Research

Repeatability of nest predation in passerines depends on predator species and time scale

Karel Weidinger and Radim Kočvara

K. Weidinger (weiding@prfnw.upol.cz) and R. Kočvara, Dept of Zoology and Laboratory of Ornithology, Faculty of Science, Palacky Univ., Tr Svobody 26, CZ–771 46 Olomouc, Czech Republic.

It has been proposed that some specific locations of bird's nests have higher intrinsic chances of being depredated than other locations. This predicts that fates of consecutive nesting attempts at the same site should be repeatable. We used 20 pairs of old thrush nests to simulate repeated nesting attempts at the same sites, both within and between breeding seasons (n = 40 sites × 2 trials × 2 years = 160). Each nest was monitored by a camera to record multiple predation events and to identify predators. Predation by all predator species was repeatable during a 15-day trial. Predation by principal predators (jay *Garrulus glandarius*, marten *Martes martes/foina*) and total predation (all species combined) was not correlated within pairs of simultaneously exposed nests or within samples of nests from particular study plot, and not repeatable for individual nests between-trials or between-years. These findings suggest short-term effect of predator memory causing revisitation of previously depredated nests during a current nesting trial (all predators); do not support an effect of nest site features on multiple nest discoveries and/or an effect of nest location on repeated random encounters with the same nest (principal predators). Long-term repeatability and correlation within pairs of simultaneously exposed nests was detectable only in occasional predators (great spotted woodpecker *Dendrocopos major*, possibly also squirrel *Sciurus vulgaris*), which suggests effect of nest location combined with site fidelity and individual foraging specialization of these predators. We conclude that repeatability of nest predation depends on the time scale considered and the local predator community. We caution against spurious findings of repeatable nest predation resulting simply from statistical properties of correlation in binary data (nest fates).

Understanding the selection of nesting habitat is a central issue in avian ecology. Because predation is one of the major causes of nesting failure and because risk of nest predation varies among nest sites (Fontaine et al. 2007), selection of safe nesting sites is assumed to be adaptive (Martin 1998, Forstmeier and Weiss 2004, Caro 2005). Yet, studies looking for associations between various nest site features and predation risk yielded remarkably inconsistent results. For example, evidence for seemingly obvious antipredator function of good nest concealment is conflicting (Martin 1992, Burhans and Thompson 1998, Remeš 2005), while nest predation unrelated to vegetation characteristics of nest site has often been reported (Wilson and Cooper 1998, Braden 1999, Davis 2005). This has been traditionally attributed to diversity of local predators using multiple cues to locate nests, resulting in absence of safe sites (Liebezeit and George 2002, King and DeGraaf 2006), and to variation of predators among studies. Another possibility is that the nest site characteristics measured so far by human observers differ from those used by predators searching for nests.

An alternative view of the problem was introduced by Martin et al. (2000) who proposed that some specific nest locations have higher intrinsic chances of being depredated than other specific locations. If so, then consecutive nesting attempts at the same site should be consistently either successful or depredated – nest fates should be repeatable. This prediction is testable even without knowledge of specific nest site features associated with predation risk. Yet, these experiments also yielded conflicting results, unrepeatable nest fates being more common (Cresswell 1997, Ortega et al. 1998, Weidinger 2002, 2004, Remeš 2005, Styrsky 2005) than repeatable fates (Martin et al. 2000, Muchai and du Plessis 2005).

The same pattern of repeatable nest fates may result from several different mechanisms. First, successive nesting attempts at the same site share the same set of nest site features, which increases probability of repeated independent discoveries by predators using these features as searching cues (Santisteban et al. 2002). Second, successive nesting attempts at the same site share the same location relative to spatial distribution of predators and their foraging activity. This increases probability of repeated random encounters of predators with these nests. For example, nests as incidental prey will be robbed consistently more often if located in high-use area within predator home ranges (Vigallon and Marzluff 2005, Schmidt et al. 2006). Third, repeatable nest fates may result from a memory

effect of individual predators revisiting sites with previously depredated nests, independent of nest site features and location. An effect of predator memory was suggested in martens preying upon cavity nests (Sonerud 1993, Sorace et al. 2004) and crows preying on eggs (Sonerud and Fjeld 1987). The above mechanisms are not mutually exclusive and their effects are hard to separate in observational data. Yet, they predict different effects on different time scales and for different categories of predators. To our knowledge, all previous studies evaluated repeatability of overall predation by anonymous predators (without species identification) and no single study considered multiple time scales.

