance of these two species may vary with locality and habitat.

Raptors are seldom considered as important nest predators of woodland songbirds, but available data suggest that they could contribute significantly to the overall nest losses (Liebezeit & George 2002, Williams & Wood 2002). Buzzards breeding in

contiguous forest were shown to feed primarily on birds, including juveniles, during the breeding season (based on analysis of diet, Jedrzejewska & Jedrzejewski 1998). Here I documented Buzzards regularly preying on woodland songbird nests even in a landscape dominated by arable land, which is in agreement with results of dietary analyses from Central Europe (Voříšek *et al.* 1997). Observations from several distant study plots exclude unusual behaviour of specialized individuals. Moreover, Buzzard predation on nests was recorded in four consecutive years, indicating that it is not confined to years of low abundance of rodents, the Buzzard's primary prey (Jedrzejewska & Jedrzejewski 1998, but see Selås 2001).

Woodpeckers are known to destroy nests in cavities/nest-boxes (Michalek & Mietinen 2003), but predation of open songbird nests is still poorly documented (Hazler *et al.* 2004, Požgayová *et al.* 2005, Stevens *et al.* 2008). Great Spotted Woodpeckers accounted for a similar percentage of total predation as Buzzards, but their predation was clearly spatially clumped (Table S2). Given their breeding occurrence on all study plots, a likely explanation may be individual foraging specialization and site fidelity. Most records of Woodpecker predation probably resulted from repeated sampling of the same breeding pair on a single study plot. Birds of both sexes were found depredating nests (identified at eight nests: 7F, 1M), but multiple visits to the same nest were always by either the female or the male. In addition, a study of artificial nests showed that predation by Woodpeckers was consistently repeatable, both within and between breeding seasons (K. Weidinger & R. Kočvara unpubl. data).

Crows and Eurasian Magpies *Pica pica* are the principal avian predators of (artificial) nests in agricultural landscapes (Angelstam 1986, Andrén 1992), and location of their territories was shown to be associated with an increased predation on natural shrub (Roos & Pärt 2004) or artificial ground (Šálek 2004) nests. Yet, I found that their predation on songbird nests was negligible and confined to the early part of the nesting season (before full development of canopy foliage). Hooded Crows *Corvus cornix* are abundant in the study area: their breeding was observed/suspected on all study plots. Yet, visual observations suggested that crows did not enter dense vegetation below the canopy level, either inside woodlots or along forest-field edges. Contrary to expectations based on

habitat use data and predation rates on artificial ground nests (Angelstam 1986, Andrén 1992, Smedshaug *et al.* 2002), this study suggests that Hooded Crows do not present a serious threat to shrub-nesting songbirds, even in edge habitats (for similar findings on wader nests see Teunissen *et al.* 2008). Magpies were locally much less abundant than Jays and Hooded Crows (ratio < 1 : 10) and their breeding was not recorded within *c.* 100 m of any study plot. Unlike crows, the low ratio of Magpie to Jay predation roughly reflected the local abundance of these two species.

Of note are the frequently suspected predators that were not detected in this study – mice. The role of mice as predators of active (as opposed to artificial) shrub nests is still unclear (Thompson & Burhans 2004), though predation on various songbird nests has been documented in North America (Thompson 2007). In Europe, dormice (Gliridae) are known to destroy cavity nests (Adamík & Král 2008), voles (*Microtus* spp.) are suspected predators of ground-nesting songbirds (Bureš 1997), but there is almost no definitive video evidence for mouse predation on open songbird nests (Schaefer 2004). The Wood/Yellow-necked Mouse *Apodemus sylvaticus/flavicollis* and Bank Vole *Clethrionomys glareolus* occurred on all study plots at moderate population levels, without marked population outbreaks/crashes during the five study years. Mice were often found resting in old natural nests and they readily visited artificial nests of various types (Weidinger 2002). Mice were recorded during 56% of trials at 93% of nests (natural thrush nests baited with quail eggs) monitored by automatic still cameras in a similar habitat (K. Weidinger & R. Kočvara unpubl. data). In spite of comparatively high effort (Weidinger 2008a) and diversity of monitored nests, I did not record any predation by mice upon an active nest. Given their abundance, it seems unlikely that mice do not interact with nesting songbirds simply due to random encounters with active nests. Because active (vs. artificial) nests are attended/defended by parents, most encounters with mice probably did not result in nest loss and remained undetected. Though scarce, evidence exists that mice are able to flush nest-attending parents and old nestlings ('forced fledging'; K. Weidinger unpubl. data), or even take nest content from an active nest (Schaefer 2004), but the frequency of such behaviour and impact on nesting success is open to further study. Nevertheless, the results of this and

