

# Complex habitat patterns create unpredictable nest predation risk – an artificial nest experiment

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Although birds might increase nesting survival by selecting safe sites, nest predation is a major limiting factor in natural bird populations. We investigated how forest structure, predator distribution, and nest location contribute to nest predation risk, and whether lower predation probabilities characterize formerly “safe” sites. We distributed 304 artificial ground and tree nests in a forest landscape, following the previous year locations of forest grouse observations (with and without broods). We modelled nest predation incidence using generalized mixed models; we also identified potential nest predators by tooth/bill marks on plasticine eggs. We found complex habitat effects: nest predation depended non-linearly on the stand age (low risk in post-clear-cut stands; peak values in middle-aged stands) and there were no simple relationships with predator proximity or nest concealment. Predation probabilities were higher in tree nests than in ground nests, and did not differ in the locations where broods had been observed or not. The results can be partly explained by the behaviour of the most frequent nest predator species, the pine marten, that forages both on the ground and in the canopy and avoids open areas. We suggest that large-scale modifications in forest age structure can alter not only landscape-scale predation pressure on bird nests, but also small-scale distribution and predictability of the predation, which can explain declining numbers of forest-specialist bird species.



## 1. Introduction

Nest predation is the most frequent proximate cause of reproductive failure in birds and a major factor of their population status (Martin 1993, Robinson & Wilcove 1994). Nest predation risk is affected by habitat factors at multiple scales, and birds can increase their nest survival by predicting safer sites (Martin 1995, Eggers *et al.* 2005, Mönkkönen *et al.* 2007). The effect of nest concealing structures (e.g., canopy cover and ground vegetation) on nest predation has been widely studied (Storch 1994, Delong *et al.* 1995, Hanski 1996, Seibold *et al.* 2013). Profound indirect ef-

fects, which can emerge from landscape changes (e.g., decreasing nesting habitats and increasing edge habitats), are also well-documented (Donovan *et al.* 1997, Huhta *et al.* 1996, Chalfoun *et al.* 2002, Stephens *et al.* 2004). However, there has been less attention on the predictability of nest safety in relation to anthropogenic factors.

Nest predation gradients are widely documented in forest-farmland mosaics (Wilcove 1985, Andrén *et al.* 1985, Andrén 1992, Svobodová *et al.* 2012), but less studied along managed forest mosaics, including stands of various age and human influence (such as artificial drainage). Some artificial nest experiments have described

increased predation risk due to landscape fragmentation caused by logging (Yahner & Scott 1988, Wegge *et al.* 2012), which has been confirmed in several forest-specialist birds (e.g., Hoover *et al.* 1995, Huhta *et al.* 2004, Poulin & Villard 2011). In contrast, local habitat factors (e.g., distance from edge, stand age) have shown inconsistent relationships with nest predation in forests (Hanski *et al.* 1996, Zanette & Jenkins 2000, Lahti 2001). Forest structural transformation, for example, can change the relative vulnerability of tree-nests vs. ground nests. In a managed landscape, Wegge *et al.* (2012) found twice higher losses of ground nests compared with nests above ground, whereas no such difference was found in pristine forest inhabited by different predators. Poor nest concealment might explain why ground nests suffer from high predation in open early-successional (Einarsen *et al.* 2008) or sparsely stocked stands (Martin & Roper 1988, Seitz & Zegers 1993). These results imply that even partial harvesting can alter the safety of nests (Morris & Conner 2016).

In addition to changing nest concealment, production forestry may create habitats favoured by common generalist mesopredators (Rolstad & Wegge 1989, Kurki & Linden 1995, Červinka *et al.* 2011). In Europe, such predators include the red fox (*Vulpes vulpes*) (Kurki *et al.* 1998, Jahren 2012) and corvids, such as the hooded crow (*Corvus cornix*) and the Eurasian jay (*Garrulus glandarius*) (Andrén 1992). For instance, opportunistic nest predation may increase where logging creates extensive early-successional areas favoured by foxes (Kurki *et al.* 1998, Savola *et al.* 2013).

