1   **Influence of landscape features on nest predation rates of grassland-breeding waders**

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14  Land use change and agricultural intensification have greatly reduced the area of natural and semi-
15  natural habitats throughout the developed world. Populations in small areas of remaining habitat
16  can experience increased rates of predation which can threaten population sustainability,
17  particularly if the surrounding landscape is inhospitable to prey and predators. Excluding predators
18  to reduce impacts of predation can be a short-term solution but is often not feasible or desirable.
19  Consequently, there is growing interest in identifying landscape-scale habitat management
20  techniques that could be used to reduce rates of predation on species of concern, for example
21  through altering predator distribution and activity. In Europe, lowland wet grasslands have
22  become increasingly fragmented, and populations of waders in these fragments are subject to
23  unsustainably high levels of nest predation. Patches of tall vegetation in these landscapes can
24  support small mammals, which are the main source of prey for many predators. Providing such
25  patches of small mammal habitat could potentially reduce levels of nest predation if predators
26  preferentially target small mammals. However, predator attraction to patches of tall vegetation
27  for foraging, shelter, perching and/or nesting opportunities that they provide, could also result in
28  local increases in predation rates, as a consequence of increased predator densities or spillover
29  foraging from the surrounding area.  Here we explore the influence of the presence of tall
30  vegetation on wader nest predation rates, and the capacity for managing vegetation structure to
31  alter predator impacts. Between 2005 and 2011, the nest distribution and hatching success of
32  Northern Lapwing, *Vanellus vanellus*, which nest in the open, and Common Redshank, *Tringa*
33  *totanus*, which conceal their nests in vegetation, were measured on a 487 ha area of wet grassland
34  in eastern England that is primarily managed for breeding waders. The likelihood of Lapwing nests
35  being predated increased significantly with distance from tall vegetation patches, and decreased
36  with increasing area of tall vegetation within 1 km of the nest, while neither proximity to, nor area
37  of, nearby tall vegetation influenced Redshank nest predation probability These findings suggest
38  that the distribution and activity of wader nest predators in lowland wet grassland landscapes may
39  be influenced by the presence and distribution of areas of tall vegetation. For Lapwing at least,
40  there may therefore be scope for landscape-scale management of vegetation structure to
41  influence levels of predation in these habitats.

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46    The impact of predators can be a major driver of local population abundance among prey
47    populations. Predator pressure can drive population cycles of small mammals (e.g. Korpimäki &
48    Krebs 1996), and can result in local extirpation of prey populations, for example following predator
49    introduction to previously predator-free areas (Blackburn *et al*. 2004, Sih *et al*. 2010), or following
50    habitat fragmentation (Crooks & Soulé 1999, Chalfoun *et al*. 2002). The impact of predators on the
51    sustainability of prey populations can be of particular concern in relation to species of economic
52    value (e.g. gamebirds; Tapper, Potts, & Brockless 1996) or species of conservation concern (Tucker
53    & Heath 1994). As many species of conservation concern are now restricted to small fragments of
54    appropriate habitat (Wilson *et al.* 2005), there may be disproportionate impacts of predators on
55    vulnerable populations (Fischer & Lindenmayer 2007), especially within the context of agricultural
56    landscapes (Chalfoun *et al*. 2002).

57    A reduction in the impacts of predation on local prey populations can sometimes be achieved
58    through reductions in predator numbers in areas surrounding populations of conservation concern
59    (Fletcher *et al.* 2010), or through local predator eradication (Oppel *et al.* 2011). However, these
60    methods are time consuming, expensive and often controversial, with the potential for unforeseen
61    increases in other predator or competitor species (Bodey *et al.* 2009). In addition, the impact of
62    predator control is often dependent on initial predator densities (Bolton *et al.* 2007), which can be
63    difficult to assess. Predator exclusion has been found to be effective at improving avian hatching
64    success (Smith *et al.* 2011). For example, fenced exclosures to exclude mammalian predators
65    increased the hatching success of Piping Plovers *Charadrius melodus* (Maslo & Lockwood 2009),
66    and nest survival and fledging success of Northern Lapwing *Vanellus vanellus* have also been found
67    to be higher within fenced plots that exclude mammalian predators (Rickenbach *et al.* 2011,
68    Malpas *et al.* 2013). However, as fencing of sufficiently large areas is not likely to be a practical
69    option in the wider countryside, there is growing interest in developing management techniques
70    that can influence predator distribution and activity. Of particular interest are changes in habitat
71    structure that may influence predator activity and distribution, and may thus provide a means of
72    diverting predators away from areas with species of conservation concern (Seymour *et al.* 2004).
73
74    Many ground-nesting wader populations in North West Europe have been in sharp decline in
75    recent decades (Wilson *et al.* 2004, Roodbergen *et al.* 2012), and breeding populations of several
76    species are increasingly constrained to protected areas (Ausden & Hirons 2002, Smart *et al.* 2008,
77    2014). Impacts of predators within these landscapes have been identified as the key issue
78    constraining the recovery and sustainability of several of these wader populations (MacDonald &

79    Bolton 2008, Malpas *et al.* 2013). The predators of both chicks and eggs of ground-nesting waders

80    comprise a range of generalist predators, including   Red Foxes *Vulpes vulpes*, Stoats *Mustela*

81    *erminea*, Weasels *Mustela nivalis*, Marsh Harriers *Circus aeruginosus* and corvids, particularly

82    Carrion Crow *Corvus corone.* These generalists predators have a varied diet including lagomorphs,

83    birds and small mammals (Holyoak 1968, Underhill-Day 1985, McDonald *et al.* 2000, Kidawa &

84    Kowalczyk 2011). In particular, small mammals are often a key component of the diet of generalist

85    predators (Underhill-Day 1985, McDonald *et al.* 2000, Dell'Arte *et al.* 2007), and variation in the

86    availability of small mammal prey has been linked to predator impacts on bird productivity. For

87    example, temporal variation in lemming abundance in the high Arctic has been related to nest and

88    chick predation of Dark-bellied Brent Geese *Branta bernicla bernicla* as a consequence of predator

89    switching (Summers 1986). The availability of small mammal prey could therefore potentially

90    influence levels of predation on nests and chicks of ground-nesting waders.