other studies (Schaefer 2004, Stevens *et al.* 2008) suggest that the importance of mice as predators of open songbird nests in woodland habitats of Europe has been overestimated in artificial nest studies (e.g. Weidinger 2002, Remeš 2005).

Variation in predator composition

The proportional species composition of videotaped predators varied among study plots and categories of prey (species of the monitored nest); it did not depend on year or time of season. The overall variation among plots could be partly due to the unequal distribution of the sampling effort, e.g. a low number of records for some plots. As all major and perhaps most of the other predator species are common in the whole study area, I suspect that predation by these species would be eventually recorded on all adequately sampled plots (Weidinger 2008a), yielding similar qualitative composition of nest predators. However, the ratio of the two dominant predators (Pine Marten, Jay) varied markedly even among similarly sampled plots, suggesting that spatial variation in quantitative composition of nest predators is real and probably attributable to local habitat characteristics (e.g. Thompson & Burhans 2003).

The second best explanatory variable of predator composition was the species of the monitored nest. It appears that large and strong predators (carnivores, raptors) can take any discovered songbird nest and that the ratio of different prey species in their diet depends on their nest-searching abilities. Carnivores (Pine Marten) were important nest predators of all studied species, whereas raptors (Buzzard) preyed mainly on the nests of thrushes. On the other hand, small avian predators (woodpeckers, shrikes) were obviously constrained by prey size and/or parental nest defence. Unexpected in this respect was the low predation by Jays upon thrush nests. This cannot be attributed to size constraints (Jays readily took comparatively large quail eggs from artificial nests) or thrush nest-site characteristics (similar to those of frequently robbed species). The most plausible explanation is an efficient nest defence of breeding thrushes against Jays, although such behaviour is difficult to document and quantify by video recording (Pietz & Granfors 2005). Indirect support comes from the fact that Jays took thrush eggs mostly from deserted (not defended) nests (Table 1). If real, the effect of parental nest

defence may partially explain the differences in predator composition between nests of large (thrushes) and small prey species. I suspect that predator composition differs also among similarly sized species (with similar nest defence ability), presumably due to variation in nest and nest-site characteristics. However, such an effect was not detectable in grouped data (*Sylvia* warblers vs. other small birds), and sample sizes for most individual species were too low (Table S1).

The equivocal evidence for an overall effect of nesting stage on predator species composition is probably a consequence of the coarse grouping of the data. Ungrouped data are too sparse to allow for rigorous analysis but suggest relatively higher vulnerability of thrush eggs to those predators (Jay, Magpie, Great Spotted Woodpecker) for which old thrush nestlings may represent too large a prey item.

Although the monitoring effort increased throughout the five study years, the proportional species composition of predators varied little among years or with accumulating total sample size (Weidinger 2008a). Low support for seasonal variation could be due to low sample sizes at both ends of the nesting season. The possibly higher predation by corvids early in the season was due to Magpies and Hooded Crows (see above), who avoided the interior of woodlots later in the season. Predation by Jays, a woodland species, remained relatively consistent throughout the whole season.

Comparison with other studies

The only comparable study from Europe (Schaefer 2004) was conducted in the same geographical area (Central Europe), in similar habitat (deciduous woodland) and on the same prey species (shrub-nesting Blackcap). This and the study of Schaefer (2004) revealed a similar (considering the sample size) number of predator species and almost the same ratio of mammalian to avian predators. The two principal predators (martens, Jay) were common to both studies, but the ratio of martens to Jays and carnivores to corvids was markedly higher in the present study (Table 2). Compared to similar studies from North America (e.g. Farnsworth & Simons 2000; Peterson *et al.* 2004) and Europe (Schaefer 2004), I found on average a higher ratio of carnivores to corvids in my study, whereas the ratio of mammalian to avian predation was similar.