In turn, because clear-cuts are avoided by another opportunistic predator, pine marten (*Martes martes*) (Storch *et al.* 1990, Brainerd & Rolstad 2002), this species may forage more intensively within the remnant forest patches (Červinka *et al.* 2011). Thus, nest predation in production forests can re-organize spatially and increase in frequency, for example due to reduced habitat patch sizes (Seymour *et al.* 2004). So far, such landscape dynamics of nest predation in relation to forest management have been insufficiently studied.

The current study focuses on the predictability of nest predation risk from a multi-factor perspective in a variably managed forest-wetland mosaic.

We used artificial nests to examine four predictions:

- (i) We proposed that predation risk is a stable, habitat-related characteristics of the sites where birds have recently bred successfully, i.e., safe sites are predictable by the birds (see Storch 1991). We used data on forest grouse broods to address this prediction, given that long-term population declines in the capercaillie (*Tetrao urogallus*) and black grouse (*Tetrao tetrix*) are often associated with increased nest and brood predation in managed forests (Marcström *et al.* 1988, Kurki *et al.* 1998, Kauhala & Helle 2002).
- (ii) Since ground nests are accessible to all terrestrial predator species, these would be more vulnerable to predation than nests built on trees or shrubs (Burke *et al.* 2004, Wegge *et al.* 2012).
- (iii) At the stand scale, predation risk is higher in the habitats created by modern even-aged forestry, notably in clear-cut edges and young regenerating forests.
- (iv) At the landscape scale, nest predation is higher in human-modified forest landscapes than in near-natural ones.

## 2. Methods

### 2.1. Study area and sampling design

We conducted our study in a low-lying (25–32 m a.s.l.), sparsely inhabited forest-wetland landscape in the Soomaa region, south-western Estonia (ca. 58°20' N, 25°00' E). The landscape (ca. 100 km<sup>2</sup>, Fig. 1) consisted of densely drained wetland forests around pine bogs of the West-Estonian plateau type (Paal & Leibak 2011) and coniferous forests on mineral soils. The forests had been drained between 1960s and 1980s and were dominated by Scots pine (*Pinus sylvestris*) and downy birch (*Betula pubescens*). The landscape hosts dense populations of three forest grouse species: capercaillie, black grouse and hazel grouse (*Tetrastes bonasia*) (e.g., Oja *et al.* 2018).

On 7–22 June 2015, the dataset of capercaillie, black grouse and hazel grouse was collected by systematic mapping of grouse individuals. The

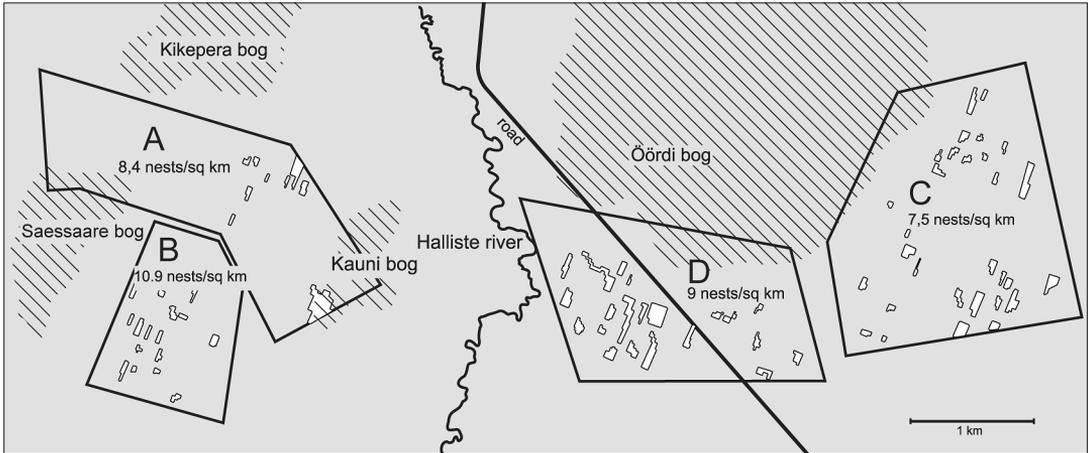


Fig. 1. Map of the study landscape. Bogs are marked as dashed areas, < 10 year-old clear-cuts as white patches. The sub-areas (A–D) are delineated with black lines and the densities of established artificial nests (nests/km<sup>2</sup>) are indicated for each sub-area.

