Landscape and habitat affect frequency of artificial duck nest predation by native species, but not by an alien predator

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3 by an alien predator

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10   **Abstract**

11   Annual Finnish breeding duck surveys over the last 30 years show declining abundance among

12   several species and greater declines on eutrophic waters than oligotrophic lakes. It has been

13   suggested that habitat-related differences in the rate of increase in predation pressure is a potential

14   explanation for contrasting duck population trajectories between habitats. We assessed potential

15   duck nest predation risk and predator presence in various duck breeding habitats in Finland and

16   Denmark by monitoring 333 artificial duck nests with wildlife cameras during 2017-2019.

17   Predation rates differed between landscapes and habitats: nest predation rate and predator diversity

18   were lowest in forested habitats and highest in agricultural landscapes. Forest nests further from

19   water bodies survived better than nests around shorelines of permanent lakes. Of the 16 different

20   predator species detected, the most common were Eurasian magpie (*Pica pica*), hooded crow

21   (*Corvus corone*) and raccoon dog (*Nyctereutes procyonoides*). While predation by specific native

22   predator species was typically associated with particular habitats and landscapes, the alien raccoon

23   dog appeared to be a true habitat generalist, ubiquitous and common across all habitats and

24   landscapes. Based on these results, the higher duck nest predation pressure along shorelines,

25   especially in agricultural landscape lakes, due to increased diversity and abundance within the

26   predator community, may contribute to the declining population trends of ducks.

27

29   Running headline: Habitat related frequency of duck nest predators at artificial nests

30

31

Introduction

Nest predation is an important determinant of avian reproductive output (Newton 1998). Predation pressure seems to be the most important factor affecting boreal duck nest site selection and nesting success (Holopainen et al. 2015). Thirty years of annual Finnish breeding duck pair surveys show declining trends across several species and greater declines on eutrophic waters than oligotrophic lakes (Pöysä et al. 2013; Lehikoinen et al. 2016). Habitat-related differences in the rate of increase in predation pressure has been suggested as a potential explanation for contrasting duck population trajectories between habitats (Pöysä et al. 2019).

Predator presence and densities vary between habitats, affecting local avian nest predation rates (Stephens et al. 2005). Landscape productivity affects general prey abundance and therefore predator abundance. Fragmented agricultural landscapes in particular, offer landscape complexity and a rich energy/prey base, and hence high predator densities compared to continuously uniform forested areas (Andrén 1992; Roos 2002).

Several invasive alien predator species have become dispersed widely in Europe during the last five decades, particularly the raccoon dog (*Nyctereutes procyonoides*) and American mink (*Neovison vison,* Kauhala 1996). Invasive species affect native ecosystems by complex interactions with native species (McGeoch et al. 2010), of which predation is among the most profound direct effects (Mooney & Cleland 2001). Alien species can have greater effects on prey species than native predators (Salo et al. 2007). However, the role of alien species as nest predators remains largely unknown. Reviews show American mink have significant effects on ground nesting birds (Bonesi & Palazon 2007), but while the raccoon dog has been reported to affect native fauna locally, it has not been proved as harmful to prey populations in Europe (Mulder

54 2012). However, recent studies have raised concerns about the raccoon dog as a duck nest predator

55 (Dahl & Åhlen 2019; Nummi et al. 2019).

56 To understand the relative levels of predator species abundance and potential predation pressure

57 at duck nests situated in different breeding habitats in Finland and Denmark, we established large

58 numbers of artificial duck nests monitored by wildlife cameras. We were especially interested in

59 predation rates and habitat use by raccoon dogs in relation to native predator species. Although

60 vegetation structure and productivity affect nest detectability and predator behaviour at nest-site

61 level (Ringelman et al. 2018), we predict a more abundant and diverse predator community in

62 eutrophic agricultural areas than in forested areas, potentially exacerbated by density-dependent

63 nest predation rates (Lariviére & Messier 1998; Gunnarsson & Elmberg 2008; Devries et al. 2018).