In this study we used artificial nests to simulate repeated nesting attempts at exactly the same sites both within and between breeding seasons. Each nest was monitored by a camera to record multiple predation events and to identify predators. First, we asked whether predation events were distributed randomly among the available nests during the current nesting attempt (short-term repeatability). Presence of overdispersion would indicate that some nests were robbed more/less frequently that expected. Second, we examined whether fates of paired (in terms of location and site features) and simultaneously exposed artificial nests were correlated. Absence of such correlation would suggest that short-term repeatability is mainly an effect of predator memory, while positive correlation would suggest that an effect of nest site features and/or an effect of location are involved. Third, we evaluated whether nest fates are repeatable between consecutive trials, both within and between breeding seasons. Because open-nesting songbirds rarely reuse the same site for subsequent nesting, we assume little selection on predators to revisit previously depredated sites over periods longer than the duration of one nesting attempt. If so, then long-term repeatability would indicate an effect of site features and/or location, rather than an effect of predator memory. Finally, we compared repeatabilities of nest predation among predator species. We expect that long-term repeatability by principal nest predator species (all individuals regularly prey upon nests) would indicate an effect of nest site features rather than an effects of specific location, because most nests are located within the foraging range of a predator individual of these species. Alternatively, long-term repeatability in occasional predator species (given that they are similarly abundant as principal predators but not all individuals prey upon nests) would indicate an effect of specific nest location, because only some nests are located within the foraging range of a predator individual.

Methods

Study area

The study was conducted in central Moravia, Czech Republic (49°21′N, 17°21′E, altitude 190 m) in May–July 2004 and 2005. The landscape is characterized by a mosaic of arable land and managed floodplain forest with oak Quercus spp., ash Fraxinus excelsior, lime Tilia spp. and poplar Populus spp. as dominant trees and bird cherry Padus racemosa and elder Sambucus nigra as dominant shrubs. We collected data each year on three study plots – isolated forests (approximately 2, 8 and 10 km²) separated by distances of 5.5, 7.5 and 12 km. None of these plots represents a convex area of continuous forest; all forests are highly fragmented by clearcuts, dense network of roads and strips (width 10–20 m) of young spruce Picea abies plantations. Consequently, the size of homogeneous forest patches and amount of edge habitat was similar across the study plots.

Artificial nests and cameras

We used undamaged real nests of song thrush Turdus philomelos and European blackbird T. merula collected in the study area before the start of experiments (most of the early nesting attempts are usually lost to predators). Nests of these two species are of about the same size and external appearance, and predation rate in this study system was not influenced by nest size and design (Weidinger 2004). All nests were replaced after each trial to reduce accumulation of scent that may potentially attract predators. The nests were baited with four Japanese quail Coturnix japonica eggs. We replaced missing (depredated) eggs on each nest check. Although this is an artificial situation, replacing eggs and thus keeping the nest active throughout the entire experimental trial is a fundamental feature of our experimental design (Leimgruber et al. 1994). In this way we were able to record multiple predatory events (by multiple predator species) per nest, which allowed us to examine the distribution of predation events among nests and to analyse repeatabilities of nest fates separately for different predator species. At the same time, our predation rates are directly comparable to those measured by conventional artificial nests (without egg replacement), because we considered only the first predation event by any (total predation) or particular (species-specific predation) predator species for calculation of predation rates.

Quail eggs are acceptable surrogates of real eggs for the present purposes. Larger size of quail eggs does not present a problem for the local nest predators (Discussion), all of which can handle eggs of this size. Brownish coloration of quail eggs, though different from the blue-green thrush eggs, represents the colour type of many other woodland open-nesting songbirds. Moreover, a previous study showed that predation rate in this study system was not influenced by egg colour (Weidinger 2001). Each nest was monitored by a still image camera triggered by a photocell positioned across the nest cup. Cameras were housed in a plastic box (14 × 10 × 7 cm) placed ca 2 m from a nest and connected to the trigger by a cable. All system components were camouflaged by brown-green spotted painting and natural material. Nests were visited every five days to check eggs and functioning of the camera (replacement of film and batteries).

To validate results from artificial nests we used two other data sets for comparison. First, predation rate on a control sample of active nests of the two thrush species was estimated for the period of this study – nests of open-nesting songbirds have been monitored on these study plots since 2000. Second, predators of active open songbird nests, including the two thrush species, were identified

during a five-year video study in a similar type of habitat (Weidinger 2009).

Experimental design

Nests were distributed in pairs – one nest ('natural') was left in its natural position, the second nest of the same species ('artificial') was placed 10–15 m apart. Natural nests were removed and replaced before the first trial to arrange the photocell trigger, thus controlling the amount of manipulation among treatment groups for all trials. We tried to keep the type of nest supporting plant, height above ground (mean $= 1.4 \pm 0.5$ SD, range 0.2–2.4 m) and overall vegetation concealment similar within nest pairs, as much as possible. Nest pairs within a study plot were located > 160 m (median $= 480$ m) apart. In total we used 40 nest sites (20 pairs) distributed equally between deciduous forest and spruce plantations (10 + 10 pairs) and the three study plots (6 + 6 + 8 pairs). Nests were exposed during two 15-day trials separated by a 15-day period, when the nest and camera were completely removed from the site. Nests of the same species were used for all trials conducted on a particular nest site. The experiment started each year after full development of foliage in the shrub undergrowth. Timing of trials was 7 May – 8 June and 9 June – 11 July in 2004 and 19 May – 22 June and 18 June – 24 July in 2005. Nest sites were marked by natural material to enable accurate relocation for subsequent trials. The experiment was replicated in two consecutive years, resulting in four trials (two per year) at each of the 40 nest sites (Fig. 1).