whole landscape was subdivided into 53 plots (mean size 50 ha), each of which was searched by one observer during one day at approximately 50-m intervals. The observers recorded coordinates, numbers, sex, and brood incidence of the grouse individuals seen. In addition, all the predator tracks and signs were recorded, photographed or collected.

In May 2016, we placed 304 artificial nests in the field for 20 days. We established four nests in each of the 76 locations where female forest grouse had been detected in the previous year, with or without broods. The majority of female grouse mate (Wittenberger 1978), hence we assumed that the nests or broods of solitary hens were depredated. The observation spots were re-located in the field using GPS, and two pairs of ground and tree nests were placed at a distance of 70–75 m from the original observation. This distance was a compromise between spacing out for observa-

tional independence (see Degraaf *et al.* 1999), while still representing the original brood observation site. Within each pair, the distance between a ground and tree nest was 3–5 m (Fig. 2).

We mimicked natural forest grouse nests, by creating simple scoops into semi-concealed sites with shrubs, underneath or close to the Scots pine or Norway spruce (*Picea abies*). To mark nest locations, we binded tapes around neighbouring trees at 1.5 m height. We created tree nests by binding plastic coated 3 mm wire around the tree or snag at 1.8–2 m height and filled the ring with immediate surrounding material, such as moss and leaves (see Degraaf *et al.* 1999). Each nest contained 2 quail eggs (30 × 22 mm, 10 g) and 1 brown plasticine egg of similar size. After 20 days, we revisited the nests and recorded these as depredated (at least one egg missing) or intact. We collected the plasticine eggs present for identification of tooth/bill marks of predators.

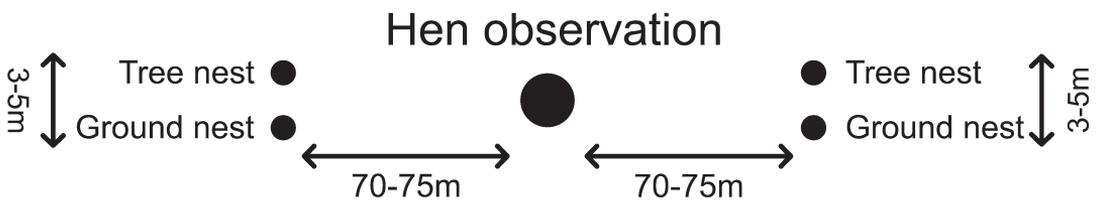


Fig. 2. Experimental design of the artificial nest set around a location of a female grouse observation from 2015 ("hen observation").

Table 1. The four sub-areas ordered by naturalness and their key characteristics.

Sub-area	Naturalness	Key characteristics
A	1	Continuous multi-aged forest mosaic with old-growth stands, bogs
B	2	Mildly managed multi-aged forest with old-growth stands, no bogs
C	3	Middle-aged production forest, fragmented old-growth stands, protected bog edge
D	4	Fragmented and logged production stands, protected bog edge

## 2.2. Recording predator information

To detect numerically dominant predator species in the sub-areas, we used predator observations and signs, including tracks, faeces and feathers of raptors and corvids (see Oja *et al.* 2018). The observations were systematically recorded and digitized as a part of the landscape-scale grouse survey in 2016 (a survey repeated within the same area and using the same methods as in 2015). We calculated the number of predator observations ( $N = 165$ ) per km<sup>2</sup> for a landscape index of predator abundance (Appendix 2). For a nest-location scale index of predator proximity, we measured the distance (m) from each artificial nest to the nearest mammalian predator observation and nearest avian predator observation.