91

92    In lowland wet grasslands managed to encourage breeding wader populations, grazing is typically

93    used to maintain short swards that are attractive to waders (Fisher *et al.* 2011). Tall vegetation

94    (defined here as greater than 15 cm height) is typically rare and  limited to areas outside fields in

95    these landscapes, and small mammals are almost entirely restricted to these tall vegetation

96    patches (Laidlaw *et al.* 2013).  Tall vegetation can also provide shelter and perching or nesting

97    locations for predators (Lucherini *et al.* 1995), around which they may concentrate their foraging

98    activities.  Consequently, the presence of tall vegetation in these landscapes could increase or

99    decrease local levels of nest predation, depending on the extent to which predators concentrate

100   their activities either within or around the patches.

101

102   Here we assess the influence of landscape-scale vegetation structure on nest predation rates of

103   breeding waders. We use a seven-year dataset of wader breeding distribution and demography for

104   one of England's largest remaining wader populations, to quantify the probability of nest

105   predation for Northern Lapwing (hereafter Lapwing) and Common Redshank *Tringa totanus*

106   (hereafter Redshank) in (i) fields with and without adjacent tall vegetation patches, and areas with

107   differing (ii) amounts of and (iii) distances to tall vegetation, at different spatial scales.

108

109   **METHODS**

110   **Study site**

111    The influence of the area and distribution of tall vegetation on nest predation in Lapwing and

112    Redshank in a wet grassland landscape was explored at Berney Marshes RSPB reserve (52°35'N

113    01°35'E, National Grid reference TG4605). Previous work on this reserve has found that nocturnal

114    predation by mammals accounted for 77% of predation events (Eglington *et al.* 2009) and nest

115    cameras on Lapwing nests have only recorded Red Foxes as nest predators  (RSPB unpublished

116    data). Numbers of Red Foxes in the area are unknown but numbers shot during regular predator

117    management in the pre-wader breeding season are relatively constant between years (mean ± SD:

118    6.9 ± 2.3, range = 2-9 individuals shot per year between 2005 and 2011). Within-field management

119    on this reserve is predominantly aimed at providing suitable nesting conditions for breeding

120    waders, through maintaining short swards and surface wet features throughout the wader

121    breeding season (Eglington *et al.* 2008).  Grazing pressure from commercial livestock on the

122    reserve is typically ~1 Lu (livestock units) ha$^{-1}$ (Bodey *et al.* 2010), which resulted in within-field

123    sward heights of ~5-15 cm across most of the reserve. However, ~5% of the reserve is comprised

124    of patches of taller vegetation, which range from verges with vegetation > ~15 cm bordering

125    roads, tracks, riverbanks and railways, to copses with trees and dense undergrowth (Figure 1).

126

127    **Wader nest monitoring and survival**

128    The nesting success of breeding waders has been monitored intensively at Berney Marshes since

129    2003 (Smart *et al.* 2006, Eglington *et al.* 2009, Bodey *et al.* 2010). In each year, between 33 and 52

130    fields with breeding waders were studied intensively as part of the reserve's scientific monitoring,

131    with surveys being carried out every 4-5 days to locate as many nesting attempts as possible.

132    Lapwing nest in short, open grassland and their visible nests are primarily located through

133    observation of incubating adults from a vehicle. In contrast, Redshank nest in taller vegetation,

134    and are not visible when incubating eggs. A late flushing response to disturbance in this species

135    means that nests are located by systematic searching and incidental flushing of adults from

136    concealed nests. Nest locations have been spatially referenced using GPS since 2005 for Lapwing

137    (n = 977 nests) and 2007 for Redshank (n = 290 nests), and these are the nests which are used in

138    the analyses reported here (Figure 1).

139

140    The wader breeding season at these latitudes typically ranges from March to July, with pairs

141    capable of renesting following losses at the egg stage, although the probability of re-nesting

142    decreases later in the season (Beintema & Muskens 1987). The date on which each nest was first

143    located (termed FIND DAY in analyses) provides an indication of the period during the season in

144    which nests were active (the majority of nests are found within 10 days of laying). All nests were

145      mapped using GPS, marked using a cane placed > 10 m away in a random direction and visited a

146      minimum of every five days, and more regularly near their estimated hatch date (calculated from

147      egg measurements following Smart 2005), to determine their fate. Nests were considered

148      successful if one or more eggs hatched and predated nests were defined as those that were empty

149      without any eggshell fragments in the nest to indicate successful hatching (Green *et al.* 1987).

150

151      To determine the time and date of nest failures, ibutton dataloggers (Maxim Integrated Products

152      Ltd, CA, USA) have been placed in a random selection of nests (between 40 – 85% of all nests

153      monitored) since 2007. These loggers record a temperature trace at specified intervals (every

154      seven minutes in this study). For empty nests with no evidence of hatching (i.e. small fragments of

155      shell or alarming adults nearby), and no evidence of trampling (flattened nest) or flooding (wet

156      nest contents), a sharp and permanent decline in nest temperature below incubation temperature

157      indicates nest predation (Bolton *et al.* 2007), allowing the date, time and nest fate to be recorded.

158      For predated nests in which the exact date of predation was not known (e.g. dataloggers not

159      deployed), the failure day was taken as the midpoint between the final two visits. Only nests that

160      hatched (n = 586) or were predated (n = 681) were included in the analysis (Table 1; Figure 2a and

161      3a).