64 *A priori,* we hypothesized that nests in open agricultural areas would show the poorest survival,

65 while forest nests would survive better because of lower predator diversity and densities.

66 Furthermore, we also expected as a null hypothesis that alien predators would make no greater or

67 lesser impact on nest survival than native predators.

68

69 **Materials and methods**

70 *Study areas*

71 We established artificial nests in wetland habitats along the macro-environmental gradient from

72 temperate broadleaf to boreal forest (each surrounded by varying proportions of forest versus

73 agricultural land) within two areas in Denmark (eastern and western Jutland) and three areas in

74 Finland (North-Savo, Häme, Uusimaa; Fig. 1), further subdivided in 11 subareas based on location

75 and landscape (Appendix Table 1). In all areas, we established artificial nests around two discrete

76 types of wetland, which we analysed separately: (i) those characterised by shallow water with

77 varying shorelines and (ii) permanent lakes retaining constant water levels throughout the summer.

78 The former group included seasonal ponds, beaver ponds (made by American beavers *Castor*

79 *canadensis* in Finland and Eurasian beavers *C. fiber* in Denmark), man-made ponds and/or larger

80 flooded wetland complexes with varying water levels and therefore varying shorelines.

81 The predator species potentially present to threaten nesting ducks differed naturally between the

82 study areas (see Appendix A for the species-specific trends). In both Finland and Denmark red fox

83 (*Vulpes vulpes*), pine marten (*Martes martes*), European badger (*Meles meles*) and Eurasian otter

84 (*Lutra lutra*) were widespread (Lindén, Hario, & Wikman 1996; Baagøe & Jensen 2007). In

85 addition, Denmark has stone marten (*Martes foina*) and European polecat (*Mustela putorius*) as

86 native species (Baagøe & Jensen 2007). Alien mammals included American mink and raccoon dog

87 in Denmark and Finland (Kauhala 1996; Kauhala & Kowalczyk 2011), as well as raccoon

88 (*Procyon lotor*) in Denmark (Salgado 2018). Finland and Denmark supported a range of avian

89 predators, including the common corvids: hooded crow (*Corvus corone*), common raven (*Corvus*

90 *corax*), Eurasian magpie (*Pica pica*), Eurasian jay (*Garrulus glandarius*) and western jackdaw

91 (*Corvus monedula*) as well as the commoner gull species: e.g. common gull (*Larus canus*), herring

92 gull (*L. argentatus)*, lesser black-backed gull (*L. fuscus)* and great back-backed gull (*L. marinus*).

93 In addition western marsh harriers (*Circus aeruginosus*) bred in both countries (Grell 1998;

94 Valkama, Vepäläinen, & Lehikoinen 2011).

95

96 *Nest experiments*

We conducted artificial nest experiments in 2017–2019 to compare potential nest predator species presence and predation rates in different duck breeding habitats. Nests were placed where a dabbling duck hen could potentially lay a clutch, based on our own experience. Some dabbling duck species nest close to the shoreline, while others can place nests in the forest far from wetlands, so our artificial nest sites reflected this distribution.

We established paired experimental nests ("shoreline" in contrast to "forest") around lakes and ponds whenever possible (although some sites lacked forests around them; see Appendix B for more information). Shoreline nests were placed less than five metres from shorelines and forest nests at least 70 metres (range 70–1400 m) from the shoreline. In Denmark, some study areas were larger wetland complexes with shallow seasonal water bodies, so here we distributed nests evenly throughout duck nesting areas. In areas where nests were established in two years, we used the same nest sites in both years. Artificial nest density was kept low, around one nest km^{-2} (subarea average 1.1 nests km^{-2}, variance 0.5 – 1.8 nests km^{-2}, Appendix Table 1.) to avoid any density effects caused by artificial nests. We had no knowledge of natural nest densities in any of our study areas, so density dependent variation in predation rate is possible (Gunnarsson & Elmberg 2008). However, as we kept the artificial nest density constant, we feel confident in being able to compare the relative predation rates between the habitats.