Data analysis

We inspected photo images, determined predators to the lowest taxonomic level (referred to as 'species', hereafter) and recorded time of their visits. We defined 'predation event' as a nest visit by a particular predator species during a 24-h period. Position of photocells in the nest cup assured that an event was recorded only if the predator was in contact with eggs. Although we could not see in all cases whether the egg was actually removed, video records from active nests (Weidinger 2009, unpubl.) showed that such behaviour always resulted in predation. Repeated visits by the same species in a shorter time interval were omitted. We also excluded nest visits by small rodents whose role as predators of open-cup shrub nest was not supported (Discussion). We focused on predator species whose predatory behaviour was documented by videotaping of active nests (Weidinger 2009) and was seen on photographs from artificial nests (this study). We conducted analyses of all predation combined and separately for the four dominant predator species.

For each nest we recorded two response variables, 'fate' – binary nest fate (successful/depredated) and 'events' – number of predatory events. Descriptive data on proportion of depredated nests, number of events per nest and number of predator species per nest, were calculated for three inclusive time periods: 'trial' – a single continuous 15-day exposure (n $= 40$ sites $\times 2$ trials $\times 2$ years $= 160$); 'year' – pooled data from two trials per year
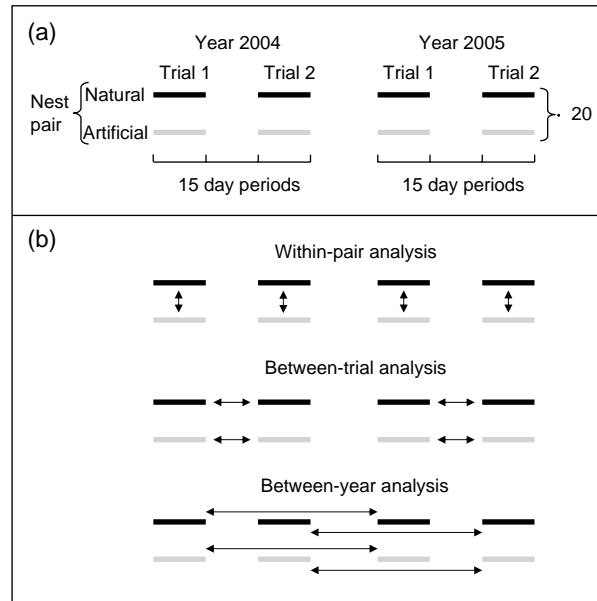

Figure 1. (a) Scheme of the experiment. Nests were distributed in pairs – one nest was left in its natural position, the second was placed 10–15 m apart. In total we used 40 nest sites (20 pairs). Nest were exposed during two 15-day trials separated by a 15-day period. Experiment was replicated in two consecutive years, resulting in four trials (two per year) at each of the 40 nest sites. (b) Scheme of the analyses. Differences in proportion of depredated nests and correlation of nest fates were evaluated in four subsets of 20 paired observations (indicated by arrows) on three time scales: (1) within-pair – between paired and simultaneously exposed nests in natural and artificial site, separately for the two trials and the two years; (2) between-trial – between the two trials on the same nest site, separately for natural and artificial nest sites and the two years; (3) between-year – between the two years on the same nest site, separately for natural and artificial nest sites and the two trials. A pooled data set consisted of 80 paired observations on each time scale.

(n $= 40$ sites $\times 2$ years $= 80$); 'experiment' – pooled data from the entire two-year experiment (n $= 40$ sites).

To assess whether predatory events were randomly distributed among the nests (n $= 160$) we compared the observed distribution with the expected Poisson distribution; the degree of clumping was expressed as variance to mean ratio. To exclude an effect of large scale spatial heterogeneity in predation rates on the repeatability of individual nest fates we checked for correlation of nest fates within the six (3 plots $\times 2$ years) or 12 (3 plots $\times 2$ years $\times 2$ trials) data samples (exact test for correlation in clustered binary data; Cytel Inc 2005).

Correlation of paired nest fates was evaluated on three time scales corresponding to different underlying hypotheses (see Fig. 1 for a scheme): (1) 'within-pair' – between paired and simultaneously exposed nests in natural and artificial sites, separately for the two trials and the two years; (2) 'between-trial' – between the two trials on the same nest site, separately for natural and artificial nest sites and the two years; (3) 'between-year' – between the two years on the same nest site, separately for natural and artificial nest sites and the two trials. We first examined whether the four subsets of paired observations (summarized as four 2×2 tables, n $= 20$ pairs per table)

available on each time scale were homogeneous (exact test of homogeneity for stratified 2 × 2 tables; Cytel Inc 2005). Next we pooled the four subsets (single 2 × 2 table, n = 80 pairs) and examined whether predation rates differ between the paired observations (exact McNemar test for paired binary data; Cytel Inc 2005). Finally, we estimated correlation of nest fates between the paired observations. In the case of binary data, all popular measures of correlation/association (Pearson and Spearman correlation coefficients, phi contingency coefficient) are numerically equivalent and yield identical exact p-values. We controlled for multiple testing problem using the sequential Bonferroni adjustment of type I error rate (Roback and Askins 2005) within each set of five tests (five predator categories) on each time scale. Generally we focused more on detecting replicated patterns in data than on significance testing. To assess potential effect sizes, we present 95% confidence intervals for the correlations of nest fates (asymptotic CI) and the differences in predation rates between paired observations (exact CI; Cytel Inc 2005).