## 2.3. Nest site and habitat characteristics

At the location of each artificial nest pair, the same observer made visual estimates of canopy cover (5% accuracy), ground visibility and evergreen shrub cover and species both at the time of nest establishment and removal. We included evergreen shrubs only since deciduous shrubs lacked leaves and did not provide much concealment in the experimental period. Canopy cover (by overstorey trees) was estimated around each nest pair in a 5 m radius. Ground-level horizontal visibility was expressed as the reverse of the visible proportion of a wooden pole (1 m tall, 6 cm wide) assessed at 1-m height and 5-m distance from the ground nest. To detect the impact of forest management to a nest site, we also measured the distance (m) between each artificial nests and the nearest clear-cut.

To assess nest predation at the landscape scale, we delineated 4 sub-areas based on overlapping polygons that were generated around the grouse observation points using 200-m radii. Each sub-

area contained at least one capercaillie lek. To illustrate landscape differences, we calculated the proportions of wetlands, clear-cuts and stand age classes in each sub-area (Table 1, Appendix 1), using MapInfo and digital maps provided by Estonian Land Board. We ranked the 4 sub-areas in the order of naturalness (A–D) based on proportions of clear-cuts and young stands.

## 2.4. Statistical processing

Predation probabilities in the locations of hens with or without broods were compared by using two-way contingency table and a chi-square test. Generalized linear mixed models (GLMM) with binomial distribution and logit link were analyzed with “lme4” package (Bates *et al.* 2014) in R 3.0.1 (R Core Team 2013) for effects of nest site characteristics on the incidence of nest predation (dependent variable). The predictors “sub-area” and “nest pair” (tree + ground nest) were included as random predictors. Independent predictors included: nest location (ground or tree), stand age, nearest clear-cut, ground visibility, canopy cover, shrub cover, nearest avian predator and nearest mammalian predator. All continuous variables (stand age, nearest clear-cut, nearest avian predator, nearest mammal predator) in the GLMMs were zero-centered. Given our focus on complex habitat effects, we also tested for square terms (non-linearity), even when linear effects were absent. For distinguishing the best model sets, we compared alternative models comprising sets of uncorrelated variables and using the small sample size corrected Akaike information criterion (AICc) with ‘MuMIn’ package (Barton 2009). We tested polynomially only those two variables that had  $\Delta AICc < 2$  (Bozdogan 1987). All the tests were two tailed. In total, 19 models were tested (Appendix 3).

Table 2. Predation probabilities and predator abundance index (no. of observations / km<sup>2</sup>) in each sub-area. Total sample sizes in each sub-area are in brackets. See Appendix 2 for details of the predator counts.

Sub-area	Predation probability			Predator observations / km <sup>2</sup>
	Total	Ground nests	Tree nests	
A	79% (68)	68% (34)	91% (34)	8.4
B	73% (58)	71% (29)	79% (29)	3.7
C	83% (92)	76% (46)	89% (46)	2.7
D	67% (86)	67% (43)	67% (43)	5.4
Total	76% (304)	70% (152)	82% (152)	4.6

### 3. Results

The total predation probability was 76% (70% in ground nests; 82% in tree nests, Table 2). Eighty of the 231 depredated nests revealed predator marks that were assigned to: unknown mammal (32%), pine marten (21%), unknown bird (15%), Eurasian jay (12%), small mustelid (9%), red squirrel (5%), raccoon dog (*Nyctereutes procyonoides*) (2.5%), large carnivore (1%) and red fox (1%). The rest of the 151 depredated nests either lacked the plasticine egg (27%), the egg had no predator

marks (41%) or the marks were unclear and probably belonged to rodents (31%). We did not observe accordance between nest predation probability and predator observation densities at the sub-area level (Appendix 2).