162

163      To determine the daily nest predation rate (DPR) for each species, the Mayfield method (Mayfield

164      1961, 1975) was used, in which the number of exposure days represents the period over which

165      each nest was monitored from discovery to predation or hatching. This method accounts for the

166      increased likelihood of locating nests that survived for longer periods:

167

$$DPR = \frac{Total\ number\ of\ monitored\ nests\ predated}{Total\ number\ of\ days\ nests\ were\ under\ observation}$$

168

169      **Scale of landscape structure and habitat assessment**

170      Patches of tall vegetation (greater than 15 cm), which are generally found in verges outside fields,

171      provide the only suitable habitat for small mammals in this landscape (Laidlaw *et al.* 2013), and

172      may therefore be a source of prey or shelter for predators. The area and distribution of verge

173      within the reserve were mapped in ArcGIS v.9.3, by digitising outlines from aerial photographs

174      (Millennium Map 2000; Figure 1). Fields that were CONNECTED (uppercase indicates model

175      predictors) to a verge, either via a gateway or other means of bridging the ditch (e.g. earth

176      bridges) were identified from aerial photographs and ground-truthing. The DIRECT DISTANCE from

177    each wader nest to the nearest verge was measured as the shortest straight line distance in

178    ArcGIS. To investigate the influence on hatching success of the amount of verge within the vicinity,

179    the AREA of tall verge vegetation within circular buffers of radius 0.2 (0.13 km$^2$), 0.5 (0.79 km$^2$) and

180    1.0 km (3.14 km$^2$) around each nest was calculated in ArcGIS. The different sized buffers represent

181    different scales at which tall vegetation could influence wader hatching success: from potential

182    local-scale effects on predator movement within wet grassland up to larger landscape-scale effects

183    on predator presence and abundance.

184

185    **Statistical analysis**

186    Variation in daily nest predation rates were explored with Generalized Linear Mixed Models

187    (GLMMs), using a formulation of Mayfield's (1961, 1975) method as a logistic model with a

188    binomial error term, in which success or failure (hatched or predated) was modelled with

189    exposure days as the binomial denominator (Aebischer 2009), and with CONNECTED or not to a

190    verge, DIRECT DISTANCE to verge and AREA of verge in the surrounding landscape (to assess the

191    effects of verges) and FIND DATE (to incorporate seasonal variation in predation risk) as

192    predictors, and YEAR and FIELD as random factors (Table 1). Separate models were constructed for

193    each species and for each of the three buffer distances for area of verge (0.2, 0.5 and 1.0 km; all

194    three spatial-scales could not be incorporated in a single model due to collinearity; Table 1). Non-

195    significant ($P < 0.05$) variables were sequentially removed from these models (although their

196    estimates and associated probabilities in maximal models are also reported, for completeness). All

197    models were carried out in R (v 2.13.1) using the lme4 package, and collinearity of model terms

198    was tested (VIF 1.01 -2.07).

199

200    Daily predation rates (DPR) predicted from these models were then transformed to predation

201    probabilities by estimating nest survival rates over the incubation period (S) by raising the daily

202    survival rate (1-DPR) to the power of the species incubation periods (from first egg laid: Redshank

203    = 30 days; Lapwing = 32 days; Crick, Baillie, & Leech 2003; Kragten & De Snoo 2007), and this was

204    used to calculate nest predation probability over the incubation period (1-S).

205

206    **RESULTS**

207    Both wader species nested in fields that were and were not connected to verges and at distances

208    up to 622 m from the nearest verge (Figures 2c,d and 3c,d). Most nests had only around ~4%

209    (5000 m$^2$) tall vegetation within the surrounding 0.2 km (Figures 2e and 3e). As the surrounding 1

210    km encompassed a large proportion of the reserve, all nests contained tall vegetation within this

211    buffer (Figures 2g and 3g).

212

213    Lapwing nests that were more distant from the nearest verge had significantly higher predation

214    probabilities in both the 0.2 and 0.5 km buffer models (Table 2a, Figure 4a). The area of verge

215    within 0.2 km and 0.5 km did not significantly influence predation probabilities of Lapwing nests

216    (Table 2a and b), but nests with larger areas of verge within the surrounding 1 km (Figure 4b) had

217    significantly lower predation probabilities (Table 2c). Distance to verge was not a significant

218    predictor of predation probability in the model that included area of verge within 1 km (Table 2c),

219    suggesting that the relative effect of area of verge at this large scale (when all nests have some

220    verge habitat in the surrounding buffer area) is greater than distance to the nearest verge. None of

221    the environmental or seasonal variables explored significantly influenced the predation probability

222    of the 255 Redshank nests in the study (Table 3).

223

224    **DISCUSSION**

225    Landscape structure has potential to influence rates and patterns of predation, which could be an

226    important management tool if predation is limiting the success of populations. Within lowland wet

227    grasslands in the UK, areas of tall vegetation are typically rare and patchily distributed within the

228    landscape, but evidence from this study suggests their presence may lower nest predation levels in

229    some species of breeding waders. The closeness and extent of patches of tall vegetation positively

230    influenced Lapwing nest survival from field-scales to landscape-scales (Figure 4). These effects of

231    the presence of tall vegetation were not apparent for Redshank, which breed at much lower

232    densities and conceal their nests in vegetation.

233

234    The location and extent of areas of tall vegetation in relation to fields that support nesting waders

235    has not previously been considered in terms of predator management, but could influence the

236    vulnerability of nests to predation. At the local-scale (0.2 km) and field scale (0.5 km), nest

237    predation rates were lower for nests closer to tall vegetation, but the amount of tall vegetation in

238    the surrounding area did not influence Lapwing nest predation rates at these scales. However,

239    Lapwing nests were significantly more likely to be predated in areas with less tall vegetation in the

240    surrounding 1 km, suggesting that patterns of predator activity across the reserve may vary in

241    relation to the vegetation structure at landscape scales.