Results

We recorded 386 predation events by 11 species of predators: European jay *Garrulus glandarius* (174, 'jay'), great spotted woodpecker *Dendrocopos major* (78, 'woodpecker'), pine/stone marten *Martes martes/foina* (46, 'marten'), red squirrel *Sciurus vulgaris* (43, 'squirrel'), racoon *Procyon lotor* (30), magpie *Pica pica* (4), hedgehog *Erinaceus europaeus* (3), buzzard *Buteo buteo* (3), honey buzzard *Pernis apivorus* (3), stoat/weasel *Mustela erminea/nivalis* (1), tawny owl *Strix aluco* (1). The four dominant predators accounted for 88% (341/386) of all predation events and 89% (94/106, trial), 96% (64/67, year) and 97% (36/37, experiment) of depredated nests.

More than one predator species was recorded at 33% (35/106, trial), 55% (37/67, year) and 78% (29/37, experiment) of depredated nests. Mean number of predator species per depredated nest increased with lengthening time scale (number of trials conducted per nest site) from trial (1.4 ± 0.6SD, max = 3) to year (1.8 ± 1.0, max = 5) and entire experiment (2.6 ± 1.4, max = 6). Similarly, proportion of depredated nests (Fig. 2a) and the number of predation events per depredated nest (Fig. 2b) increased with lengthening time scale, whether total predation or species-specific predation was considered.

Frequency distribution of predation events (n = 386) among nests (n = 160) was markedly overdispersed compared to the Poisson distribution, for total predation as well as for the four dominant predator species (Table 1; χ^2 goodness of fit test, all p < 0.01). The degree of clumping (ratio variance/mean; values rounded after calculation) was highest in woodpecker (3.4/0.5 = 7.0), followed by total predation (8.0/2.4 = 3.3), jay (3.2/1.1 = 3.0), marten (0.8/0.3 = 2.8) and squirrel (0.7/0.3 = 2.7).

Nest fates were not correlated within the six (3 plots × 2 years; all p > 0.10) or 12 (3 plots × 2 years × 2 trials; all p > 0.14) data samples for total predation as well as for the dominant predator species.
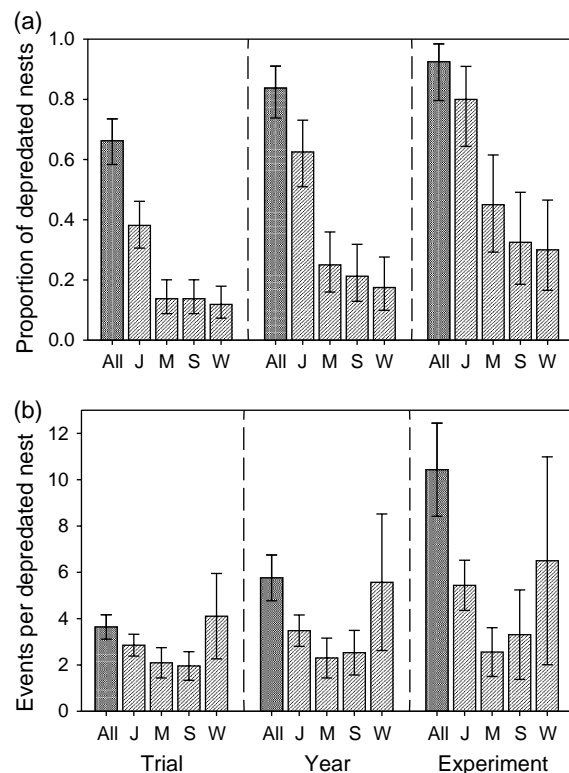

Figure 2. (a) Proportion of depredated nests and (b) number of predation events per one depredated nest. Estimates are shown for three inclusive time periods (see Fig. 1. for the scheme): (1) trial – continuous 15-day exposure (n = 40 sites × 2 trials × 2 years = 160); (2) year – pooled data from two trials per year (n = 40 sites × 2 years = 80); (3) experiment – pooled data from the entire two-year experiment (n = 40 sites). Proportions of depredated nests for individual predator species (J = jay, M = marten, S = squirrel, W = woodpecker) do not sum up to the total predation (All), because some nests were robbed by more than one predator species or by species not analyzed separately. Shown are means with 95% CI.