Each artificial nest contained two farmed mallard *Anas platyrhynchos* eggs and some clean down from shot mallard females (in Finland) or down from eider *Somateria mollissima* nests (Denmark), mimicking the situation in the early stage of egg laying by wild mallards. This is the stage where females only visit the nest when laying. Nests were constructed to resemble real ones: natural nest material from the nest surroundings was collected to form a c. 20 cm wide nest cup and used to cover the eggs slightly. Eggs were not completely covered with down since ducks do not typically

120   do so before commencing incubation. Nests were established under small trees or bushes where

121   available and within tussocks in open wetlands, to render nests almost impossible to detect from

122   directly above. Light-triggered passive wildlife cameras were mounted ca. 1–1.5 m from nests,

123   attached on trees or 1 m stakes. Cameras were active for the whole period, responded to movement

124   and were adjusted to take three pictures in a row, followed by a one-minute pause.

125   We started nest experiments to coincide with when ducks initiate egg laying locally: April in

126   Denmark and late April-June in Finland (following the ice-out phenology from south to north).

127   One sub-area (East-Uusimaa) was sampled in early July in 2017. Nests were left for seven days

128   without visit. All nests were established and deconstructed between 9 am and 16 pm.

129   Here, we report data only from the initial (primary) predators of each nest, *i.e*. when the first eggs

130   were broken, eaten or removed by any predator. Because pine and stone martens were difficult to

131   distinguish on the imagery, we combined these for the analysis (*Martes* spp.). Because of low

132   overall predation rates, we combined the three gull species too: common gull, herring gull and

133   great black-backed gull. We established 335 nests, but discarded two because of camera failure or

134   excavation activities at the nest site, hence 333 nests are reported from 274 independent nest sites

135   (78 nest sites had observations from two years; Supplementary material Table S1.).

136   We analysed nest environments at two scales: landscape and habitat. The dominant two land use

137   categories in all study areas were forestry and/or agriculture, which largely reflects landscape

138   openness. We expected landscape openness to affect predator presence and abundance, and thus

139   we instituted a landscape-level indicator (i.e. percentage area of agricultural fields, hereafter %

140   Fields) as a metric to describe the forest-agricultural land gradient. The total area of agricultural

141   land (e.g. arable crop, hay, and grazing land together) within a 1 km radius around each nest was

142   calculated (Appendix C). Average % fields in this area were 25 (variation 0-77 %) and 42 (1-100

143   %) in Finland and Denmark, respectively.

144   We classified every nest site to catch the habitat-level variance in predator community as 1) forest,

145   2) shoreline of permanent lake, or 3) wetland (seasonal pond, beaver pond, man-made pond,

146   wetland complex).

147   Artificial nests are unlikely to reflect genuine nest predation rates, so our intention here is not to

148   assess overall predation rates, but assess habitat-specific relative predation risk to duck nests,

149   relative predator presence and predation intensity. Many important differences exist between real

150   and artificial nests and it is therefore important to consider, whenever conducting artificial nest

151   experiments, that: (i) predator species may differ, (ii) duck parents may successfully defend nests,

152   (iii) human scent can attract olfactory-searching mammals, (iv) artificial nests are not equivalent

153   to the real ones, (v) observations are not independent or (vi) the eggs were not those normally

154   encountered, all potentially affecting bias relative to predation at natural nests (Whelan et al. 1994;

155   Butler & Rotella 1998; Wilson, Brittingham, & Goodrich 1998; Pärt & Wretenberg 2002). We did

156   our best to circumvent these problems: we used real mallard eggs and can confirm that the species

157   observed in the camera pictures are known predators of real duck nests (Pöysä, Milonoff, &

158   Virtanen 1997; Opermanis, Mednis, & Bauga 2001). Our nest density was low ensuring that

159   observations were independent and the lack of an attendant hen associated with our artificial nests

160   merely "mimicked" the absence of natural females (which are not present continuously at nests

161   during early egg-laying), so in this way the experimental design resembled the realistic situation.