The absolute contribution of carnivores/mammals and corvids/birds to the overall predation was higher in this and the study of Schaefer (2004) (Table 2), mainly due to the complete absence of snake predation in Central Europe. Snakes account for a significant part of nest predation in temperate North America (Thompson 2007), whereas their impact on nest success in Europe is poorly documented (e.g. Sorace *et al.* 2000).

In spite of considerable monitoring effort, the resulting predator list is certainly incomplete. Because nest predation is mostly opportunistic, the regional pool of potential predators is usually rich, whereas the number of species found in a sample is a function of sample size (Weidinger 2008a). The relatively high number of predator species found in this study simply reflects the high sampling effort and its distribution among multiple study plots, various nest-sites and prey species, rather than an exceptionally rich local predator community. The quantitative results underline the findings of previous studies (e.g. Schaefer 2004, Teunissen *et al.* 2008) that a large part of total nest predation is attributable to a small number of predator species, regardless of predator species richness.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1.

Numbers of identified nest predators of open-nesting songbirds in woodland habitats in the Czech Republic, cross-tabulated by species of the depredated nest and stage of the nesting cycle.

Table S2.

Numbers of identified nest predators of open-nesting songbirds in woodland habitats in the

Czech Republic, cross-tabulated by study plot, year and month.

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Table S1

Numbers of identified nest predators of open nesting songbirds in woodland habitats in the Czech Republic, cross-tabulated by species of the depredated nest and stage of the nesting cycle.

Predator species		Depredated species ^a													Stage ^b		Total
		1	2	3	4	5	6	7	8	9	10	11	12	13	E	N	
Pine/Stone Marten	<i>Martes sp.</i>	12	11	9	2	1	-	3	4	3	1	1	-	1	16	32	48
Pine Marten	<i>Martes martes</i>	5	3	6	-	-	-	1	1	1	-	-	-	-	5	12	17
Stone Marten	<i>Martes foina</i>	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	1
Jay	<i>Garrulus glandarius</i>	22	5	4	9	8	1	3	-	-	-	-	-	-	25	27	52
Buzzard	<i>Buteo buteo</i>	2	7	3	1	-	-	-	-	-	-	-	-	-	1	12	13
Great Spotted Woodpecker	<i>Dendrocopos major</i>	7	1	1	-	3	-	-	-	-	-	-	1	-	7	6	13 ^c
Weasel/Stoat	<i>Mustela sp.</i>	-	2	-	-	-	1	-	-	-	-	-	-	-	1	2	3
Weasel	<i>Mustela nivalis</i>	-	-	-	-	-	2	-	-	-	-	-	-	-	-	2	2
Stoat	<i>Mustela erminea</i>	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	1
Magpie	<i>Pica pica</i>	-	1	3	-	-	-	-	-	-	-	-	-	-	4	-	4
Red Squirrel	<i>Sciurus vulgaris</i>	1	-	1	-	1	-	-	1	-	-	-	-	-	2	2	4
Red-backed Shrike	<i>Lanius collurio</i>	1	-	-	1	-	-	-	-	1	-	-	-	-	-	3	3
Domestic Cat	<i>Felis catus</i>	1	-	-	1	-	1	-	-	-	-	-	-	-	-	3	3
Sparrowhawk	<i>Accipiter nisus</i>	-	1	1	-	-	-	-	-	-	-	-	-	-	-	2	2
Tawny Owl	<i>Strix aluco</i>	2	-	-	-	-	-	-	-	-	-	-	-	-	-	2	2
Hedgehog	<i>Erinaceus sp.</i>	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1	2 ^d
Goshawk	<i>Accipiter gentilis</i>	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
Honey Buzzard	<i>Pernis apivorus</i>	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	1
Long-eared Owl	<i>Asio otus</i>	-	-	-	-	1	-	-	-	-	-	-	-	-	1 ^e	-	1
Hooded Crow	<i>Corvus cornix</i>	-	-	1	-	-	-	-	-	-	-	-	-	-	1	-	1
Badger	<i>Meles meles</i>	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	1
Mink	<i>Mustela vison</i>	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1	1
Polecat	<i>Mustela putorius</i>	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1	1
Fox	<i>Vulpes vulpes</i>	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1
Total		55	33	28	16	14	8	8	6	5	1	1	1	1	67	110	178

