1   **Landscape effects on nest site selection and nest success of Lapwing *Vanellus vanellus* in lowland**

2   **wet grasslands**

3   Nikolas P. Bertholdt[1], Jennifer A. Gill[1], Rebecca A. Laidlaw[1] & Jennifer Smart[2]

4   [1]School of Biological Sciences, University of East Anglia, Norwich Research Park, Norwich, NR4 7TJ,

5   UK

6   [2]RSPB Centre for Conservation Science, Royal Society for the Protection of Birds, The Lodge, Sandy,

7   SG19 2DL, UK

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10   **Capsule**: Northern Lapwing *Vanellus vanellus* avoid nesting close to small woodland patches but nest

11   predation rates do not vary with distance to woodland patches, either because risky areas are

12   avoided or perceived nest predation risk doesn't reflect actual risk.

13   **Aims**: To explore the effects of woodland patches in wet grassland landscapes on nest distribution

14   and success of Lapwings.

15   **Methods**: We quantified the effect of woodland patches on the distribution and outcome of Lapwing

16   nests across four wet grassland sites by mapping nest distribution and monitoring nest outcomes.

17   **Results**: Lapwing nested significantly further from woods than expected by chance. Neither nest

18   predation rates nor the probability of predation occurring at night (thus primarily mammalian

19   predators) or day (primarily avian predators) varied in relation to distance from woodland patches.

20   **Conclusions**: High levels of nest and chick predation in wet grassland landscapes limit the capacity

21   for breeding wader populations to be self-sustaining. Consequently, identifying manageable

22   landscape features that influence predation rates is an important focus of conservation research.

23   Lapwing avoid breeding close to woodland but, as nest predation rates don't vary with distance from

24   woodland patches, their removal may increase the area of suitable nesting habitat but is unlikely to

25   substantially influence productivity.

26   **Introduction**

27   Global declines in wader populations are a major current conservation concern (Stroud. *et al*. 2008).

28   In Europe, long-term population declines are evident in 11 of the 12 wader species monitored within

29   the Pan-European Common Bird Monitoring Scheme (European Bird Census Council 2014) and, in

30   the UK, populations of Lapwing, Common Snipe *Gallinago gallinago*, Common Redshank *Tringa*

31   *totanus*, and Eurasian Curlew *Numenius arquata* have all declined to such an extent that they are

32   now either red- or amber-listed (Hayhow *et al.* 2015). These declines have largely been driven by

33   land drainage and intensification of agricultural management removing the resources required for

34   nesting and chick-rearing (Wilson *et al.* 2005, Eglington *et al.* 2008, Amar *et al.* 2011).

35   Habitat fragmentation is resulting in once-widespread species being increasingly confined to

36   remaining pockets of suitable habitat, and such fragmentation generally leads to reduced nest

37   survival due to predation (Stephens *et al*. 2004). This, combined with increases in generalist predator

38   **number**s, can result in unsustainably high levels of wader clutch loss (Macdonald & Bolton 2008),

39   making predation a significant limiting factor for these species. In these circumstances, increasing

40   the availability of suitable habitat is typically insufficient to arrest population declines without also

41   identifying means of reducing levels of nest predation (Smart *et al*. 2013).

42   The effectiveness of direct predator control at reducing levels of wader nest predation varies

43   depending on the local predator community and context (Bolton *et al*. 2007), is time consuming and

44   therefore costly and any benefits are lost when control ceases. If predation rates vary in relation to

45   manageable landscape characteristics, these could potentially offer longer-term, more sustainable

46   means of improving productivity and aiding recovery of wader populations.

47   Landscape structure could influence wader nest success by altering predator distribution, abundance

48   or activity, and thus the risk of nests being located by predators (e.g. (Whittingham & Evans 2004),

49   Eggers *et al.* 2006, Laidlaw *et al.* 2015). However, such effects may be masked if areas in which

50   predation risk is high are avoided as breeding locations (Martin 2011, Lima 2009, Zanette *et al.* 2011,

51   Lima 2009). Avoidance behaviour could thus reduce the impact of habitat-specific nest predation

52   risk. For example, nesting close to habitat edges may increase exposure of nests to predators from

53   the surrounding landscape. Elevated levels of predation of artificial nests have been recorded near

54   to habitat edges in forest fragments (Hartley & Hunter 1998), in open prairie habitats (Burger *et al.*

55   1994) and, for artificial and real nests, in marshlands (Batáry & Báldi 2004). However, other studies

56   have reported little or no evidence for variation in nest predation rates with distance from habitat