162   Finally, we did our best to avoid leaving any scents at the nest sites.

163   Compared to natural nests, mere camera presence may affect nest survival, typically by decreasing

164   predation rate (Richardson, Gardali, & Jenkins 2009), a potential shortcoming unavoidable with

165   this study design. The study design potentially emphasises the role of visual predators, such as

166   corvids, as our nests were not necessarily hidden as efficiently as that of an experienced dabbling

167   duck hen. However, high corvid predation rates at duck nests have been recorded in North America

168   during the early part of the breeding season, which was positively related to American crow

169   (*Corvus brachyrhynchos*) activity (Johnson, Sargeant, & Greenwood 1989).

170   While we accept that there remain uncertainties associated with data from monitored artificial

171   nests, considering problems identified in earlier studies and having tried to minimize differences

172   between real and artificial nests, we suggest that our data are suitable for assessing trends in

173   relative predation rates in relation to habitat (Wilson, Brittingham, & Goodrich 1998).

174

175   *Statistical methods*

176   We undertook our numerical analyses at two levels. First, we studied overall nest survival in

177   different landscapes and habitats, and secondly we studied the effect of landscape and habitat on

178   species-specific predation occurrence.

179   Initial data exploration showed that habitat-specific predation rates differed in Finland and

180   Denmark, so Finnish and Danish data were analysed separately. Depredated nests where memory

181   cards failed were excluded due to their unknown predation date ($N = 2$ in 2017, $N = 1$ in 2018 and

182    $N = 2$ in 2019). We compared daily nest survival in different habitats (forest, shoreline and

183   wetland), based on 123 nests in Denmark (25, 58 and 40 nests) and 205 nests in Finland (103, 57

184   and 45 nests) which survived the entire study period or with the known predation time (55 and 91

185   predated nests in Denmark and Finland respectively).

186   We used a generalized linear (mixed) model (GL(M)M) framework to calculate daily nest survival

187   probability by using modified logistic regression which incorporates the number of exposure days

188   into the link function (i.e. link function includes an exponent $1/t$ indicating the observation time,

189   Shaffer 2004), based on the entire data set for seven days, each beginning at 12 pm. The logistic

190   exposure method is a modification of logistic regression and maximizes the use of nest survival

191   data by treating each measurement day as a discrete trial. Daily nest fate was analysed as a binary

192   response variable (1 = survived, 0 = depredated). The explanatory variables were "Day" (1,…7),

193   "Habitat" (forest, shoreline, wetland) and "%Field" (percentage area of fields around the artificial

194   nest). Data exploration suggested that the effect of %Field was non-linear, but with possible

195   threshold values. For both countries, we therefore used models including %Field as a factor

196   variable: using 10% as the Finnish threshold and 20% for Danish data. Because nests were

197   established at the same sites in Finland in two years, Nest_ID was used as a random factor for

198   Finnish data (Appendix D). We used the package lme4 (Bates et al. 2015) and all analyses were

199   carried out in R 3.5.2 (R Development Core Team 2018).

200   The second step was to study nest predator species-specific occurrence in different landscapes and

201   habitats. Landscape association with species-specific nest predation or survival was analysed with

202   linear mixed-effects modelling (nlme package, Pinheiro et al. 2018, again using Nest_ID as a

203   random factor for Finnish data). We used nest-specific %Field as an independent variable and

204   predator species as an explanatory variable. We considered only predator species that predated

205   more than three nests (see Table 1.). As we were especially interested in the relationship between

206   raccoon dog and native species, nests predated by raccoon dog were used as the intercept, so that

207   the results showed if %Field at the nest predated by other species differed from %Field of nests

208   predated by the raccoon dog.

209   To study the species-specific habitat associations of nest predators, we used the *G*-test of goodness-

210   of-fit: we studied how well the observed predation reflected the expected rates. This was done by

211   assuming that in an expected situation, nest predation by a certain predator species would have

212   been divided evenly between the three habitats.