242

243    Potentially, an increase in the amount of tall vegetation in the landscape could alter the predation
244    pressure on breeding waders. However, differences in timing of breeding, nest concealment and
245    behavioural responses to predators could all influence these relationships. Our results suggest that
246    establishing patches of tall vegetation in the vicinity of breeding waders population could
247    potentially benefit nesting Lapwing, while not negatively affecting breeding Redshank. The
248    influence of landscape structure on wader nesting success, and the type of management that may
249    be appropriate, may therefore differ among species, and such actions could also have
250    unintentional impacts on other non-target species, including other predators.

251

252    **Potential mechanisms influencing verge effects on nest predation**
253    The possible mechanisms through which patches of tall vegetation could influence predation rates
254    include altering prey densities, predator behaviour or the carrying capacity of landscapes for
255    predators. Understanding the relative importance of different mechanisms is likely to be key in
256    predicting the consequences of future habitat manipulations (Norris 2004).

257

258    Tall vegetation in road and field verges has been found to support several small mammal species
259    in Britain, including bank voles *Clethrionomys glareolus*, wood mice *Apodemus sylvaticus* and field
260    voles *Microtus agrestis* (Bellamy *et al.* 2000). Within areas managed for breeding waders, small
261    mammals are generally restricted to tall vegetation patches which typically occur in fields verges,
262    and these are likely to provide the primary prey source for the main predators of wader nests
263    (Laidlaw *et al.* 2013). The lower predation of Lapwing nests closer to verges could result from
264    increased availability of small mammal prey within these verge habitats reducing the need for
265    predators to search in open fields for wader nests. As tall vegetation patches are not available
266    continuously through the landscape, searching for wader nests may be relatively more profitable
267    for predators when far from tall vegetation and the small mammal prey it supports. Predator
268    switching in response to prey density is common (van Baalen *et al.* 2001, Kjellander & Nordström
269    2003), and the relative profitabilities of searching for small mammals in enclosed vegetation and
270    wader nests in the open may well differ substantially, particularly given the effectiveness of the
271    anti-predator mobbing behaviour shown by many waders (Elliot 1985, Jónsson & Gunnarsson
272    2010).

273

274    Areas of tall vegetation within lowland wet grasslands will also increase spatial heterogeneity in
275    habitat structure, which has been found to alter prey availability, leading to modified encounter,
276    kill and consumption rates in predator-prey interactions (see Gorini *et al.* 2011 for review).

277   Predation rates are often observed to increase along habitat edges, with more fragmented
278   habitats being more heavily predated (Batáry & Báldi 2004). In fragmented agricultural landscapes,
279   carnivores (especially mustelids) have been found to use narrow strips of shrubby vegetation and
280   dense long-stemmed grasses more often than the hayfield matrix (Sálek *et al.* 2009). The
281   intersection between tall verge vegetation and shorter within-field vegetation may therefore
282   provide predators with more prey options, and decreased predation of Lapwing nests closer to
283   verges could simply reflect the broader range of available prey rather than specialisation on small
284   mammals.
285
286   Alternatively, individual predators may specialise on wader nests during the breeding season, and
287   these individuals may be less likely to focus their activities around tall vegetation. Generalist
288   predators could have specialised hunting behaviours to locate and predate wader nests, for
289   example there are anecdotal records of individual crows specialising in predating Lapwing eggs
290   (Ausden *et al.* 2009). Individuals specialising on wader nests may also favour large, open areas of
291   grassland without tall vegetation obscuring their view of incubating adults or areas with high
292   breeding densities.
293
294   Finally, tall vegetation patches may also provide shelter for predator species, and may thus attract
295   predators irrespective of their foraging opportunities. However, the reduced levels of predation of
296   Lapwing nests close to tall vegetation suggests that Red Foxes, at least, are likely to concentrate
297   their activities within these patches, as there is no evidence of an increase in levels of nest
298   predation  in areas close to tall vegetation for either Lapwing or Redshank. Foxes may use the
299   patches of tall vegetation distributed throughout this wet grassland landscape as corridors
300   through which they can move safely around their home range, in which case establishing corridors
301   of tall vegetation in areas with high breeding densities could be particularly effective in reducing
302   nest predation rates.
303
304   In open habitats, such as blanket bogs, waders have been found to selectively occupy areas further
305   from forest fragments (Wilson *et al.* 2014). Similarly, in wet grasslands, waders nest further from
306   raised structures that avian predators can use for searching for prey (Wallander *et al.* 2006). In the
307   UK uplands, the nesting success of curlew has been found to be lower when the area of woodland
308   surrounding sites is larger (Douglas *et al.* 2014). The lack of similar evidence of increased predation
309   close to tall vegetation in our study may reflect the differences in scale of these studies, the type
310   of vegetation being investigated (many of the verges do not contain trees suitable for nesting or

311    perching) or the suite of predators. Alternatively, the tall grass verges in our study may support

312    more abundant small mammal populations than woodlands, and thus predators in our landscape

313    may be more likely to concentrate their foraging within, rather than around, the verges.