The paired observations of nest fates were homogeneous among various subsets of data (Fig. 1) on all time scales (Table 2a), hence we proceeded with analyses of pooled data sets. Proportion of depredated nests generally did not differ significantly between paired observations on any time scale; effect sizes were in both directions and tended to increase from within-pair to between-year comparison. (Fig. 3a, Table 2b). The only exception was a significant increase in a proportion of nests depredated by woodpecker between the two years. Correlations of nest fates between the paired observations were generally positive and varied consistently among predator species. On all time scales, the effect size (correlation coefficient) was highest in woodpecker and squirrel, lowest in jay and marten and intermediate in the total predation (Fig. 3b, Table 2c). We found heterogeneity among subsets of data in only total predation on a between-year scale. Analyses conducted separately on each subset of data revealed no significant differences in proportion of depredated nests (Fig. 4a); a single significant (exact p < 0.001) correlation of nest fates was found in the subset of data from the second trial at artificial nest sites (Fig. 4b).

Table 1. Distribution of predation events (n =386, all predators combined) among nests (n =160). Shown are the observed frequencies of nests with a given number of predation events and the deviations from frequencies predicted by the Poisson distribution (in parentheses, rounded after calculation). The cumulative frequency of nests with one or more predation events is equal to the proportion of depredated nests shown in Fig. 2a.

No. events	All predators	Jay	Marten	Squirrel	Woodpecker
0	54 (40)	99 (45)	138 (18)	138 (16)	141 (40)
1	22 (−13)	14 (−45)	10 (−25)	12 (−21)	5 (−41)
2	19 (−23)	20 (−12)	7 (2)	4 (0)	4 (−7)
3	23 (−11)	12 (0)	2 (2)	4 (4)	3 (1)
4	12 (−8)	4 (1)	0 (0)	0 (0)	2 (2)
5	12 (2)	3 (2)	2 (2)	1 (1)	0 (0)
6	7 (3)	5 (5)	1 (1)	1 (1)	1 (1)
7	3 (2)	2 (2)	0 (0)	0 (0)	0 (0)
8	1 (1)	0 (0)	0 (0)	0 (0)	0 (0)
9	3 (3)	1 (1)	0 (0)	0 (0)	3 (3)
≥10	4 (4)	0 (0)	0 (0)	0 (0)	1 (1)

Discussion

Short-term repeatability

Distribution of predation events among individual nests was overdispersed (clumped) for total predation as well as for individual predator species – about 34% of nests exposed for a 15-day trial escaped predation altogether, while other nests were depredated multiple times (mean = 3.6 events per depredated nest). This indicates that once depredated, a nest had a higher probability of being depredated again during the current trial (nesting attempt). In contrast, predation on pairs of simultaneously exposed nests, sharing similar nest site features and location within a habitat matrix, was only weakly correlated (except for woodpecker). From this we conclude that the short-term repeatability could be better explained by a memory effect – revisitation of previously depredated nests by the same predators (but note that individual identity was unknown) rather than by multiple independent discoveries due to specific nest site features or by repeated random encounters

due to specific nest location. Although the study was conducted on three separate study plots (forests), the short-term repeatability of nest fates could not be explained as an artifact of spatial heterogeneity in predation rates, because the overal predation did not differ apreciably (given the sample size) among the three study plots (0.58 vs 0.64 vs 0.77; n =48, 64, 48; p =0.13) and nest fates were not correlated within samples of simultaneously exposed nests on individual study plots.

Multiple visits to the same nests during a period no longer than the mean duration of one nesting attempt (25–30 days in most open-nesting songbirds) may represent an adaptive foraging strategy for those predators that do not take all nest contents at once. For instance, jays and woodpeckers were videotaped revisiting active nests during 2–4 subsequent days, taking one egg/nestling at a time (KW, unpubl.). Video studies of active nests suggests that such behaviour could be frequent but difficult to quantify (Farnsworth and Simons 2000, Sanders and Maloney 2002, Stake and Cimprich 2003), while most artificial nest studies were not designed to record multiple predation

Table 2. Analyses of paired binary data (nest successful/depredated) on three different time scales. Shown are exact p-values for: (a) test of homogeneity for stratified 2 ×2 tables (stratum =subset of 20 paired observations, four subsets); (b) McNemar test (pooled data, 80 paired observations); (c) correlation of nest fates (pooled data, 80 paired observations). Test specific p <0.05 shown in bold; asterisk indicates where p <0.05 after the sequential Bonferroni adjustment applied to the set of five tests on each time scale. See Fig. 1 for a scheme of the experiment and Fig. 3 for estimated effect sizes.