213

214   **Results**

215   From the 333 nests, 151 (45%) were predated (in Finland 45% and in Denmark 46%), involving

216   16 species of primary predators (Table 1., Appendix E). On this basis, the most common predators

217   were Eurasian magpie (21% of the predated nests), hooded crow (19%), raccoon dog (13%),

218   *Martes* spp. (8%) and western marsh harrier (8%). There were geographical differences in the most

219   common nest predators: Eurasian magpie and raccoon dog were more prevalent in Finland, while

220   western marsh harriers and red foxes more commonly predated nests in Denmark.

221   The %Field had a significant negative effect on overall nest survival, both in Finland and

222   Denmark (Table 2.). In Denmark, forest nests survival rate was significantly higher than nests on

223   shorelines and wetlands. In contrast, Finnish forest and wetland nest survival did not differ, but

224   shoreline nests had lower survival than nests in the two other habitats (Appendix F; see also the

225   results for the optional model where wetland habitat was used as an intercept Appendix Table 2).

226   Overall survival increased over consecutive days, as indicated by the positive Day-variable

227   estimate (Table 2.).

228   Data exploration revealed that %Field seemed to have a threshold effect on predator presence:

229   above 30% field area, forest predator species disappear to be replaced by more typical predators

230   of agricultural land (Fig. 2). In marked contrast to all other species, raccoon dog predation was

231   distributed widely around the threshold value. Nests that survived tended to be situated within
232   forested landscapes.

233   Red fox, hooded crow, Eurasian magpie, western marsh harrier and gulls predated nests in
234   landscapes with significantly greater %Fields than the raccoon dog (Table 3.). In landscape terms,
235   raccoon dog predation did not significantly differ from *Martes* spp., common raven and Eurasian
236   jay predation (Table 3.). European badger predated nests much more in agricultural landscapes
237   than the raccoon dog, but because of the small badger sample size, the result was only of marginal
238   significance.

239   Habitat analysis revealed that the predation rates by mammals did not differ significantly from
240   those expected, although predation by red fox was just on the limit: fox predation was concentrated
241   more on wetlands and lakeshores than expected based on availability of nests (Table 4.). Most
242   avian predator predation differed significantly from the expected distribution: hooded crow
243   predation was greater on shorelines and common raven and gull predation was greater on wetlands,
244   while marsh harriers predated nests on shorelines and wetlands, but avoided forests. The only avian
245   predation confined largely to forests was the Eurasian jay, with Eurasian magpie predation
246   distributed evenly among all habitats.

247

248   **Discussion**

249   Using artificial nests to assess potential predation pressure and species presence in different duck
250   breeding habitats at important inland breeding sites, we showed that predation rates in Denmark
251   and Finland differed between landscape and habitat types. Nest predation rate and predator
252   community diversity increased from forested to agricultural landscapes.

253   These results suggest that agricultural landscapes maintain higher levels of potential predation

254   pressure than do forested areas. Nests further away from water bodies in forests survived better

255   than nests around the permanent lakes in both Finland and Denmark. In Finland, lake shorelines

256   of eutrophic lakes in particular, have been occupied by three novel nest predator species: American

257   mink, raccoon dog and western marsh harrier in the past 50 years (Pöysä, Linkola, & Paasivaara

258   2019, including our Finnish eutrophic study lakes, Väänänen, V.-M. unpubl.). As a result, duck

259   species nesting on eutrophic lakes and especially those preferring shorelines as nesting places

260   have, in all likelihood, experienced a major increase in predator diversity and abundance, which

261   may have contributed to their declining population trends (Lehikoinen et al. 2016; Pöysä, Linkola,

262   & Paasivaara 2019). Several currently threatened duck species in Finland typically nest close to

263   shorelines (e.g. pintail *Anas acuta*, common pochard *Aythya ferina*, tufted duck *Aythya fulicula;*

264   Lehikoinen et al. 2019), and may thus suffer greater nest predation rates than species nesting

265   further away (e.g. mallard and teal *Anas crecca*; e.g. Pöysä et al. 2019). Overall, shorebirds seem

266   to have experienced a worldwide increase in nest predation in recent decades, most pronounced at

267   high northern latitudes (Kubelka et al. 2018),

268   Complex species interactions in rich duck nesting habitats could also elevate nest predation rates.

269   In high duck nest density areas, depredated (i.e. more visible) nests potentially attract all predators

270   that employ restricted area searching, raising the odds of finding neighboring nests (Wada 1994).