57   edges ((Stroud *et al*. 1990), (Nour *et al.* 1993), (Lahti 2001)), which could reflect either no effects of

58   habitat edges on predator activity or effective avoidance of risky areas by species vulnerable to nest

59   predators. Increases in nesting density with distance from woodland edges have been shown in

60   grassland passerines (Renfrew 2005) and, in the UK uplands, breeding wader abundance increases

61   with distance from plantation edges, Wilson *et al.* 2014), suggesting either avoidance of woodlands

62   by these species or lower survival of individuals breeding close to woodlands. The landscapes in

63   which waders breed can differ greatly in the amount, type and distribution of woodland. Small

64   patches of woodland are common in lowland wet grassland landscapes, but the influence of these

65   woodland patches on the nesting distribution and nest success of the important wader populations

66   that breed in these areas is not well understood.

67   If waders in lowland wet grassland avoid nesting close to woodlands, as seen in the uplands, this

68   could render large areas of potentially suitable lowland habitat unusable, thus limiting the capacity

69   for species recovery. Similarly, if woodland patches are used by nest predators, nest predation may

70   vary with proximity to woodland. Previous studies of breeding waders on grasslands have shown

71   that mammalian predators, particularly red foxes, *Vulpes vulpes*, are responsible for the great

72   majority of wader nest losses (Macdonald & Bolton 2008), and that lapwing nests that are closer to

73   patches of tall (primarily grass) vegetation have lower predation rates (Laidlaw *et al.* 2015). As these

74   patches of tall vegetation support small mammal populations that are otherwise rare in wet

75   grasslands (Laidlaw *et al.* 2013), the greater success of wader nests close to tall vegetation may

76   result from foxes concentrating on small mammal prey in these areas. If woodland patches provide

77   similar small mammal prey resources, nest predation by mammalian predators may be lower close

78   to woodland. Alternatively, if woodland patches provide perching locations from which avian

79   predators can hunt, nest predation by avian predators may be greater for nests close to woodland

80   patches. While the identity of nest predators is rarely known, most mammalian nest predation

81   occurs at night while avian predators operate primarily during daylight, thus nocturnal and diurnal

82   nest predation are generally good proxies for mammalian and avian predators, respectively

83   (Eglington *et al*. 2009)**.** To assess the influence of woodland patches in lowland wet grassland

84   landscapes on breeding wader distribution and success, we therefore quantify variation in nest

85   location, nest predation and timing of predation (night or day) of Lapwing nests in relation to

86   proximity to woodland patches, on four sites in eastern England.

87   **Materials and Methods**

88   Four wet grasslands sites on the Alde-Ore estuary in Suffolk, UK were studied between 31st March

89   and 30th June 2014 (mean ± SD ha: 117.4 ± 67.5). These sites were at least 3 km apart and contained

90   grasslands with a mix of sward heights and wet features in the form of shallow floods and

91   footdrains. At all four sites, fields are managed by cutting or grazing with sheep or cattle, and the

92   sites are surrounded by a mix of arable farmland and dry grassland, with a vegetated sea wall

93   separating them from intertidal habitats along one boundary. Small patches of woodland are

94   present on all sites (mean number per site = 5 ± 2 SD; mean woodland patch size = 1.3 ha ± 1.1 SD)

95   (Figure 1).

96   Lapwing nests were located during twice weekly visits to each site by observing incubating adults.

97   Eggs were weighed and measured, to calculate predicted hatching dates (Smart 2005), a

98   temperature logger was inserted beneath the nest lining, and the position of the nest was recorded

99   using a Garmin Etrex 30 handheld GPS.

100   Temperature loggers recorded temperature every eight minutes, and were retrieved once the nest

101   was empty. The resulting temperature traces were used to determine the date and time of hatching

102   or failure. Hatched nests were identified as being empty within two days of predicted hatch date and

103   in which tiny eggshell fragments were found within the undisturbed nest lining. Predated nests

104   typically had remains of predated eggs or a disturbed nest lining, and were empty prior to predicted

105   hatch dates. Trampled nests (containing broken eggshell and contents) and abandoned nests

106   (containing cold, intact eggs) were also recorded.

107   The positions of all woodland patches, ditches, field margin vegetation (hedges or tall vegetation

108   fringe) and within-field tall (>50 cm) vegetation and wet features were mapped using a combination

109   of GPS and ground-truthed aerial imagery, and imported into ArcGIS along with the positions of all

110   nests. Wet features are known to attract nesting Lapwing (Eglington et al. 2010) and thus their

111   influence on nest location had to be taken into account when assessing effects of woodland patches

112   on nest distribution and success. The effects of ditches, field margin and within-field tall vegetation

113   were included in initial analyses but, as they had no significant effects on nest site selection or

114   predation, these were excluded from further consideration in this study.

