

1 **Placement, survival and predator identity of Eurasian Curlew *Numenius arquata***  
2 **nests on lowland grass-heath.**

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15 **Short title**

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17

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23 **Summary**

24 **Capsule**

25 Within the UKs largest lowland Eurasian Curlew *Numenius arquata* population, Curlew  
26 preferentially nested on physically-disturbed (treated) than undisturbed (control)  
27 grassland, and low nest survival rates were primarily attributable to Red Fox *Vulpes*  
28 *vulpes*.

29 **Aims**

30 To inform conservation interventions for Curlew within semi-natural lowland dry-  
31 grassland landscapes.

32 **Methods**

33 Across a 3,700 ha lowland dry-grassland landscape, over two years, effects of ground-  
34 disturbance management on Curlew nest placement (n=41) were examined using  
35 GLMs controlling for vegetation strata; effects of site and management on nest survival  
36 (n=44) were examined controlling for lay date and year. Nest predator identity was  
37 investigated using temperature sensors (n=28) and nest cameras (n=10).

38 **Results**

39 Curlews were five times more likely to nest on physically-disturbed than undisturbed  
40 grassland. Nest survival (overall mean  $0.24 \pm 0.07$ , SE) was not influenced by year or  
41 ground-disturbance but declined with lay date and differed markedly between the two  
42 sites, consistent with predator control. Predation accounted for 29/32 of failed nests  
43 and was predominantly at night (17/23 cases where timing was known,  $p < 0.001$ ),  
44 consistent with mammalian predators. Cameras indicated Foxes to be the main

45 predator (4/5 cases). Overall breeding productivity was  $0.16 \pm 0.01$  (SE) chicks per  
46 nesting attempt.

#### 47 **Conclusion**

48 Curlew suffered from unsustainably high rates of nest predation primarily attributable  
49 to Foxes. A combination of perimeter fencing and lethal predator control appeared to  
50 improve nest success at one site. Ground-disturbance treatment could encourage  
51 nesting attempts in areas managed to minimise predator density.

52 **Introduction**

53 Global wader (shorebird) populations are declining (Butchart *et al.*, 2010),  
54 primarily due to habitat loss and degradation through agricultural intensification and  
55 climate change (Pearce-Higgins *et al.*, 2017, Franks *et al.*, 2017). Almost half of  
56 European wader populations for which trends are known are either IUCN Threatened  
57 or declining (Stroud *et al.*, 2006) and in the UK, 16 of 20 breeding wader species are  
58 classified nationally as IUCN Threatened (Stanbury *et al.*, 2017). One such species is  
59 the Eurasian Curlew *Numenius arquata* (hereafter 'Curlew'), which has been recently  
60 classified nationally as Threatened. As a result of the species' global conservation  
61 status (IUCN Near Threatened; BirdLife International 2017), the international  
62 significance of the UK breeding population (~68,000 breeding pairs, accounting for  
63 over a quarter of the global breeding population; Musgrove *et al.* 2013, Hayhow *et al.*,  
64 2017), and its long-term decline (65% between 1970-2015; Hayhow *et al.*, 2017),  
65 Curlew are considered to be the UK's highest bird conservation priority (Brown *et al.*,  
66 2015). Although the number of Curlew in the UK uplands (including moorland: upland  
67 heath, bog and unenclosed grassland; and enclosed upland grassland) is not known  
68 with precision, these hold the majority of the population, where considerable research  
69 has focused on their breeding ecology and conservation (Douglas *et al.*, 2017;  
70 Johnstone *et al.*, 2017). Although lowland Curlew are less studied, their loss would  
71 reduce the species' breeding range, increasing the dependence on vulnerable upland  
72 populations (Baldock *et al.*, 2017).

73 The main driver of UK Curlew decline is low breeding productivity, attributable  
74 to predation and reduced quality of breeding habitats (Franks *et al.*, 2017; Hayhow *et*  
75 *al.*, 2017). Research from the uplands has informed habitat provision (e.g. controlled  
76 cutting of moorland to provide a mosaic of vegetation heights and creation of pools,

77 Fisher & Walker 2015) and demonstrated that legal predator control (of Red Fox  
78 *Vulpes vulpes*, hereafter 'Fox', Carrion Crow *Corvus corone*, hereafter 'Crow', Stoat  
79 *Mustela erminea* and Weasel *M. nivalis*) can increase Curlew breeding success and  
80 abundance (Fletcher *et al.*, 2010; Ludwig *et al.*, 2019); however, lethal control does  
81 not work in all cases (e.g. Bodey *et al.*, 2011, Bolton *et al.* 2007b). In lowland regions  
82 of the UK, recent monitoring (Smart, 2017; Curlew Call, 2017) has confirmed low  
83 breeding productivity with a mean across studies (weighted by square-root of sample  
84 sizes) of  $0.23 \pm 0.13$  SD fledged chicks nesting attempt<sup>-1</sup> year<sup>-1</sup> (Table S1),  
85 considerably less than the 0.48 - 0.62 pair<sup>-1</sup> year<sup>-1</sup> required for population stability  
86 (Grant *et al.*, 1999). Previous research into the predator assemblage and efficacy of  
87 anti-predator solutions (e.g. lethal control and anti-predator fencing, Bolton *et al.*,  
88 2007b; Malpas *et al.*, 2013) in lowland habitats, which has focused on other wader  
89 species, particularly Northern Lapwing *Vanellus vanellus* (hereafter 'Lapwing'),  
90 Common Redshank *Tringa totanus* and Common Snipe *Gallinago gallinago*, has  
91 demonstrated that nocturnal mammalian predators are the main cause of nest failure  
92 (MacDonald & Bolton 2008, Teunissen *et al.*, 2008). However, these findings may not  
93 be applicable to lowland Curlew due to differences in nest exposure (Curlew nests are  
94 less concealed compared to Common Redshank or Snipe), adult size, social  
95 aggregation and habitat preferences (Bolton *et al.*, 2007b). This, along with the  
96 vulnerability of Curlew breeding populations, emphasises the need for a study into  
97 nest predation (Leyrer *et al.*, 2018).