314

315    **Implications for wet grassland management**

316    This study provides evidence that the presence of tall vegetation in wet grassland landscapes may

317    influence the predation pressure on breeding Lapwing nests. This suggests that encouraging the

318    growth of tall vegetation could potentially be used as a tool to alter nest predation rates, which

319    are currently unsustainably high (MacDonald & Bolton 2008). Similar habitat manipulations have

320    already been promoted for other species of conservation concern, for example taller vegetation at

321    field margins is already recommended for increasing insect abundance and nesting cover for Grey

322    Partridge *Perdix perdix* (Sotherton 1998). Outside of fields, tall vegetation patches within this

323    landscape are largely present along roads, railways or riverbanks with no specific management

324    being undertaken in association with breeding waders. The amount of tall vegetation within the

325    landscape could be altered by increasing the area of verge outside of fields, or by ensuring that

326    mowing of existing verges occurs after the wader breeding season (late July). Alternatively, there

327    may be scope to provide tall vegetation within whole fields that are not appropriate for breeding

328    waders (e.g. too dry), depending on livestock grazing requirements. Whether such management

329    options result in changes in the impact of predators on wader populations is likely to depend on

330    the mechanisms underpinning the responses observed here, the nature of any consequent

331    changes in chick survival, the variability in the existing predator suite, and whether increasing

332    resources for predators simply increases the total numbers of predators and thus does not result

333    in sustained reductions in nest predation (e.g. Amar *et al.* 2011). However, manipulation of verge

334    structure and distribution is likely to be sufficiently feasible to allow exploration of these issues,

335    and thus of the capacity of this management tool to reduce wader nest losses.

336

337    Exclusion of mammalian predators with fences has been successful at reducing nest predation

338    (Malpas *et al.* 2013), but these benefits could potentially be offset by high levels of predation on

339    chicks by avian predators. However, overall productivity of Lapwing has been shown to be higher

340    in fenced areas (Malpas *et al.* 2013) , suggesting either that Red Foxes are also a major predator of

341    chicks or that the effects of avian predators at this stage are limited. While avian predators may

342    well be attracted to areas of tall vegetation containing small mammals (e.g. Amar & Redpath

343    2005),  the effective anti-predator mobbing by high densities of parents may reduce their impact

344    on wader chicks.

346 If predator impacts on waders in the wider countryside are similarly influenced by the presence
347 and amount of tall vegetation in wet grassland landscapes, spatial planning and targeting of agri-
348 environment options to provide tall vegetation alongside options specifically designed to improve
349 conditions for breeding waders could potentially be a mechanism for altering landscape structure.
350 At present, these schemes target conditions within fields only, such as surface water and sward
351 conditions, and landscape-scale issues such as proximity to tall vegetation are not considered.
352 Before specific management prescriptions can be determined, however, the mechanism by which
353 the proximity to tall vegetation impacts predation rates of wader nests needs to determined,
354 ideally through manipulations of landscape structure at different scales.

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502

**Table 1** Descriptions of response and explanatory variables and model structures used in analyses of nest predation probabilities of Lapwing and Redshank. The numbers of wader nests used in each analysis are shown separately for fields with (V) or without (NV) a verge connected. GPS = spatially referenced nests.

| Model response | Lapwing | | Redshank | | Model structure |
|---|---|---|---|---|---|
| | V | NV | V | NV | |
| Nest predation rate | 308 | 669 | 98 | 192 | Find day + Verge connection + Distance to verge + Verge within 0.2 km + (1\|Year) + (1\|Field) |
| | | | | | Find day + Verge connection + Distance to verge + Verge within 0.5 km + (1\|Year) + (1\|Field) |
| | | | | | Find day + Verge connection + Distance to verge + Verge within 1.0 km + (1\|Year) + (1\|Field) |

| Type | Variable | Distribution (link) | Explanation |
|---|---|---|---|
| Response | Nest predation rate | Binomial (logit) | Nest outcome (Predated or Hatched) accounting for exposure days ; (cbind(predated outcome, exposure days) |
| Explanatory | Year | | Lapwing: 2005-2011; Redshank 2007-2011 |
| | Field | | Nest field identity |
| | Find date | | Day after March 1$^{st}$ when nest was found |
| | Verge connected | | Nest field connected or not to a verge (e.g. gateway or other entrance). |
| | Direct distance to verge | m | Straight line distance between nest and nearest verge. |
| | Verge within 0.2 km | m$^2$ | Area of verge within a buffer of 0.2 km radius centred on each nest |
| | Verge within 0.5 km | m$^2$ | Area of verge within a buffer of 0.5 km radius centred on each nest |
| | Verge within 1 km | m$^2$ | Area of verge within a buffer of 1 km radius centred on each nest |

**Table 2** Results of binomial models of nest survival for Lapwing with differing areas of verge habitat in the surrounding (0.2 km, 0.5 km and 1 km buffer models). Minimum models are shown above the dashed lines, and non-significant variables (with estimates from the full model) are shown below the dashed lines. Estimates and se are logits. Marginal ($R^2_m$) and conditional ($R^2_c$) estimates of model fit are calculated following Nakagawa and Schielzeth (2013).

| | Variable | Estimate | se | z value | P |
|---|---|---|---|---|---|
| **a** | 0.2 km buffer model ($R^2_m = 0.006$, $R^2_c = 0.046$) | | | | |
| | (Intercept) | -3.533 | 0.151 | -23.423 | < 0.001 |
| | Direct distance to verge | 0.001 | 0.000 | 2.718 | 0.007 |
| | Find date | 0.005 | 0.003 | 1.739 | 0.082 |
| | Verge connected | -0.239 | 0.145 | -1.643 | 0.100 |
| | Verge in 0.2 km buffer | 0.000 | 0.000 | 0.670 | 0.503 |
| **b** | 0.5 km buffer model ($R^2_m = 0.006$, $R^2_c = 0.046$) | | | | |
| | (Intercept) | -3.533 | 0.151 | -23.423 | < 0.001 |
| | Direct distance to verge | 0.001 | 0.000 | 2.718 | 0.007 |
| | Find date | 0.005 | 0.003 | 1.747 | 0.081 |
| | Verge connected | -0.160 | 0.136 | -1.176 | 0.239 |
| | Verge in 0.5 km buffer | 0.000 | 0.000 | -1.363 | 0.173 |
| **c** | 1 km buffer model ($R^2_m = 0.012$, $R^2_c = 0.048$) | | | | |
| | (Intercept) | -2.701 | 0.193 | -13.970 | < 0.001 |
| | Verge in 1 km buffer | 0.000 | 0.000 | -3.740 | < 0.001 |
| | Find date | 0.004 | 0.003 | 1.657 | 0.097 |
| | Verge connected | -0.158 | 0.129 | -1.220 | 0.222 |
| | Direct distance to verge | 0.001 | 0.000 | 1.133 | 0.257 |