Landscape-scale depredation probabilities varied from 67% to 83%, being lowest in the sub-area D that had the highest proportion of young stands, and highest in the sub-area C with highest cover of middle aged stands (Table 2). The depre-

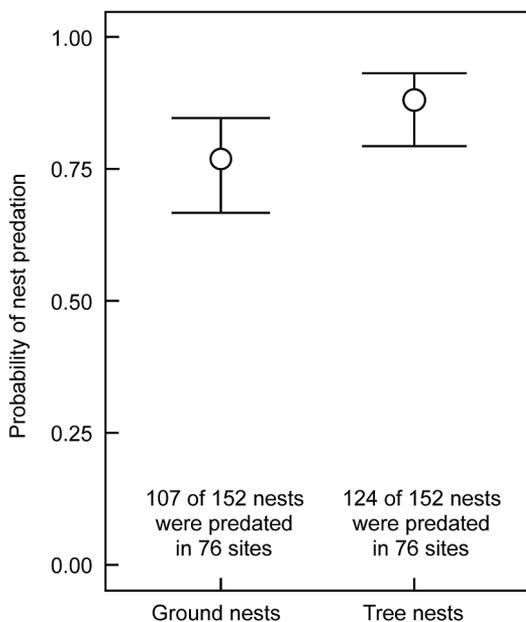


Fig. 3a. Mean predation probability ( $\pm$  SE) of ground and tree nests; dots represent mean values (back-transformed from the logit model to linear scale).

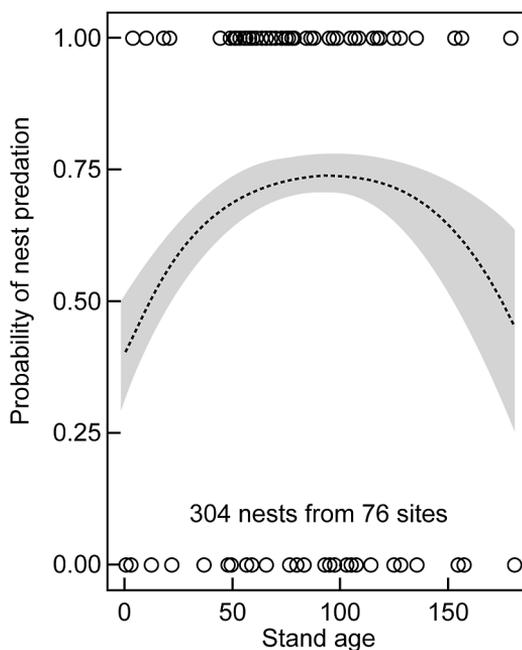


Fig. 3b. Relationship between the nest predation probability (304 nests in 76 sites) and stand age (years). Grey area denotes standard error estimate for the fit. The values are back-transformed from logit models to linear scale.

Table 3. Fixed effects of the best mixed logit models of predation probability.

Fixed effects	Estimate±SE	Z	P
Intercept	0.99±0.23	4.20	< 0.001
Nest location (Tree nests)	0.81±0.30	2.64	0.008
Stand age	4.16±2.63	1.58	0.114
(Stand age) <sup>2</sup>	-6.19±2.62	-2.37	0.018

Fixed effects	Estimate±SE	Z	P
Intercept	0.99±0.27	3.61	0.001
Nest location (Tree nests)	0.81±0.31	2.64	0.008
Shrub cover	-0.30±0.16	1.91	0.056

dation probabilities did not differ in the locations with previous year's grouse broods (78%) vs. the locations of single females without brood (75%;  $\chi^2_1 = 0.2, p = 0.65$ ).

Among alternative logit models of predation incidence, the best model incorporated the variables "stand age" and "nest location" (ground vs tree) (Fig. 3a–b). This model contained a non-linear (unimodal relationship) with stand age: low predation in the youngest stands and high predation in mid-aged stands (Fig. 3b, Table 3). However, a later decrease of predation in old forests could not be confirmed due to high variation of nest predation probability for old-aged stands. Another model, where the factor "nest location" was combined with "shrub cover" did not differ from the best model in terms of AICc ( $\Delta AICc = 1.84$ ) but the negative effect of "shrub cover" was only marginal ( $p = 0.056$ ). Incorporating an interaction between the factors did not improve the latter model. We did not find any significant relationships between nest predation and ground visibility, canopy cover, nearest clear-cut, nearest avian predator or mammal observation.