271   Furthermore, Pöysä et al. (2019) speculated that the presence of American mink and raccoon dog

272   might cause serious reductions in breeding numbers of inland black-headed gull (*Chroicocephalus*

273   *ridibundus*) colonies. Disappearance of gull colonies is thought to expose nests of associated

274   waterbirds to greater predation threat caused also other species, such as corvids, which are

275   normally driven off by mobbing gulls protecting their own nests (Väänänen 2000).

276   We acknowledge that predator species of artificial nests very likely differ from those at real nests

277   for several reasons. Mammal predation has been observed to be greater and avian predation lesser

278   at real nests (with incubating females) than artificial nests (*e.g.* MacIvor, Melvin, & Griffin 1990).

279   We strongly suspect that our experimental design may over-emphasize the effect of visually

280   searching avian predators, compared to mammals, which use more olfactory cues (Willebrand &

281   Marcström 1988; Butler & Rotella 1998). Ideally, artificial nest predation rates should be

282   compared and calibrated simultaneously with those at real nests (Major & Kendal 1996). We have

283   not had the possibility to measure predation rates at real nests at our study areas, but the

284   comparative data from Holopainen et al. (submitted) suggests that, by using our method, the

285   artificial nest predation rate reflects roughly the difference in brood production of ducks in forest

286   and agricultural landscapes. Furthermore, as our nests were distributed over large areas at very low

287   densities, we assume that the predator-specific nest predation rate is a reasonable reflection of the

288   predator species' local density and relative nest predation effort (i.e. we are assuming that both

289   predator species density and effort contribute to the overall predation rate witnessed in the

290   experimental results).

291   Predation caused by native species was typically concentrated in certain habitats and landscapes.

292   Red fox, hooded crow, western marsh harrier and gulls were common predators in agricultural

293   landscapes on wetlands and along shorelines, contributing to high overall nest predation rates in

294   these habitats. Eurasian magpie was more prevalent in agricultural landscapes, where its predation

295   was evenly distributed among the studied habitats. Overall, the predator community consisted of

296   fewer species and individuals in forest than in agricultural landscapes, reflected in lower overall

297   nest predation rates in the forest landscape. The main native forest predators were Eurasian jay

298   and *Martes* spp., with common ravens predating a few wetland nests with some surrounding forest.

299 Our results support earlier studies showing that the raccoon dog is truly a habitat generalist species

300 (Kauhala & Kowalczyk 2011). Our limited results found it inhabiting all studied breeding duck

301 habitats independent of landscape. Raccoon dog predation rate was low only in the most

302 agricultural of landscapes, perhaps because of habitat preference (Mulder 2012) or heavy raccoon

303 dog control on the studied Danish grazed wetlands (personal communication). Overall, raccoon

304 dogs predated more nests than any other mammalian species, although more marked in Finland

305 while red fox was the most common mammalian predator at Danish artificial nests.