| Predator	Within pair	Between trial	Between year
(a) Homogeneity of data subsets			
all predators	0.823	0.523	**0.028**
jay	0.324	0.689	0.137
marten	1.000	0.578	0.154
squirrel	0.638	0.082	0.082
woodpecker	1.000	1.000	1.000
(b) Difference in proportion of depredated nests			
all predators	0.797	0.138	0.158
jay	0.915	0.293	0.924
marten	0.685	0.532	0.249
squirrel	0.685	0.265	0.265
woodpecker	0.532	0.824	**0.002***
(c) Correlation of nest fates			
all predators	0.079	**0.046**	0.135
jay	0.155	1.000	1.000
marten	0.345	0.634	0.685
squirrel	**0.038**	**0.005***	**0.005***
woodpecker	**0.001***	**0.001***	**0.020**
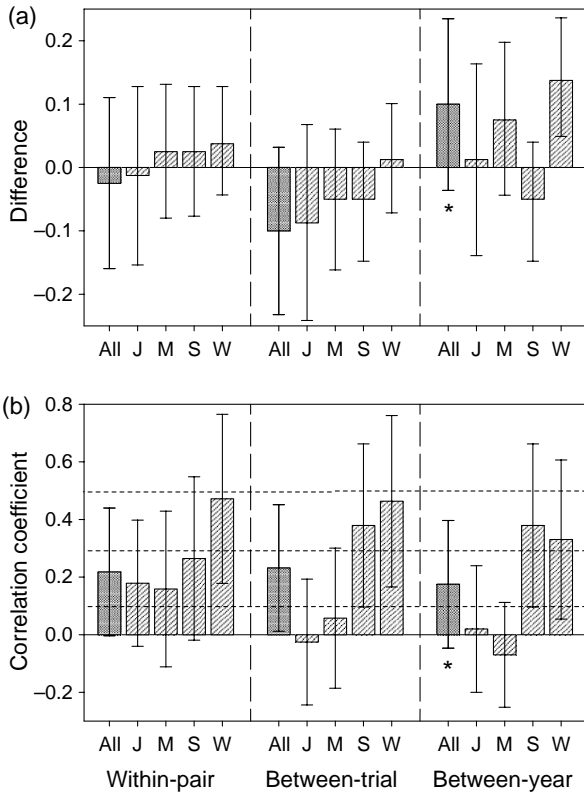
Figure 3. (a) Differences in proportion of depredated nests (with exact 95% CI) and (b) correlations of nest fates (with asymptotic 95% CI) evaluated on three different time scales. Estimates are shown for the total predation (All) and four dominant predator species (J = jay, M = marten, S = squirrel, W = woodpecker). Positive values in (a) indicates higher predation on: natural versus artificial nest sites, in second versus first trial, in second versus first year. Horizontal dotted lines in (b) correspond to small (0.1), medium (0.3) and large (0.5) standardized effect size. Data set for each analysis (column) consisted of 80 paired binary observations (nest successful/depredated); asterisk indicates heterogeneity among four subsets of 20 paired observations, that were reanalyzed separately (Fig. 4). See Fig. 1 for a scheme of the experiment and Table 2 for exact p-values.

events on the same nest within an experimental trial (Leimgruber et al. 1994).

Long-term repeatability

Ultimately, over 92% of nest sites were depredated at least once during the two-year experiment, but repeatability of predation between consecutive nesting trials was generally low. Overall proportion of depredated nests did not increase between trials throughout the experiment (Fig. 3a; Yahner and Mahan 1999) but the turnover of predators was high – from 1.4 (one trial) to 2.6 (entire experiment) species per depredated nest (also Leimgruber et al. 1994). We did not expect a long-term effect of predator memory – open-nesting songbirds in natural habitats (but see Wysocki 2004 for urban habitat) rarely reuse nest sites for repeated nesting attempts and there is generally little reward for predators revisiting previously used nest sites. Hence, the absence of long-term repeatability (except for woodpecker and squirrel) suggests that nest site features and/or nest
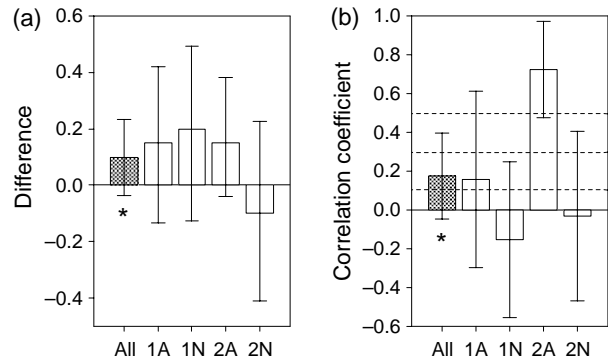

Figure 4. (a) Differences in proportion of depredated nests (with exact 95% CI) and (b) correlations of nest fates (with asymptotic 95% CI) estimated for the total predation on a between-year scale. Positive values in (a) indicates higher predation in second versus first year. Horizontal dotted lines in (b) correspond to small (0.1), medium (0.3) and large (0.5) standardized effect size. Asterisk indicates the estimates based on pooled data set of 80 paired binary observations (Fig. 3). The four open columns represent separate estimates for the four subsets of 20 paired observations (1A = trial 1 at artificial nest sites, 1N = trial 1 at natural nest sites, 2A and 2N = the same for trial 2). See Fig. 1 for a scheme of the experiment.

location did not influence the probability of multiple discoveries and/or random encounters with the same nests in this study.