#### 4. Discussion

The predation probabilities were not lower in the sites where grouse had formerly been observed with broods compared to sites where only grouse without broods were observed. This result contrasts with our prediction (i); as well as with Brittas and Willebrand (1991) and Storch (1991) who

showed that capercaillie hens tend to select less predated nest sites. Instead, our key results support the idea that local risk of opportunistic predation is difficult to predict for breeding birds and, thus, can set limits to active nest site selection as a buffering mechanism (Filliater *et al.* 1994, Forstmeier & Weiss 2004).

In intensively managed areas another mechanism may be a lack of high-quality breeding habitats, so that birds selecting safer habitats are facing a more severe trade-off with other conditions needed for successful breeding (Misenhelter & Rotenberry 2000). One factor contributing to this difficulty is probably the study landscape characteristics. Another study in the same landscape confirmed that nest predation pressure varies at broad scales and comprises multiple predators (Oja *et al.* 2018). Our study tentatively supported that result and highlighted some potentially important landscape differences (but we acknowledge our small sample size).

In contrast to our initial prediction (ii), but supporting the idea of highly variable predation risk, we found tree-nests significantly more depredated than ground nests. While tree nests are accessible to a subset of predators (notably avian and arboreal mammal predators), elevated tree nest predation has been repeatedly reported in heterogeneous temperate forest landscapes (Yahner & Wright 1985, Rudnický *et al.* 1993, Seitz & Zeger 1993, Sloan *et al.* 1998, Flaspohler *et al.* 2001). Perhaps, when such predators are abundant, they can be more efficient in finding the nests on discrete structures, such as trees, than a wider range of predators in the ground vegetation.

Wegge *et al.* (2012) elaborated that artificial ground nests can be more vulnerable in a managed than a natural forest landscape due to different predator faunas. Managed forest landscapes can host increased numbers of mammalian ground nest predators (e.g., red fox; Kurki *et al.* 1998, Jahren 2012), while natural forests can host more arboreal predator species (e.g., pine marten; Storch *et al.* 1990, Brainerd & Rolstad 2002). Based on four sub-areas, our results suggest the opposite: the least logged sub-area A had the most pronounced difference in predation probabilities (23% higher in tree nests), while near-equal probabilities were observed in the most extensively logged sub-area D. We also found that, while higher shrub cover

tended to associate with less frequent predation, this relationship was not distinct for tree nests and ground nests (no interaction detected). Thus, the importance of concealment specifically for ground nests (as reported by, e.g., DeLong *et al.* 1995, Coates & Delehanty 2010, Huhta *et al.* 2015) was not supported in our system.

Nest predation probabilities were highest in mid-aged post-clear-cut stands, but lowest in early-successional stands – a similar result to Storch (1991). At the landscape scale, this corresponded to a similar contrast between the sub-area D vs. the sub-area C (rich in middle-aged stands; high risk). Hence, we obtained mixed results for our predictions (iii–iv) of high predation probability in the most managed nest sites and sub-areas. Further, we did not find a relationship between predation probabilities and clear-cut vicinity, and we could not separately confirm the tendency of reduced risk in old stands. The latter could be due to our small sample size from old stands and the pattern deserves further study. However, the high risk of nest predation in the sub-area C, which comprised extensive areas of fragmented old stands, may refer to a specific edge effect between clear-cuts and mature stands (Yahner & Scott, 1988, Huhta *et al.*, 2004, Poulin & Villard, 2011). As fragmented forest stands can both attract mesopredators (Seymour *et al.* 2004, Červinka *et al.* 2011) and provide nest sites in the reduced forest patches, habitats like our sub-area C can develop into ecological traps for forest birds.

The main nest predation patterns detected suggest a key role of the pine marten – the most frequent nest predator in our study area as revealed both by field observations and tooth marks on plasticine eggs (see also Summers *et al.* 2009). Specifically, this species forages both on the ground and in the canopies (explaining high predation probabilities of tree nests) and avoids clear-cuts and early-successional forests (Brainerd & Rolstad 2002, Červinka *et al.* 2011). Red fox – a major ground-nest predator in North-Europe (Marcström 1988, Wegge & Rolstad 2011, Jahren 2012) – was rare in our landscape in 2015 and 2016 (detected just once by marks on plasticine eggs). The lack of a relationship between nest predation and predator vicinity or density can probably be attributed both to the mobility of individual predators and their incomplete detection during

single-visit surveys. Yet, the lack of these effects supports the idea that predator presence is difficult to predict also for nesting birds (see also Storaas & Wegge 1987).

