

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.

42

43 **Keywords:** Shorebirds, predator-prey interactions, foodwebs, wetlands, habitat management

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45

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 \pm 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, $\sim 5\%$ of the reserve is comprised
124 of patches of taller vegetation, which range from verges with vegetation $> \sim 15$ 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 re-nesting 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

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

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 km²), 0.5 (0.79 km²) and
180 1.0 km (3.14 km²) 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 ($1 - \text{DPR}$) 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 m²) 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 predated 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.

345

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 be determined,
354 ideally through manipulations of landscape structure at different scales.

355

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361

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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).

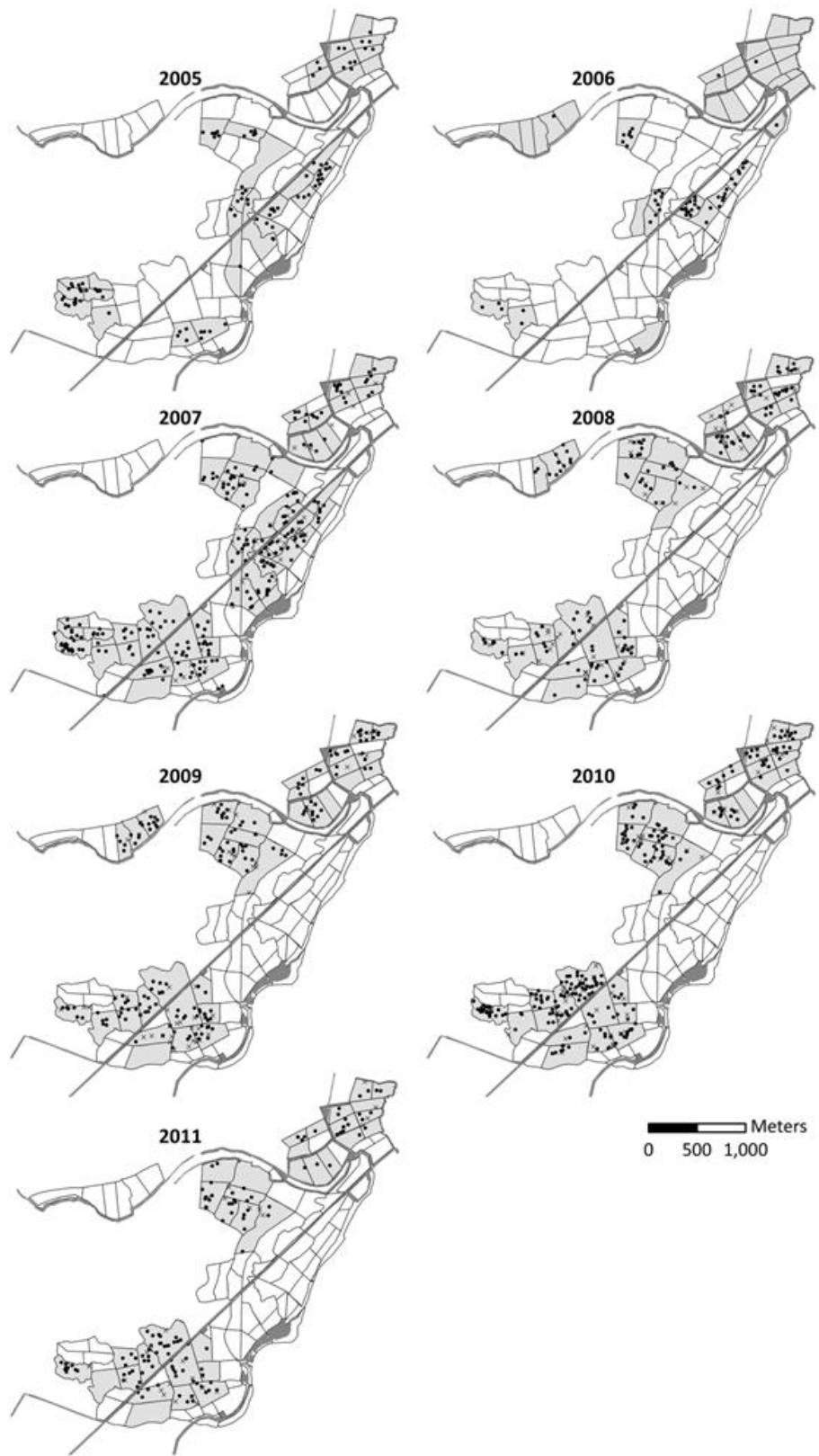


Figure 1

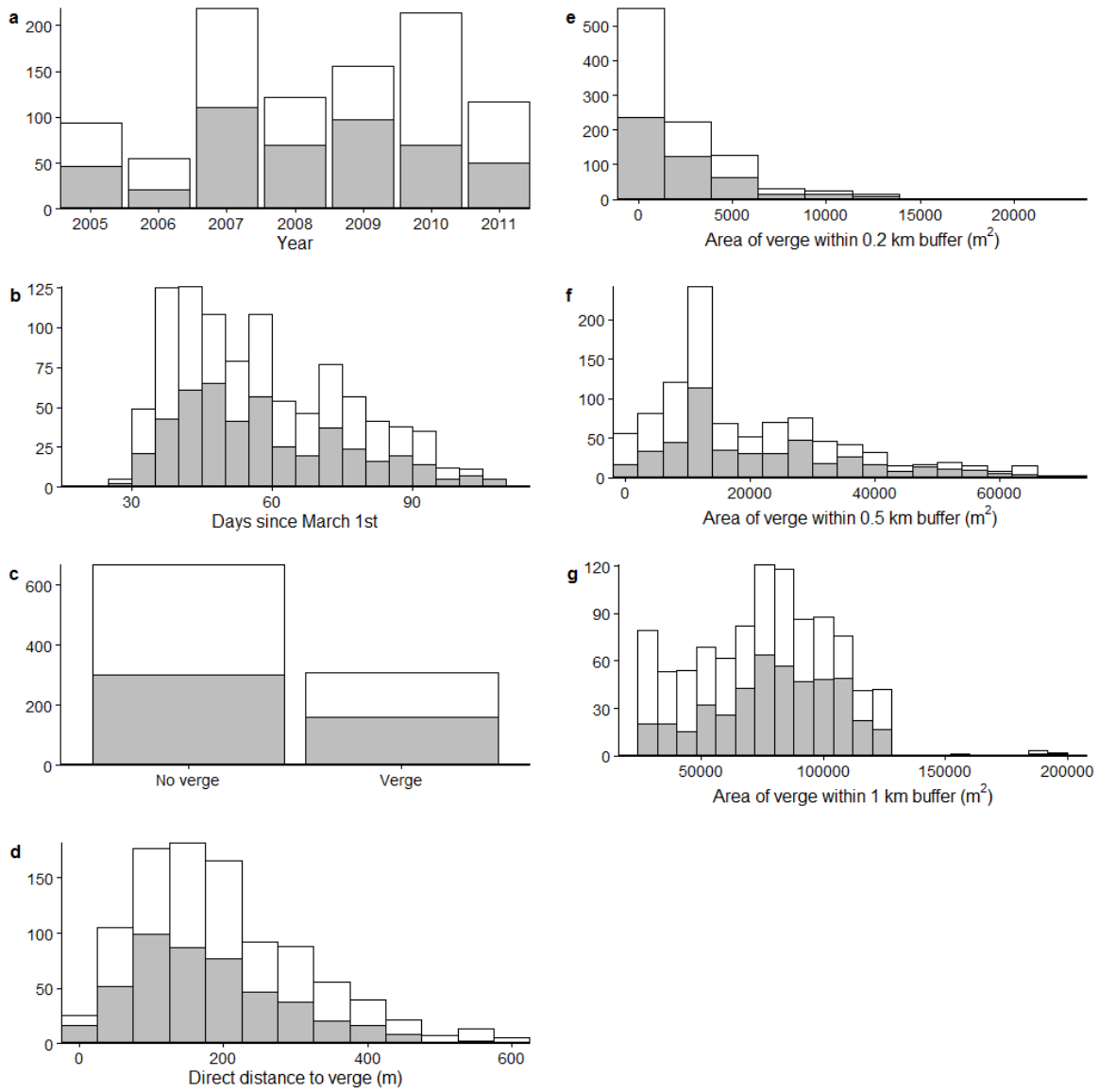


Figure 2

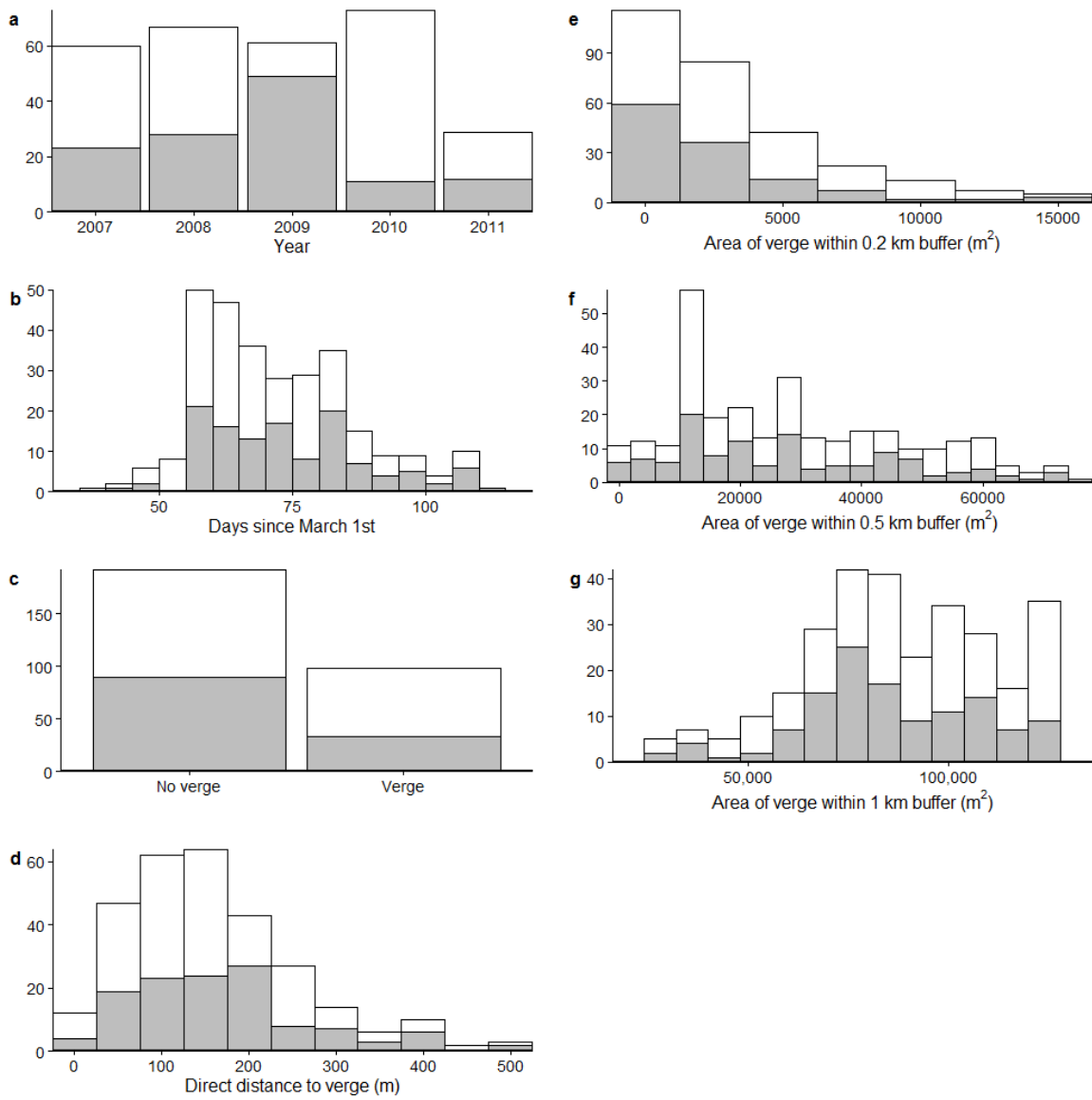


Figure 3

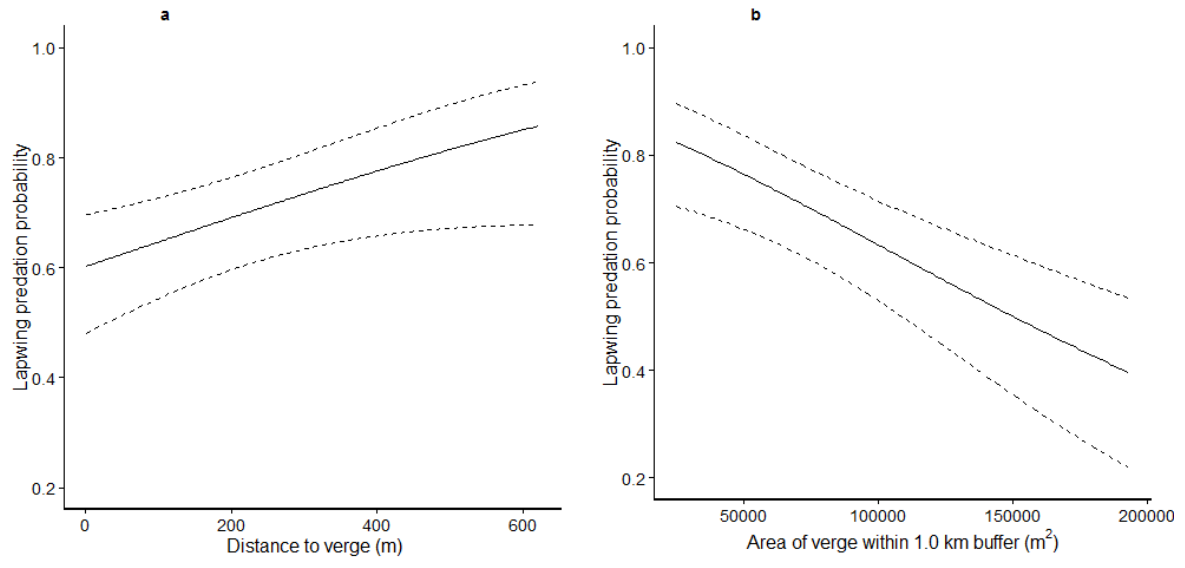


Figure 4