115   The effects of woodland patches on (1) nest site selection, (2) daily nest predation rate and (3) time

116   of nest predation were assessed using generalised linear models with a logit link function and

117   binomial error distribution. Daily predation rate was calculated using the extension to Mayfield

118   estimate methods described by (Aebischer 1999) (Table 1). Nest locations were compared to

119   randomly located points generated using the Create Random Points function in ArcGIS. The number

120   of random points generated for each site reflected the number of nests at that site (rounded up to

121   the nearest five), and random points were excluded from areas of unsuitable nesting habitat

122   (standing water and vegetation height greater than 15 cm) (Winspear & Davies 2005). The timing of

123   nest predation was classified as day or night, as defined by the hours of civil twilight.

124   **Results**

125   Across all sites, a total of 77 nests were monitored (12, 28, 13 and 24 per site) of which 32% hatched,

126   53% were predated, 9% failed due to trampling and 5% failed due to flooding or abandonment.

127   Nests were found, on average, 8.7 days (± 8.2 SD) from the start of incubation, and were located

128   between 71 and 1815 m from woodland patches (mean 717 m ± 327 SD), with 88% being located

129   over 500 m from the nearest woodland. The maximum distance of potential nesting habitat to

130   woodland patches was 2065 m. Nests were distributed closer to wet features and further from

131   woods than randomly located points (full model: $\chi^2_5=34.7$, p<0.001, Table 2.1, Figure 2.1). This

132   model successfully classified 63.5% of nests and 74% of random points.

133   For the 65 nests for which outcome (hatched or not) was known (Figure 2.2) and exposure days

134   could be calculated (12 of the 77 nests were excluded from this analysis due to being found at or

135   after hatching or data loggers failed, and hence outcome dates were lost), the Mayfield estimate of

136   mean daily predation rate was 0.05 (± 0.008 SE). There was no significant variation in daily

137   predation rate of these nests between sites or in relation to either distance to the nearest woodland

138   patch or wet feature (Table 2.2).

139   Predation events occurred throughout the breeding season and, of the 39 predated nests for which

140   time of predation was available, 68% were predated at night (Figure 2.3 and Figure 3). However,

141   there was no significant difference in the relative frequency of nocturnal and diurnal predation

142   events among sites or in relation to either distance to the nearest woodland patch or the nearest

143   wet feature (Table 2.3).

144   **Discussion**

145   In wet grassland landscapes in which small woodland patches are common, Lapwing nests were

146   located significantly further from woods than expected by chance, however the rate and timing of

147   predation did not vary in relation to these landscape features. In this study the presence of

148   woodland patches did not therefore appear to strongly influence the probability of Lapwing nests

149   being predated in these landscapes.

150   Avoidance of woodland patches was quite strong (only 12% of nests were within 500 m of woods

151   despite ~30% of the suitable nesting habitat being within 500 m of woods at these sites (mean site

152   area = 42.2 ha ± 32.4 SD). The spatial scale of this avoidance of woodlands is similar to that

153   previously found in a range of wader species breeding at higher elevations (Stroud *et al*. 1990,

154   Wilson *et al.* 2014). Lapwing nests were significantly more likely to be located closer to in-field wet

155   features (as has also been shown elsewhere; Eglington *et al.* 2010), and so it is not clear whether the

156   removal of woodland patches alone would necessarily increase the area for nesting Lapwing at these

157   sites, unless in-field wet features were already present or were subsequently developed within the

158   areas previously close to woodland.

159   Increased levels of predation of Lapwing nests close (< 50 m) to trees and other avian perches have

160   been reported (Berg *et al*. 1992) but in our study all nests were located more than 70 m from

161   woodland patches, and thus particularly risky locations may well have been avoided by these birds

162   prior to our study. Waders have also previously been shown to avoid nesting close to tall structures

163   which can potentially be used as perches by avian predators (Wallander *et al.* 2006). Other than

164   woodlands there were very few structures, apart from gateposts which were less than 2 m high,

165   across the sites so tall structures were unlikely to have been important in this study.