We also acknowledge that artificial nest experiments may not fully reflect birds' opportunities to address predation risk. Specifically, artificial nests disregard parental defence and behavioural nest concealment, which can increase the survival of natural nests (Faaborg 2004, Hu *et al.* 2017). Human scent and high density of nests can potentially attract mammalian predators and overestimate predation probability (Small & Hunter 1988, Major & Kendal 1996, Burke *et al.* 2004). However, our sampling locations were based on actual grouse observation sites and the 76% total predation probability observed is similar to the ca. 75% share of Capercaillie females without broods in June as reported in the area (Löhmus 2016, see also Jahren 2002 for similar estimates elsewhere). Additionally, the effects studied are only based on the assumption that artificial nests reveal habitat related *differences* in predation pressure, which are otherwise difficult to study in infrequent species (see Villard & Pärt 2004).

In conclusion, we can see multiple nest predation gradients not only in forest-farmland mosaics, but also in managed forest-wetland landscapes. In forest-farmland mosaics, the gradients are created by edges between agricultural lands and reduction of forest patches; in forested wetlands, the gradients are primarily driven by forest age and successional changes, including their silvicultural modification. More specifically, we tentatively conclude that intensive clear-cutting based forestry can change not only landscape-scale predation probabilities, but also small-scale distribution and predictability of nest predation by breeding birds (see also Yahner & Scott 1988).

Large clear-cuttings may create dynamic spatial contrasts in the predation pressure, which concentrates into mid-aged and fragmented mature forests that are used both by forest specialist birds (Huhta *et al.* 2004, Poulin & Villard 2011) and nest predators (Červinka *et al.* 2011, Payer & Harrison 2003). In a time perspective, post-harvest succession of clear-cuts and new harvest entries maintain a rapid turnover of the landscape, its predator assemblages, and possibilities of birds to find safe nesting sites (Franklin & Forman 1987).

It is possible that some bird species, such as grouse (Kämmerle *et al.* 2017), cannot cope with these changes, even if safe nest sites exist (see also Schmiegelow & Mönkkönen 2002). Thus, forest managers should pay attention to nest predation as a possible cause of bird declines. For instance, reducing clear-cut size and decreasing the proportion of logged areas on landscapes creates less spatial contrasts, and protecting larger contiguous patches may relieve possible aggregation of predation.

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### Heikosti ennustettava saalistusriski monimuotoisissa elinympäristöissä – kokeellinen lähestymistapa

Vaikka linnut voivat parantaa pesimämenestystään valitsemalla turvallisia pesäpaikkoja, saalistus on silti usein tärkein populaatiokokoa säätelevä tekijä. Tässä tutkimuksessa selvitimme miten metsän rakenne, saalistajien jakautuminen ja pesän sijainti vaikuttaa pesäpredaatioon, ja ovatko aiemmat pesimäpaikat vähemmän vaarallisia. Sijoitimme 304 keinopesää maastoon ja puihin, puolet näistä paikoille, joilla oli edellisenä vuonna havaittu pesiviä metsäkanalintuja, ja analysoimme pesäpredaatiota sekamallien avulla. Selvitimme myös saalistajien ryhmiä keinomunien avulla, nokan/hampaanjalkien perusteella.

Havaitsimme, että saalistus riippui habitaatista: Avohakkuualueilla oli alhainen riski kun taas keski-ikäisessä metsässä korkein pesäpredaatio-riski. Pedon läheisyys tai pesän suojaisuus ei merkittävästi vaikuttanut pesäpredaatioon. Predaatio oli suurempaa puissa kuin maapesissä, mutta ei ollut yhteydessä aiempien metsäkanalintujen havaintopaikkoihin.