**Table 3** Results of binomial models of nest survival for Redshank with differing areas of verge habitat in the surrounding (0.2 km, 0.5 km and 1 km buffer models). Minimum models are shown above the dashed lines, and non-significant variables (with estimates from the full model) are shown below the dashed lines. Estimates and SE are logits.

| | Variable | Estimate | Std. Error | z value | P |
|---|---|---|---|---|---|
| **a** | 0.2 km buffer model | | | | |
| | (Intercept) | -2.929 | 0.311 | -9.421 | < 0.001 |
| | Find date | -0.003 | 0.006 | -0.476 | 0.634 |
| | Verge connected | 0.234 | 0.219 | 1.068 | 0.285 |
| | Distance to verge | 0.001 | 0.001 | 0.956 | 0.339 |
| | Verge in 0.2 km buffer | 0.000 | 0.000 | 1.359 | 0.174 |
| **b** | 0.5 km buffer model | | | | |
| | (Intercept) | -2.929 | 0.311 | -9.421 | < 0.001 |
| | Find date | -0.002 | 0.006 | -0.327 | 0.744 |
| | Verge connected | 0.243 | 0.224 | 1.083 | 0.279 |
| | Distance to verge | 0.001 | 0.001 | 0.488 | 0.625 |
| | Verge in 0.5 km buffer | 0.000 | 0.000 | 0.454 | 0.650 |
| **c** | 1 km buffer model | | | | |
| | (Intercept) | -2.929 | 0.311 | -9.421 | < 0.001 |
| | Find date | -0.002 | 0.006 | -0.386 | 0.700 |
| | Verge connected | 0.249 | 0.228 | 1.094 | 0.274 |
| | Distance to verge | 0.001 | 0.001 | 0.622 | 0.534 |
| | Verge in 1 km buffer | 0.000 | 0.000 | 0.938 | 0.348 |

**Figure 1** The distribution of monitored fields (light grey) and Lapwing (●) and Redshank (X) nests at Berney Marshes between 2005 and 2011, and of tall vegetation outside fields (dark grey).

**Figure 2** Number of Lapwing nests that were predated (white) and hatched (grey) for different a) years, b) find dates (days since the 1st March), c) presence of attached connected verge, d) direct distance from nest to verge, e) area of verge within 0.2 km of nest, f) area of verge within 0.5 km of nest, and g) area of verge within 1 km of nest.

**Figure 3** Number of Redshank nests that were predated (white) and hatched (grey) for different a) years, b) find dates (days since the 1st March), c) presence of attached connected verge, d) direct distance from nest to verge, e) area of verge within 0.2 km of nest, f) area of verge within 0.5 km of nest, and g) area of verge within 1 km of nest.