166   A wide range of potential predator species were observed across the sites, including Red foxes

167   *Vulpes vulpes*, Eurasian badgers *Meles meles*, Eurasian otters *Lutra lutra,* Carrion crows *Corvus*

168   *corone*, Herring gulls, *Larus argentatus*, Greater black -backed gulls *L. fuscus*, Lesser black -backed

169   gulls *L. marinus*, Grey herons *Ardea cinerea* and Marsh harriers *Circus aeruginosus*. The majority

170   (68%) of nest predation events occurred during the hours of darkness, suggesting that mammalian

171   predators were responsible for most of the nest losses, and Red foxes have been shown to be the

172   main nest predator of waders on grasslands across Western Europe (Macdonald & Bolton 2008).

173   However, diurnal predation events were also recorded in this study, and thus avian predators may

174   also be involved. This range of both diurnal and nocturnal potential predator species, and the likely

175   differences in how they interact with woodland patches, may contribute to the absence of an overall

176   effect of woodlands on the timing of nest predation.

177   The absence of any change in nest predation rates with distance from woodland patches suggests

178   that the lack of nests close to woods is more likely to result from lapwing actively avoiding these

179   areas than from nests close to woods being predated prior to being detected. Avoidance of areas

180   close to woods could reflect a greater perceived predation risk in these areas, perhaps because trees

181   prevent clear lines of sight from nest locations and thus increase the perceived vulnerability to

182   predators of incubating adults.

183   A previous study of breeding lapwing on lowland wet grasslands has shown lower nest predation

184   rates close (within ~100-200 m) to areas of tall vegetation such as field verges (Laidlaw *et al.* 2015),

185   potentially reflecting predators concentrating on small mammal prey in these areas (Laidlaw *et al.*

186   2013). The lack of association between proximity to woodland patches and nest predation rates or

187   timing of predation suggests that woodland patches may either (a) not provide the same conditions

188   for small mammals as grassy field verges, (b) attract avian predators and thus offset any benefit of

189   reduced mammalian predator impact or, alternatively, (c) the avoidance of woodland patches by

190   nesting lapwing may constrain the capacity to identify their influence on nest predation rates. Our

191   analyses of distance to woodland used the straight-line distance which presumes that predator

192   movement around the sites is not constrained by any landscape features. While ditches could

193   potentially constrain the movement of mammalian predators between fields, previous studies have

194   found no evidence of foxes concentrating their activity along these features (Eglington *et al.* 2009),

195   and, in these study areas, the distance of many of the woodland patches from the study fields

196   (Figure 1) meant that direct and indirect (avoiding ditches) distances were very similar.

197   We have shown that the presence of woodland patches in lowland wet grassland landscapes may

198   influence the distribution of breeding Lapwing and could result in large areas of potentially suitable

199   habitat being unused for nesting. Consequently, in these landscapes, restoration of wet grassland

200   habitats might be best located away (i.e. > 500 m) from woodland and woodland creation away (i.e.

201   > 500 m) from fields suitable for breeding waders, and incorporating these criteria into agri-

202   environment options designed to support breeding waders may help to avoid habitat creation in

203   areas where parts of the landscape may be effectively unavailable to nesting lapwing. However, our

204   findings also suggest that such habitat modifications may be unlikely to reduce nest predation rates,

205 and thus the presence of woodland patches is not sufficient to inform or target predator control

206 strategies, and other management practices that increase productivity, such as predator control or

207 landscape manipulation to provide ample alternative food resources for predators, will still be

208 needed to reverse wader population declines.

217 **References**

218 **Aebischer, N.J.** 1999. Multi-way comparisons and generalized linear models of nest success:

219   extensions of the Mayfield method. *Bird Study* **46**: 22–31.

220 **Amar, A., Grant, M., Buchanan, G., Sim, I., Wilson, J., Pearce-Higgins, J.W. & Redpath, S.** 2011.

221   Exploring the relationships between wader declines and current land-use in the British

222   uplands. *Bird Study* **58**: 13–26.

223 **Batáry, P. & Báldi, A. 2004.** Evidence of an edge effect on avian nest success. *Conservation Biology*

224   **18:** 389–400.

225 **Berg, Å., Lindberg, T. & Källebrink, K.G.** 1992. Hatching success of Lapwings on farmland:

226   Differences between habitats and colonies of different sizes. *Journal of Animal Ecology* **61**:

227   469–476.

228 **Bergin, T.M., Best, L.B., Freemark, K.E. & Koehler, K.J.** 2000. Effects of landscape structure on nest

229   predation in roadsides of a midwestern agroecosystem: a multiscale analysis. *Landscape*

230   *Ecology* **15**: 131–143.

231 **Bolton, M., Tyler, G., Smith, K. & Bamford, R.** 2007. The impact of predator control on lapwing

232   *Vanellus vanellus* breeding success on wet grassland nature reserves. *Journal of Applied*

233   *Ecology* **44**: 534–544.