306 Studies of raccoon dog effects on waterfowl nesting on inland wetlands have produced contrasting

307 results (Kauhala 2004; Nummi et al. 2019), while raccoon dog nest predation on islands has been

308 shown to be highly destructive (Dahl & Åhlen 2019). Raccoon dogs exploited the most abundant

309 locally available food resource (Kauhala & Kowalczyk 2011) and, for example, wetland area

310 increased consumption of avian prey (Sidorovich et al. 2008). While we accept that our study does

311 not constitute proof that raccoon dogs are harmful to duck populations, the results show that it is

312 a widely spread, effective and frequent potential egg predator. Alien predators invading new

313 habitats can potentially be more successful than native predators in utilising certain prey resources

314 (*e.g.* Dick et al. 2013). Nests are a limited resource in time and space for many predators, which

315 may enable those that show innate explorative, opportunistic behaviour, such as the raccoon dog,

316 to be efficient at finding such resources. Whatever the explanation, our results imply that compared

317 to native species, the threat from the raccoon dog to breeding ducks is potentially greater than that

318 posed by any other single native species.

319 Some predator species made lesser contributions to nest predation than expected. European

320 badgers appeared to be uncommon duck nest predators in at our sites. Despite the role of American

321 mink implied by other studies on freshwater ducks (Zschille et al. 2014; Brzezinski et al. 2019)

322 and especially on maritime islands (Nordström et al. 2002), the species was rarely encountered

323 and very rarely as an initial nest predator in this study. No European polecats or Eurasian otters

324 predated any of our monitored artificial nests, but eggs play a minor role in the diets of both species

325 (Hammershøj, Thomsen, & Madsen 2004; Malecha & Antczak 2013; Krawczyk et al. 2015).

326

327 **Conclusions**

328 Important bird lakes in Northern Europe are often eutrophic and occur usually in agricultural

329 landscapes (Jeppesen et al. 1999; Leivo et al. 2002). Twelve of the 19 duck species breeding in

330 Finland are already classified as threatened to some degree (Lehikoinen et al. 2019). Declining

331 trends underline the urgent need for conservation actions to safeguard these species.

332 Nest predation is a natural limiting factor acting upon duck nesting success (Newton 1998), so

333 introducing novel alien predators into ecosystems likely enhances nest predation rates (Zschille et

334 al. 2014; Dahl & Åhlen 2019). Current high waterfowl nest predation rates, especially in

335 agricultural landscapes, may result from increases in predator species number and abundance in

336 response to resources offered by fragmented agricultural habitats (Lariviére & Messier 1998). The

337 situation was different in forested landscapes where duck densities are low; as predator richness

338 was observed to be low, effects of species interactions are less likely.

339 Assuming that declines in nesting duck populations do result from increases in predator diversity

340 and abundance, preventing the continued spread of alien predators should be a priority. In Finland,

341 eradicating the already well-established raccoon dog population has proved difficult (Nummi et

342 al. 2019), but in Sweden where the species is only in the early stages of colonisation, a successful

343 eradication programme has been maintained (Dahl & Åhlen 2019). Given its ubiquity across

344 landscapes and habitats and frequency as predator of ducks nests, we emphasise the potential effect

345 of the raccoon dog as a nest predator and the danger it poses to future breeding populations of

346 ducks.

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360 Appendix A-F; Appendix Tables 1-2. Supplementary data

361 Supplementary data associated with this article can be found, in the online version, at XXXXX."

362

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525 **Web references for the geographical data**

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534

535   Table 1. The number of artificial nests predated by different species in Finland and Denmark. In

536   total the data consist of results from 208 and 125 nests from Finland and Denmark, respectively.

Species	Denmark	Finland	Total	Total %
Mammalian predators				
Raccoon dog *Nyctereutes procyonoides*	3	17	20	13,2
Red fox *Vulpes vulpes*	10	1	11	7,3
Pine or stone marten *Martes martes/foina*	5	7	12	7,9
European badger *Meles meles*	4	1	5	3,3
American mink *Neovison vison*	0	1	1	0,7
Domestic dog *Canis lupus familiaris*	0	1	1	0,7
Avian predators				
Eurasian magpie *Pica pica*	0	31	31	20,5
Hooded crow *Corvus corone cornix*	12	17	29	19,2
Western marsh harrier *Circus aeruginosus*	11	1	12	7,9
Eurasian jay *Garrulus glandarius*	2	8	10	6,6
Common raven *Corvus corax*	2	5	7	4,6
Common gull *Larus canus*	4	0	4	2,6
Herring gull *Larus argentatus*	1	0	1	0,7
Great black-backed gull *Larus marinus*	1	0	1	0,7
Common crane *Grus Grus*	0	1	1	0,7
Unknown	2	3	5	3,3
Sum	57	94	151	100