^a Depredated species: 1, Blackcap *Sylvia atricapilla*; 2, Song Thrush *Turdus philomelos*; 3, Blackbird *Turdus merula*; 4, Yellowhammer *Emberiza citrinella*; 5, Chaffinch *Fringilla coelebs*; 6, Chiffchaff *Phylloscopus collybita*; 7, Dunnock *Prunella modularis*; 8, Icterine Warbler *Hippolais icterina*; 9, Garden Warbler *Sylvia borin*; 10, Marsh warbler *Acrocephalus palustris*; 11, Nightingale *Luscinia megarhynchos*; 12, Goldfinch *Carduelis carduelis*; 13, Jay *Garrulus glandarius*.

^b Stage of nesting cycle: E, eggs; N, nestling.

^c Including two events directly observed during the video study.

^d Including one event directly observed before beginning of the video study.

^e Predation on incubating female, eggs were left intact.

Table S2

Numbers of identified nest predators of open nesting songbirds in woodland habitats in the Czech Republic, cross-tabulated by study plot, year and month.

Predator species		Study plot ^a									Year ^b					Month ^c					Total
		1	2	3	4	5	6	7	8	9	02	03	04	05	06	A	M	J	J	A	
Pine/Stone Marten	<i>Martes sp.</i>	6	23	10	6	1	1	-	-	1	2	4	16	16	10	3	12	21	11	1	48
Pine Marten	<i>Martes martes</i>	2	5	7	2	1	-	-	-	-	-	2	3	9	3	-	6	6	4	1	17
Stone Marten	<i>Martes foina</i>	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	1	-	-	1
Jay	<i>Garrulus glandarius</i>	18	5	7	2	5	8	6	1	-	1	7	11	15	18	3	16	19	13	1	52
Buzzard	<i>Buteo buteo</i>	5	2	2	-	1	-	2	1	-	-	3	1	2	7	1	4	5	1	2	13
Great Spotted Woodpecker	<i>Dendrocopos major</i>	1	10	-	2	-	-	-	-	-	2	-	4	3	4	-	2	8	3	-	13
Weasel/Stoat	<i>Mustela sp.</i>	3	-	-	-	-	-	-	-	-	-	-	1	-	2	-	1	1	1	-	3
Weasel	<i>Mustela nivalis</i>	1	-	-	1	-	-	-	-	-	-	1	1	-	-	-	-	-	2	-	2
Stoat	<i>Mustela erminea</i>	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	1
Magpie	<i>Pica pica</i>	3	-	-	-	1	-	-	-	-	-	-	-	2	2	2	2	-	-	-	4
Red Squirrel	<i>Sciurus vulgaris</i>	-	-	-	2	1	1	-	-	-	-	-	1	2	1	-	1	1	2	-	4
Red-backed Shrike	<i>Lanius collurio</i>	1	-	2	-	-	-	-	-	-	-	-	-	3	-	-	-	1	1	1	3
Domestic Cat	<i>Felis catus</i>	3	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	2	1	3
Sparrowhawk	<i>Accipiter nisus</i>	2	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	1	1	-	2
Tawny Owl	<i>Strix aluco</i>	1	-	-	-	1	-	-	-	-	-	-	-	-	2	-	-	-	2	-	2
Hedgehog	<i>Erinaceus sp.</i>	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	2	-	-	2
Goshawk	<i>Accipiter gentilis</i>	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	1	-	1
Honey Buzzard	<i>Pernis apivorus</i>	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	1
Long-eared Owl	<i>Asio otus</i>	-	1	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	1
Hooded Crow	<i>Corvus cornix</i>	-	1	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	1
Badger	<i>Meles meles</i>	-	-	-	-	1	-	-	-	-	-	-	-	-	1	-	-	1	-	-	1
Mink	<i>Mustela vison</i>	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-	1
Polecat	<i>Mustela putorius</i>	-	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	1	-	1
Fox	<i>Vulpes vulpes</i>	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	1	-	-	-	1
Total		49	47	28	15	13	11	11	2	1	5	21	40	55	56	11	46	68	46	7	178

^a Nine study plots representing distinct woodland patches.

^b Years 2002 to 2006.

^c Months April to August.