234 **Burger, L.D., Burger, L.W. & Faaborg, J.** 1994. Effects of prairie fragmentation on predation on

235   artificial nests. *The Journal of Wildlife Management* **58**: 249.

236 **Eggers, S., Griesser, M., Nystrand, M. & Ekman J.** 2006. Predation risk induces changes in nest-site

237   selection and clutch size in the Siberian jay. *Proceedings of the Royal Society B: Biological*

238   *Sciences* **273**: 701–706.

239 **Eglington, S.M., Bolton, M., Smart, M.A., Sutherland, W.J., Watkinson, A.R. & Gill, J.A.** 2010.

240   Managing water levels on wet grasslands to improve foraging conditions for breeding

241   Northern lapwing *Vanellus vanellus*. *Journal of Applied Ecology* **47:** 451–458.

242 **Eglington, S.M., Gill, J.A., Bolton, M., Smart, M.A., Sutherland, W.J. & Watkinson, A.R.** 2008.

243   Restoration of wet features for breeding waders on lowland grassland. *Journal of Applied*

244   *Ecology* **45**: 305–314.

245 **Eglington, S.M., Gill, J.A., Smart, M.A., Sutherland, W.J., Watkinson, A.R. & Bolton, M.** 2009.

246   Habitat management and patterns of predation of Northern Lapwings on wet grasslands:

247   The influence of linear habitat structures at different spatial scales. *Biological Conservation*

248   **142**: 314–324.

249 **European Bird Census Council.** 2014. Trends of common birds in Europe, 2014 update. Available

250   from http://www.ebcc.info/index.php?ID=557 (accessed October 8, 2014).

251   **Hartley, M.J. & Hunter, M.L.** 1998. A meta-analysis of forest cover, edge effects, and artificial nest

252   predation rates. *Conservation Biology* **12**: 465–469.

253   **Lahti, D.C.** 2001. The "edge effect on nest predation" hypothesis after twenty years. *Biological*

254   *Conservation* **99**: 365–374.

255   **Laidlaw, R.A., Smart, J., Smart, M.A. & Gill, J.A.** 2015. The influence of landscape features on nest

256   predation rates of grassland-breeding waders. *Ibis* **157**: 700–712.

257   **Lima, S.L.** 2009. Predators and the breeding bird: behavioral and reproductive flexibility under the

258   risk of predation. *Biological Reviews* **84**: 485–513.

259   **Macdonald, M.A. & Bolton, M.** 2008. Predation on wader nests in Europe. *Ibis* **150**: 54–73.

260   **Martin, T.E.** 2011. The cost of fear. *Science* **334**: 1353–1354.

261   **Nour, N., Matthysen, E. & Dhondt, A.A.** 1993. Artificial nest predation and habitat fragmentation:

262   different trends in bird and mammal predators. *Ecography* **16**: 111–116.

263   **Renfrew, R.B., Ribic, C.A. & Nack, J.L.** 2005. Edge avoidance by nesting grassland birds: A futile

264   strategy in a fragmented landscape. *The Auk* **122**: 618–636.

265   **Smart, J. 2005.** Strategies of sea-level rise mitigation for breeding Redshank. PhD Thesis. University

266   of East Anglia Norwich. Available from http://www.bou.org.uk/student-post-docs-early-

267   career-researchers/branta/smart/ (accessed February 1, 2015).

268   **Smart, J., Bolton, M., Hunter, F., Quayle, H., Thomas, G. & Gregory, R.D.** 2013. Managing uplands

269   for biodiversity: Do agri-environment schemes deliver benefits for breeding lapwing *Vanellus*

270   *vanellus*? *Journal of Applied Ecology* **50**: 794–804.

271 **Stephens, S.E., Koons, D.N., Rotella, J.J. & Willey, D.W.** 2004. Effects of habitat fragmentation on

272   avian nesting success: a review of the evidence at multiple spatial scales. *Biological*

273   *Conservation* **115**: 101–110.

274 **Stroud, D.A., Baker, A., Blanco, D.E., Davidson, N.C., Delany, S., Ganter, B., Gill, R., González, P.,**

275   **Haanstra, L., Morrison, R.I.G., Piersma, T., Scott, D.A., Thorup, O., West, R., Wilson, J. &**

276   **ZöcklerStroud, C.** 2008. The conservation and population status of the world's waders at

277   the turn of the millennium. *Waterbirds around the world.* Eds. Boere, G.C., Galbraith, C.A. &

278   Stroud, D.A.. The Stationery Office, Edinburgh, UK. 643–648.

279 **Stroud, D.A., Harding, N.J. & Reed, T.M.** 1990. Do moorland breeding waders avoid plantation

280   edges? *Bird Study* **37**: 177–186.