Whatever the mechanism underlying repeatable predation, its effects are expected to diminish with lengthening time period between the consecutive nesting trials. Possible reasons include turnover of individuals in predator populations (diminishing memory effect), changes of spatial distribution of predators (repeated random encounters) and changes of nest site features due to vegetation development (multiple independent discoveries). Surprisingly, the reports of repeatable nest predation (Martin et al. 2000, Muchai and du Plessis 2005) come from between-year comparisons. Our findings of low between-trial and between-year repeatability are consistent with results of previous within-year comparisons (artificial nests: Angelstam 1986, Cresswell 1997, Ortega et al. 1998, Weidinger 2002, 2004, Remeš 2005; active nests: Styrsky 2005). In contrast to single-use open cup nests, predation on multiple-use cavity nests is more likely to be repeatable, because predators might learn location of cavities (repeated visits are rewarding) and depredate them from year to year (nest boxes: Sonerud 1993, Sorace et al. 2004; natural cavities: Nilsson et al. 1991, but see Wesolowski 2006).

Effect of predator species

The major predators of open songbird nests in woodland of central Europe are jay and marten (Weidinger 2009). We showed that both these species revisited previously depredated nests during a nesting trial, but their predation was not repeatable between trials or years. The only species whose predation was consistently and significantly repeatable on all time scales was woodpecker and, to a lesser extent, squirrel. Predation by woodpeckers was disproportionally low (30% of depredated nest sites vs
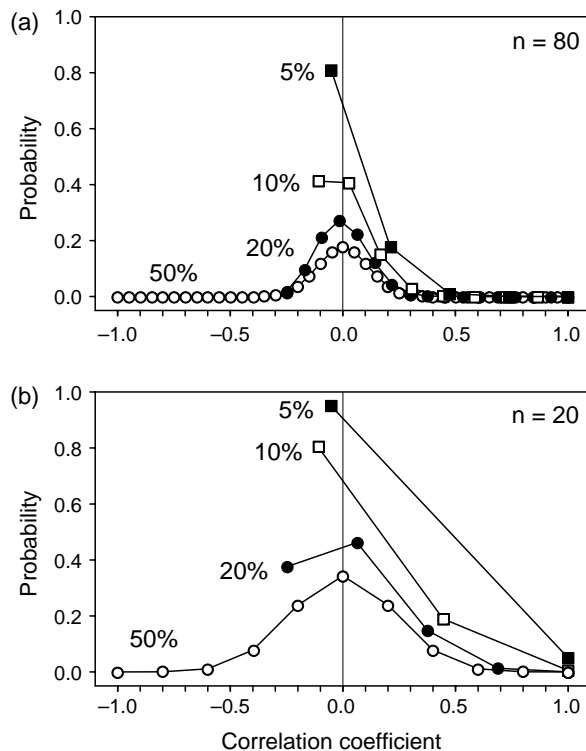
Figure 5. The exact frequency distribution of correlation coefficient between two binary variables. Sample size decreasing from 80 paired observations (a) to 20 paired observations (b) and an increasing imbalance in the frequency of binary responses within a sample (from 50% to 5%) cause the distribution to be asymmetric. Note that in the case of binary data, the Pearson and Spearman correlation coefficients and phi contingency coefficient are numerically equivalent.

80% in jay) with regard to their abundance (at least 1.5 times higher compared to jay). Woodpeckers were almost evenly distributed over all study plots and their predation was not spatially clumped on this scale (correlation of nest fates within the six plot-year samples; p > 0.9). However, predation by woodpeckers was highly clumped on the smallest spatial scale – within individual artificial nests (variance/mean ratio of events per nest: 7 vs 3 in jay; Table 1) and within nest pairs (correlation of nest fates; Fig. 3b). Videotaping revealed the same spatial pattern of woodpecker predation on active passerine nests (Weidinger 2009), which we attributed to site fidelity of woodpeckers (Michalek and Mietinen 2003) and individual foraging specialization. Similar interpretation of squirrel predation would be ambiguous as we have insufficient data about its abundance and distribution. Spatially clumped predation was seen also in racoon, an introduced predator, characterized by a low abundance and patchy distribution (data not sufficient for separate analysis).

Overall predation represents combined effects of individual predator species and, possibly, effects of different underlying mechanisms. We found that repeatabilities varied consistently among predator species on all time scales. Whether overall nest predation in a particular study system is repeatable thus depends on the composition of the local predator community. Interpretation of all previous studies of nest predation repeatability suffers from the lack of predator identification or from potential biases associated with indirect predator identification.

Methodological considerations

The varied conclusions of this and the other studies may be partly artifacts of methodology. In contrast to most previous studies, we were able to record multiple predation events on the same nest and to identify predator species. Yet, we could not identify individual predators. In consequence, repeatability at the individual level, as proposed above, must be interpreted with caution.