Tuloksia voi osittain selittää alueen yleisimmän pedon, näädän, käyttäytyminen: se saalistaa sekä puissa että maassa, ja välttää avoimia alueita. Tulosten perusteella voidaan sanoa, että laajamit-

taiset muutokset metsän iässä ja rakenteessa voivat muuttaa saalistuspainetta ja sen ennustettavuutta sekä maisematasolla että yksittäisten metsiköiden tasolla. Tämä voi osin selittää metsä(kana)lintujen väheneviä kantoja.

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Appendix 1. Study area characteristics and stand age structure. OAN = Order of Area Naturalness, WG = Wetland/grassland

Area	OAN	Key characteristics	Stand age structure (years)								WG
			>121	100– 120	80– 99	60– 79	40– 59	20– 39	10– 19	0– 9	
A 830 ha	1	Continuous multi-aged forest mosaic with old-growth stands; bogs	8% 69 ha	13% 106 ha	21% 176 ha	24% 201 ha	16% 136 ha	6% 50 ha	2% 13 ha	1% 11 ha	8% 68 ha
B 534 ha	2	Mildly managed multi-aged forest mosaic with old growth stands; no bogs	2% 12 ha	20% 107 ha	28% 147 ha	22% 119 ha	13% 70 ha	7% 39 ha	7% 37 ha	1% 2 ha	0% 0 ha
C 1,211 ha	3	Middle-aged production forest, fragmented old-growth stands, protected bog edge	7% 81 ha	9% 121 ha	18% 217 ha	30% 358 ha	15% 181 ha	5% 58 ha	6% 69 ha	7% 84 ha	3% 42 ha
D 994 ha	4	Fragmented and logged production stands, protected bog edge	7% 66 ha	6% 63 ha	12% 121 ha	22% 217 ha	19% 188 ha	7% 70 ha	7% 68 ha	12% 119 ha	8% 79 ha
3,569 ha		Total area	6% 228 ha	11% 397 ha	19% 661 ha	25% 895 ha	16% 575 ha	6% 217 ha	5% 176 ha	6% 216 ha	8% 189 ha

Appendix 2. Predator observations in the study area.

Predator observations	Areas A–D (km <sup>2</sup> )				
	A (8.3)	B (5.3)	C (12.1)	D (10)	Total (4.6)
Total predator observations	61	20	30	54	165
Large carnivore	8	3	7	6	24
Mammal mesopredator	22	10	13	23	68
Raptor/corvid	23	5	6	12	46
Wild boar	8	1	4	10	23
Unknown predator		1		3	4
Total observation No./km <sup>2</sup>	8.4	3.7	2.7	5.4	4.6

Appendix 3. Overview of all tested models, including selection statistics.

Model no.	Predictor trait										Model selection statistics				
	Nest location	Stand age	Nearest clearcut	Ground visibility	Canopy cover	Shrub cover	Nearest raptor	Nearest mammalian predator	df	logLik	AICc	ΔAICc	AICcwt		
1		P							6	-158.439	329.2	0	0.266		
2									5	-160.399	331.0	1.84	0.106		
3									5	-160.721	331.6	2.48	0.077		
4									6	-159.727	331.7	2.58	0.073		
5			P						6	-159.813	331.9	2.75	0.067		
6									5	-160.945	332.1	2.93	0.062		
7									6	-159.941	332.2	3.00	0.059		
8									5	-161.105	332.4	3.25	0.052		
9									6	-160.393	333.1	3.91	0.038		
10									6	-160.705	333.7	4.53	0.028		
11									6	-160.721	333.7	4.56	0.027		
12									6	-160.853	334.0	4.83	0.024		
13									6	-160.911	334.1	4.94	0.022		
14									6	-161.040	334.4	5.20	0.020		
15									6	-161.102	334.5	5.33	0.019		
16									5	-162.180	334.6	5.40	0.018		
17									5	-162.184	334.6	5.41	0.018		
18									5	-162.238	334.7	5.52	0.017		
19									6	-162.180	336.6	7.48	0.006		

Gray fields denote effects that were included into particular models  
 P denotes second order polynomial effect