281 **Wallander, J., Isaksson, D. & Lenberg, T.** 2006. Wader nest distribution and predation in relation to

282   man-made structures on coastal pastures. *Biological Conservation* **132**: 343–350.

283 **Whittingham, M.J. & Evans, K.L.** 2004. The effects of habitat structure on predation risk of birds in

284   agricultural landscapes. *Ibis* **146**: 210–220.

285 **Wilson, A.M., Vickery, J.A., Brown, A., Langston, R.H.W., Smallshire, D., Wotton, S. &**

286   **Vanhinsbergh, D.** 2005. Changes in the numbers of breeding waders on lowland wet

287   grasslands in England and Wales between 1982 and 2002. *Bird Study* **52**: 55–69.

288 **Wilson, J.D., Anderson, R., Bailey, S., Chetcuti, J., Cowie, N.R., Hancock, M.H., Quine, C.P., Russell,**

289   **N., Stephen, L. & Thompson, D.B.A.** 2014. Modelling edge effects of mature forest

290   plantations on peatland waders informs landscape-scale conservation. *Journal of Applied*

291   *Ecology* **51**: 204–213.

292 **Winspear, R. & Davies, G.** 2005. *A management guide to birds of lowland farmland.* Royal Society

293   for the Protection of Birds, Sandy, England.

294   **Zanette, L.Y., White, A.F., Allen, M.C. & Clinchy, M.** 2011. Perceived predation risk reduces the

295   number of offspring songbirds produce per year. *Science* **334**: 1398–1401.

296

297   Table 1. Descriptions of response and explanatory variables used in models of landscape effects on Lapwing nest site selection and nest outcome. Full

298   model structures are shown for each analysis.

Analysis	Response		Explanatory variables (fixed factors)
1: Is nest site selection affected by proximity to woods and wet features?			
	Nest or random location		Distance to woods, distance to wet features, (site)
2: Is nest predation rate affected by proximity to woods and wet features?			
	Daily predation rate		Distance to woods, distance to wet features, (site)
3: Is the timing of nest predation affected by proximity to woods and wet features?			
	Day or night		Distance to woods, distance to wet features, (site)
Response variable descriptions			
Analysis	Variable	Distribution	Description
1	Nest or random	Binomial	All nests (n=77) and random points (n=85)
2	Daily predation rate	Binomial	Predated (n=39) and other outcome (n=26) accounting for exposure days
3	Day or night	Binomial	Period of failure of predated nests (night n=26, day n=13; period defined by hours of civil twilight)
Explanatory variable descriptions			
Analysis	Variable	Factor levels	Description
1,2,3	Site	Four sites	Four wet grassland sites in Eastern England
1,2,3	Distance to wet features	Continuous	Shortest linear distance to nearest within-field flood or footdrain(m)
1,2,3	Distance to woods	Continuous	Shortest linear distance to nearest wood(m)

299

300 Table 2. Results of generalised linear maximal models exploring the influence of woods and in-field

301 wet features on nest site location, daily nest predation rate and timing of nest predation (day or

302 night). Significant effects are highlighted in bold.

| Analysis	Variable				
1: Does nest site selection vary with distance to woods and wet features?					
		Wald	expB	df	p
	Constant	0.087	0.849	1	0.77
	Site	2.097	-	3	0.55
	Distance to wet features	**15.679**	**0.994**	**1**	**<0.001**
	Distance to woods	**5.375**	**1.002**	**1**	**0.02**
2: Does nest predation rate vary with distance to woods and wet features?					
		χ^2		df	p
	Constant	22.46		1	<0.001
	Site	0.81		3	0.85
	Distance to wet features	0.57		1	0.45
	Distance to woods	0.49		1	0.48
3: Does the timing of nest predation vary with distance to woods and wet features?					
		Wald	expB	df	p
	Constant	0.398	0.319	1	0.53
	Site	1.016	-	3	0.8
	Distance to wet features	2.262	1.014	1	0.13
	Distance to woods	0.087	0.999	1	0.77