**Figure 4** Predicted predation probability (dotted lines indicate 95% confidence intervals) for Lapwing nests in relation to a) distance to the nearest verge (Table 2a and b); and b) area of verge within 1 km buffer of each nest (Table 2c).
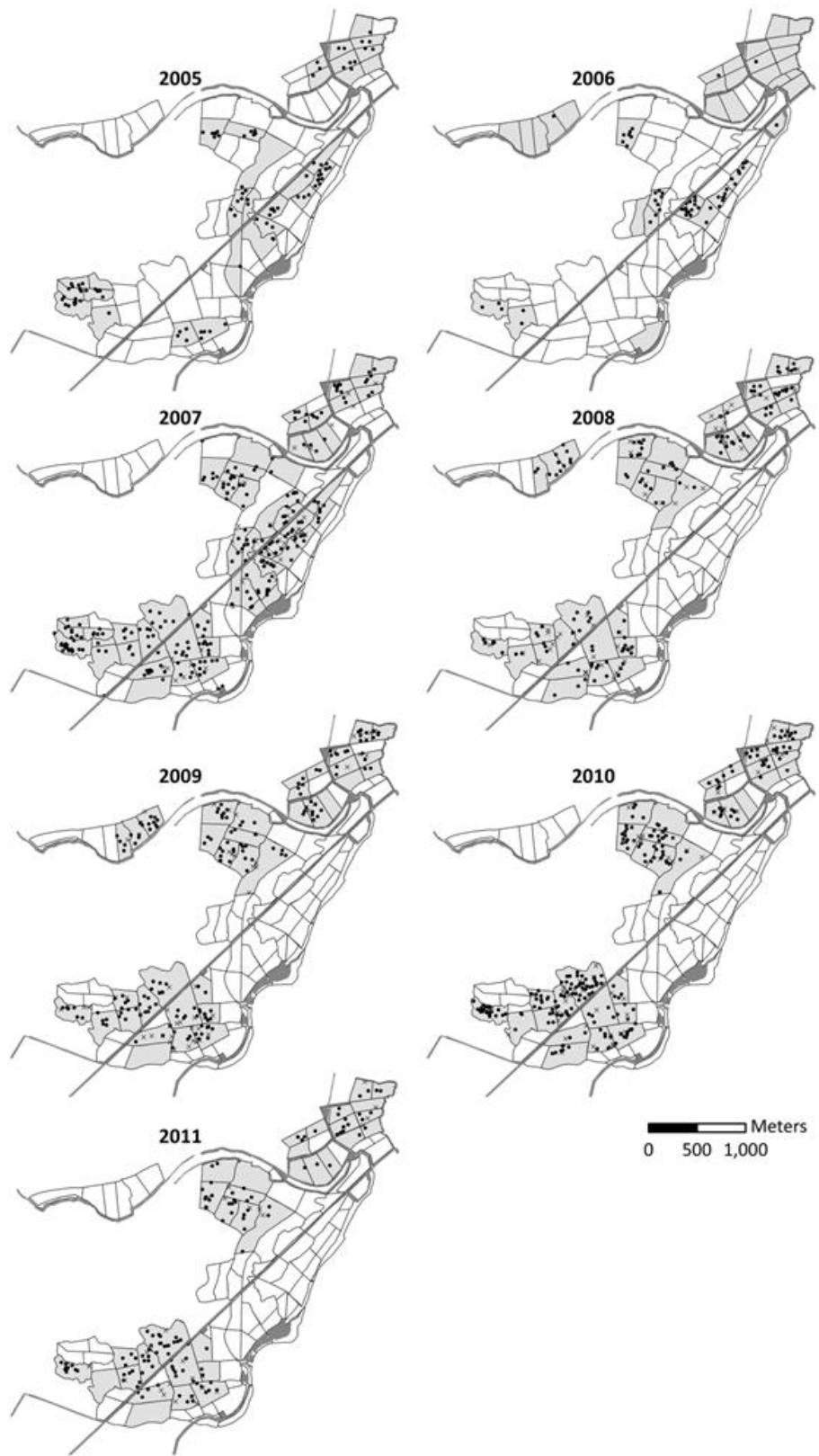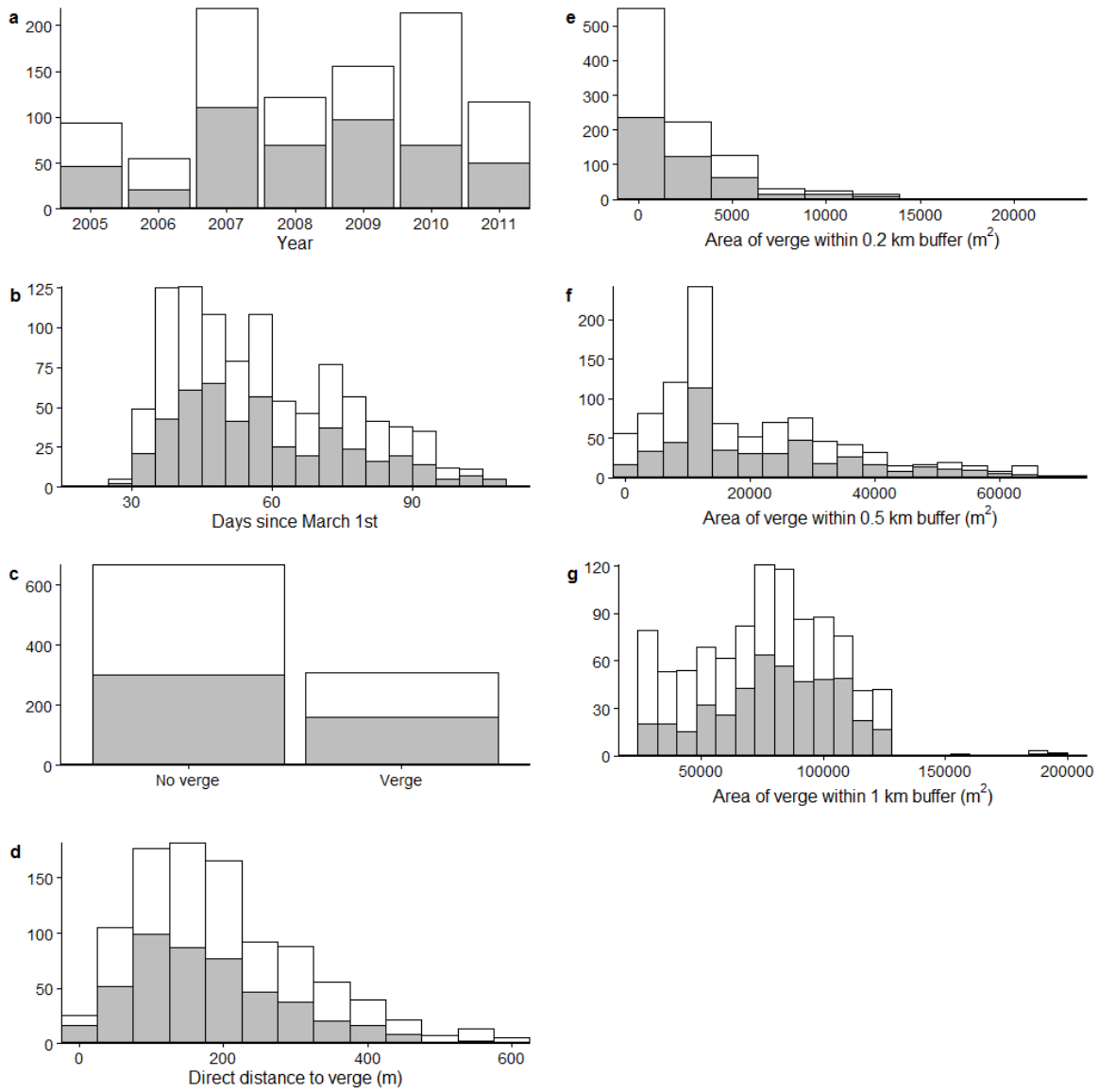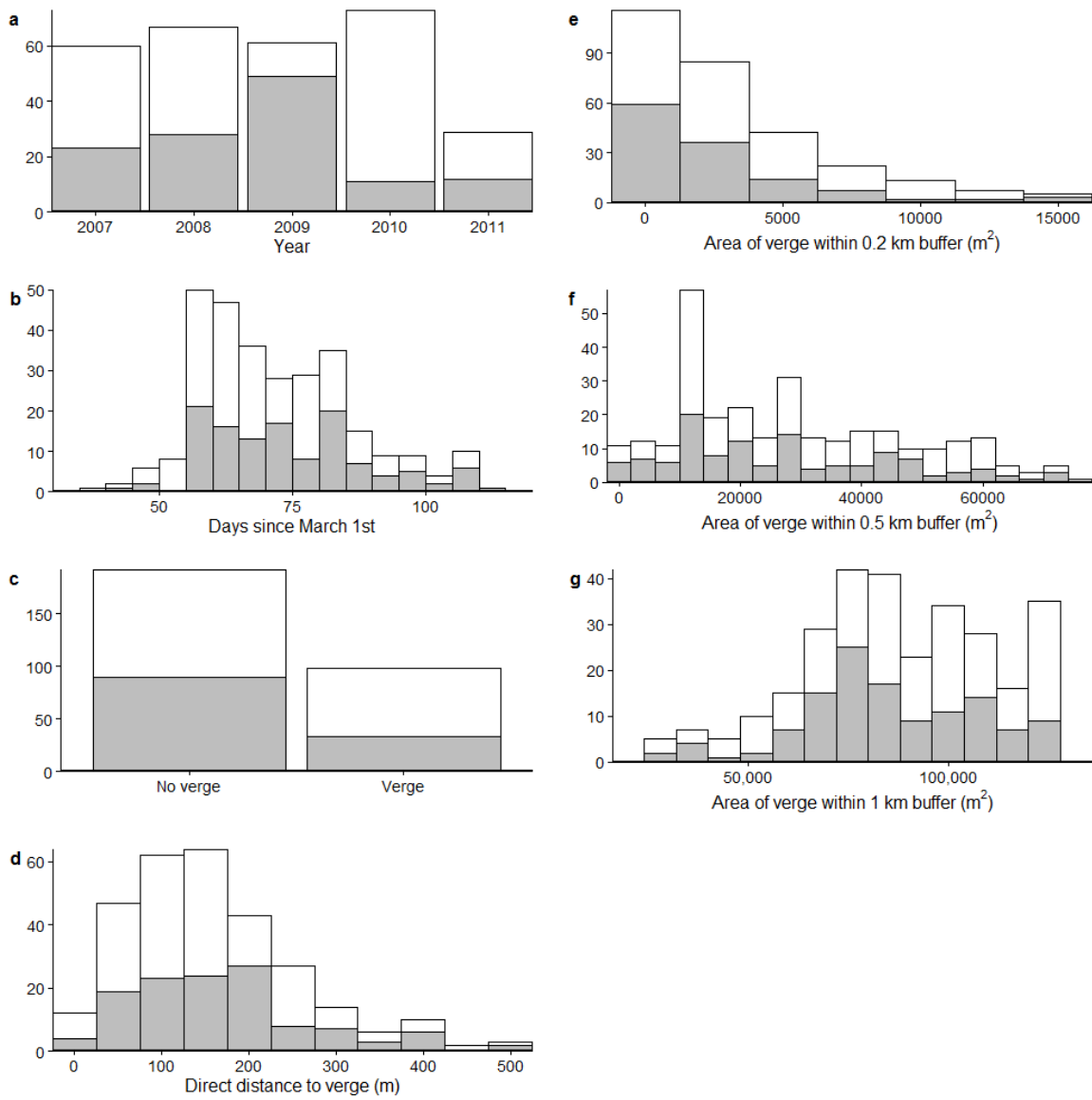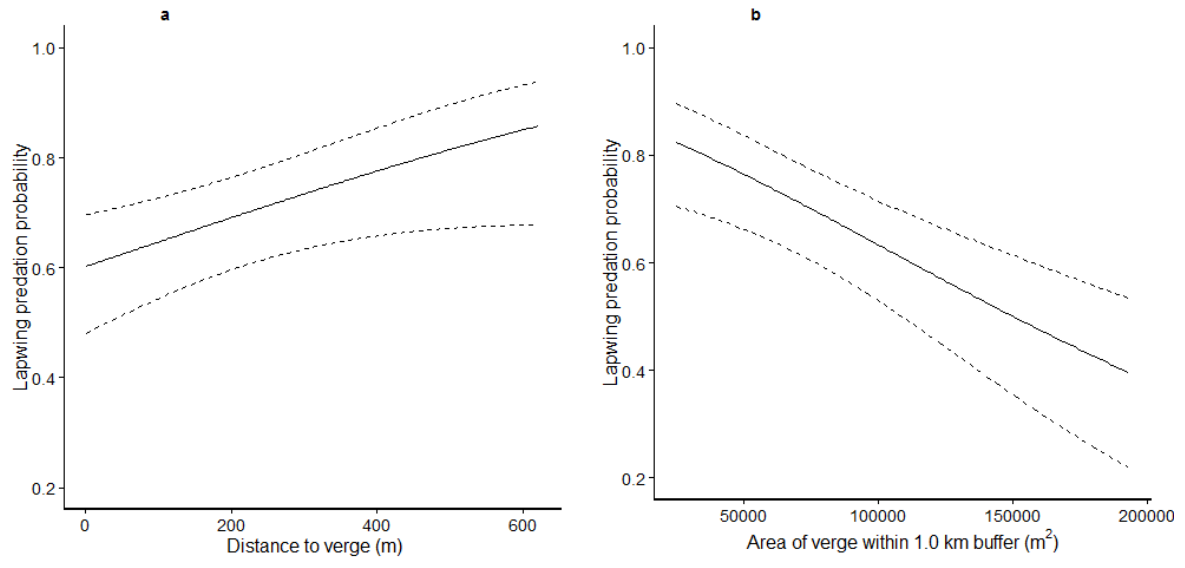
**Figure 1**

**Figure 2**

Figure 3

**Figure 4**