Repeatability of nest predation can be rarely studied on active nests (Wysocki 2004, Styrsky 2005) while artificial nests incur potential biases (Sonerud 1993, Thompson and Burhans 2004). Absence of parental behaviour, the major drawback of artificial nests, was an advantage rather than a weakness in the present study. We asked whether some specific nest locations have higher intrinsic chances of being depredated, independently of the predation risk associated with parental behaviour (for detailed reasoning see Martin et al. 2000). Most importantly, the overall daily predation rate of artificial nests in our study (0.070 ± 0.007 SE, n = 160) was close to that for control active thrush nests (0.077 ± 0.009, n = 101) and the proportional species composition of predators was similar to that at videotaped active nests (Weidinger 2009). A previous study also showed that nest predation rates were not appreciably influenced by an observer effect, either directly (observer presence at nests) or indirectly (cues left at the visited nests; Weidinger 2008).

Using comparatively large and hard shelled quail eggs in artificial nest experiments has been criticized because these eggs are difficult for small predators (rodents) to break and eat, which was suggested to underestimate the role of small predators (Maier and DeGraaf 2000). In line with this view, we recorded mice (mainly yellow-necked mouse *Apodemus flavicollis*) during 56% (90/160) trials at 93% (37/40) nest sites, while we have not recorded any successful depredation of a quail egg. However, we suggest that using mice-proof quail eggs was an advantage rather than a weakness in this study. In spite of general belief based on indirect evidence from artificial nest studies (e.g. imprints in plasticine eggs, Weidinger 2002, Remeš 2005; photographs from artificial nests, this study), we have no evidence that mice are important predators of natural (i.e. defended) open-cup nests in our study system (Weidinger 2009). We explain the frequent visits by mice to artificial (i.e. undefended) nests as a result of random encounters (mice are abundant and ubiquitous in forest undergrowth) or possibly as an active search of roost sites. Considering mice visits to artificial nests as predatory events would introduce a serious bias in the estimation of predation rates and correlation of nest fates. Taken together, we believe that our experimental design and the field protocol were adequate to the purposes of the present study.

Location of this study rather than experimental design may partly account for the lack of consistently repeatable nest predation. The managed forest habitat in our study area was characterized by high nest densities within a distinct vegetation strata and high predation rates. We

speculate that many predation events in this system result from random encounters with abundant nests, which in effect may mask any systematic patterns in predation rates. If so, then the overall predation rates as well as the proximate relationships between risk of predation and nest site characteristics, now observed in human-altered habitats (this study), may differ from those still found in historically less modified areas (Bock and Jones 2004).

Finally, the lack of unambiguously significant effects in this and similar studies may be partly attributable to low statistical power due to limited sample sizes. Although it is not clear what effect size (in terms of correlation) should be considered biologically significant in the case of nest predation repeatability, we adopted a general rule proposed by Cohen (1988) for the correlation coefficient: small effect (0.1), medium effect (0.3), large effect (0.5). According to this definition, the effect sizes found in the present study were small (overall predation and the principal predators) to medium (occasional predators). The confidence intervals around estimates of effect size mostly overlapped with zero, yet suggest potentially large effects in occasional predators (Fig. 3b). From this perspective we conclude that our study had sufficient power to detect correlations in nest fates of medium or large strength. However, presence of small effects, whether or not biologically significant, can not be excluded. Because the sample size manageable within a single study of this kind is logistically constrained, we advocate replicating studies rather than increasing sample sizes (Johnson 2002).

Analyses of repeatable nest fates (successful/depredated) often neglect the statistical properties of correlation/association between two binary variables. Decreasing sample size and increasing imbalance in the frequency of binary responses within a sample (proportion of depredated nests markedly different from 0.5) causes the exact distribution of any correlation statistic to be very asymmetric (for an example see Fig. 5). Consequently, the exact p-values are preferable to the asymptotic ones when assessing statistical significance of the correlation, while the asymptotic confidence intervals for the correlation statistic should be treated as an approximation when assessing the potential effect size (see above). In the present study the above problems apply mainly to woodpecker, the species showing consistently repeatable predation.

Conclusions

Taken together, results of this study showed that repeatability of nest predation depends on the time scale considered and the predators involved. Nest predation was repeatable on a short time scale (within-trial) in all predators, but it was not spatially correlated (within paired nests or within study plots) and not repeatable on longer time scales (between-trials or between-years) in the principal predators (jay, marten). These findings suggest short-term effect of predator memory causing revisitation of previously depredated nests during a current nesting trial (all predators), but do not support an effect of nest site features on multiple nest discoveries and/or an effect of nest location on repeated random encounters with the same nest (principal predators). Long-term repeatability and small-scale spatial correlation (within paired nests, but not within study plots) was detectable in occasional nest predators (woodpecker, possibly also squirrel). Because we do not expect long-term effect of predator memory causing revisitation of depredated nest sites, we explain the long-term repeatability as an effect of nest site location. We caution against findings of repeatable nest predation resulting simply from statistical properties of binary data (nest fates) when a small proportion of nests is located in feeding territories of specialised individuals of occasional predator species. Any future work in this area should consider the ecological context of nest predation (nest densities, predator species composition and abundance, type of habitat) and go beyond identification of predator species to identification of individuals. A practical implication for future nest predation studies is that multiple predation events on the same nest during a current trial are obviously not independent, while results of repeated trials on the same nest sites are unlikely to be strongly correlated.

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