303
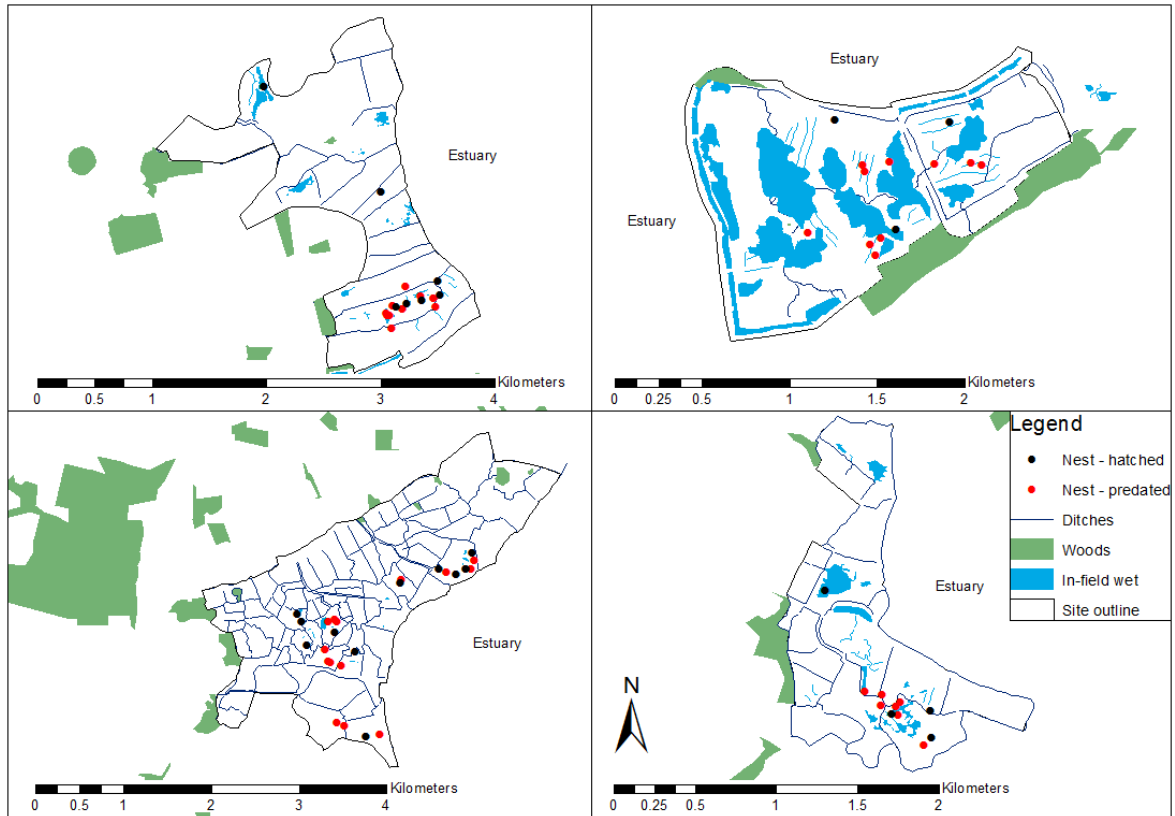
**Figure 1.** Locations of hatched and predated Lapwing nests and key landscape components at the

four study sites on the Suffolk coast, eastern England.