545 Table 2. Model estimates for the daily survival rate of artificial nests on lake and pond shoreline. Day =
546 exposure day, Habitat = a three-level factor, representing forest (Intercept), lake shoreline and wetland,
547 Field = a two-level factor, representing low %Field (low percentage area of field cover around the nest;
548 Intercept) and high %Field. Random effect standard deviation for Nest ID in Finland = 0.925.

Model	Estimate	SE	z-value	P
Finland				
(Intercept)	3.487	0.500	6.965	**< 0.001**
Day	0.431	0.079	5.473	**< 0.001**
Habitat: Shoreline	-1.288	0.394	-3.268	**0.001**
Habitat: Wetland	-0.056	0.366	-0.153	0.878
High %Field	-2.053	0.378	-5.435	**< 0.001**
Denmark				
(Intercept)	3.862	0.747	5.172	**< 0.001**
Day	0.567	0.086	6.620	**< 0.001**
Habitat: Shoreline	-1.420	0.617	-2.301	**0.021**
Habitat: Wetland	-1.664	0.626	-2.658	**0.008**
High %Field	-1.253	0.480	-2.606	**0.009**

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551

552 Table 3. Model estimates explaining the effect of field percentage on nest predation in mammal
553 and avian predator species. Intercept includes the field percentage of the nests predated by the
554 raccoon dog.

	Estimate	SE	t-value	P
Intercept (raccoon dog)	25.617	4.447	5.760	**< 0.001**
Martes spp.	-9.388	7.262	-1.293	0.198
European badger	17.399	9.944	1.750	0.083
Red fox	36.732	7.466	4.920	**< 0.001**
Hooded crow	23.727	5.781	4.104	**< 0.001**
Eurasian magpie	24.084	5.704	4.222	**< 0.001**
Common raven	-8.622	8.734	-0.987	0.325
Eurasian jay	-9.487	7.703	-1.232	0.220
Western marsh harrier	18.052	7.262	2.486	**0.014**
Gulls	58.061	9.258	6.272	**< 0.001**

558   Table 4. The results of the *G*-test of goodness-of-fit for the observed vs. expected nest predation
559   within habitats. Williams's correction was used to control small sample sizes.

Species	N	Observed deviation			df	*G*	P
		Forest	Shore	Wetland			
Raccoon dog	20	0.45	0.40	0.15	2	1.366	0.505
Martes spp.	12	0.50	0.33	0.17	2	0.770	0.681
European badger	5	0.20	0.60	0.20	2	1.212	0.546
Red fox	11	0.09	0.36	0.55	2	5.925	0.052
Hooded crow	29	0.14	0.62	0.24	2	11.016	**0.004**
Eurasian magpie	31	0.48	0.39	0.13	2	3.214	0.201
Common raven	7	0.00	0.14	0.86	2	11.434	**0.003**
Eurasian jay	10	0.80	0.10	0.10	2	6.636	**0.036**
Western marsh harrier	12	0.00	0.58	0.42	2	11.243	**0.004**
Gulls	6	0.00	0.33	0.67	2	6.604	**0.037**

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561

562   Fig. 1. Map of the study areas in Finland and Denmark: 1) North-Savo, 2) Häme, 3) Uusimaa, 4)

563   eastern Jutland and 5) western Jutland. The distance from the Danish study areas to area 1 in

564   Finland is c. 1 200 km (south-north transition c. 800 km) (Base map: Esri 2019).

565

566   Fig. 2. Distribution of survived and predated nests in relation to percentage of field around the

567   nests. Box plot shows the median, interquartile range and whiskers indicate the range. Circles

568   indicate outliers.

569