306
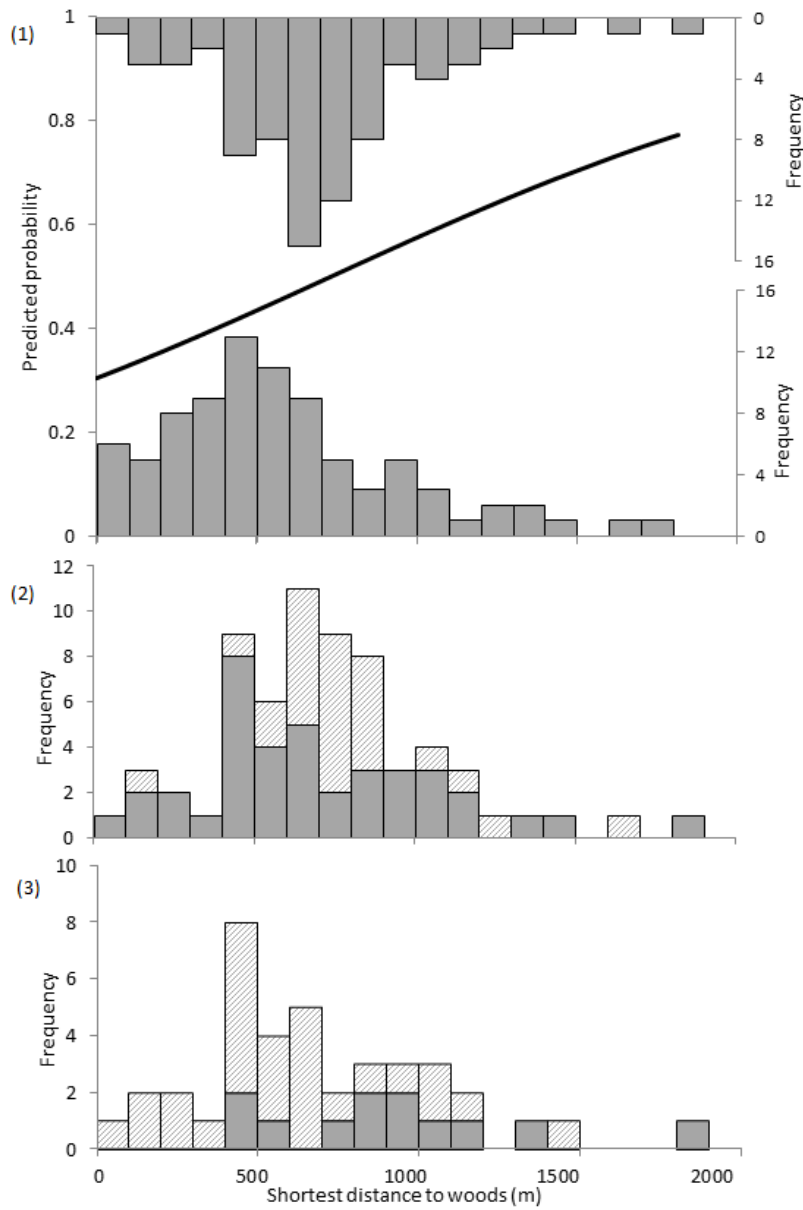
Figure 2. (1)The influence of distance to woodland patches, after controlling for site and distance to wet features, on the location of Lapwing nests (upper bars) compared to random points (lower bars), (2) the number of non-predated (shaded bars) and predated (solid bars) nests, (3) the number of nocturnal (shaded bars) and diurnally (solid bars) predated nests.
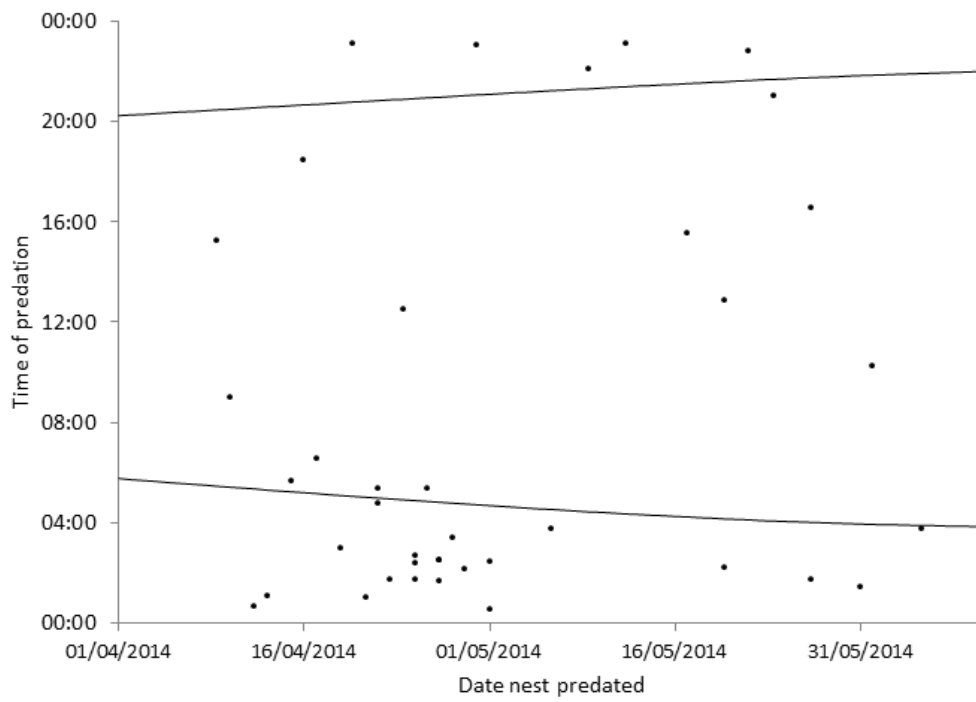
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312   **Figure 3.** Seasonal and diurnal timing of Lapwing nest predation events. Lines show the timing of

313   dawn and dusk (the beginning and end of civil twilight) throughout the breeding season.

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