98         Most lowland Curlew breed on dry grasslands and heathland (Table S1,  
99 Johnstone *et al.*, 2017) where conservation management can radically alter habitat  
100 structure. Within these habitats, physical ground-disturbance is increasingly  
101 advocated as a land management intervention for other rare, scarce and threatened

102 species, such as Stone-Curlew *Burhinus oedichnemus* and Woodlark *Lullula arborea*  
103 (Fuller *et al.*, 2017; Hawkes *et al.*, 2019b); however, it is not known whether this  
104 influences Curlew nest placement or breeding success. Understanding whether  
105 Curlew nests on disturbed grassland are easily visible to corvid nest predators, or  
106 conversely, whether placement of disturbed-plots can be used to manipulate nest  
107 placement into areas protected from mammalian predators, would better inform such  
108 management on sites with breeding Curlew.

109         To inform conservation interventions for Curlew, we studied nest placement,  
110 nest survival and nest-predator identity within the UK's largest lowland Curlew  
111 population (Breckland, Eastern England, Balmer *et al.*, 2013; holding at least 100  
112 breeding pairs but likely more, H. Ewing pers. comm.), across two extensive grass-  
113 heath sites (total c. 3,700 ha) that differed in predator density and management.  
114 Across both sites, vegetation structure was diversified prior to this study with ground-  
115 disturbance plots as part of a wider multi-taxa experiment (see Hawkes *et al.*,  
116 2019a,b), which may influence Curlew nest site selection and productivity. We *a priori*  
117 predicted that: (1) Curlew would select undisturbed grassland over disturbed  
118 grassland as nesting habitat (given that Curlew prefer rougher habitats with longer  
119 swards for nesting: Baines 1988; Ewing *et al.*, 2018), (2) nest survival would be higher  
120 on the site with lower predator density and decrease through the season (informed by  
121 Franks *et al.* 2017 and MacDonald & Bolton 2008), and (3) predation events would be  
122 attributable to nocturnal mammalian predators (as with other lowland wader species,  
123 MacDonald & Bolton 2008).

## 124 **Materials and methods**

### 125 **Study site**

126           The study was carried out in 2017 and 2018 in Breckland across the Stanford  
127 Military Training Area (hereafter 'STANTA', 52.50°N, 0.71°E) and Brettenham Heath  
128 NNR (0°83'E, 52°43'N). Both sites contain extensive areas of dry grassland and grass-  
129 heath (hereafter 'grassland', STANTA 3,500 ha; Brettenham Heath, 200 ha)  
130 surrounded by arable farmland and woodland (Fig. 1). Generalist predator control on  
131 STANTA was focussed around pheasant release pens (approximately 130 Foxes were  
132 removed annually; 0.03 ha<sup>-1</sup> year<sup>-1</sup>) but was lacking across remaining parts of STANTA  
133 and most of the surrounding arable and woodland. In contrast, Brettenham Heath was  
134 subject to continuous predator control across the whole site (10-20 Foxes were  
135 removed annually; 0.05-0.1 ha<sup>-1</sup> year<sup>-1</sup>) with similar levels of intensive control across  
136 the surrounding arable farmland (but not woodland). Brettenham Heath is also  
137 enclosed by a two-meter high deer fence with a single electric strand set half meter  
138 above the ground. Although we lacked the time and resource to compare generalist  
139 predator densities between the two sites, we saw at least one Fox during each of  
140 seven of the 75 fieldwork days on STANTA, compared to none during 23 fieldwork  
141 days on Brettenham Heath (though this ratio did not differ significantly, Fisher Exact  
142 test,  $p=0.194$ ). Both sites are sheep-grazed (approximately one ewe ha<sup>-1</sup>) with regular  
143 scrub and bracken *Pteridium aquilinum* control (see Appendix S1 for additional site  
144 management details). STANTA is subject to regular vehicle and soldier movements.

145           We used the Centre for Ecology and Hydrology Land Cover Map 2015  
146 (LCM2015, Rowland *et al.*, 2017) to identify areas of grassland and dwarf shrub heath  
147 across both study sites (hereafter collectively 'grassland', Fig. 1). Grassland was then  
148 categorised based on underlying soil type (NSRI, 2014) and age since last cultivation

149 (Sheail, 1979) to give two vegetation strata which differed in structure and vascular  
150 plant composition; 'calcareous/young' and 'older acidic' grassland. Calcareous/young  
151 grassland was characterised by shorter swards (4.15 cm, 3.77 - 4.58 95% CI; Hawkes  
152 *et al.*, 2019b), comprising a mixture of calcicolous and acidiphilous plant species  
153 developed on rendzina or following arable abandonment (73-113 years ago), whilst  
154 older acidic grassland (at least 114 years since arable cultivation) was characterised  
155 by taller swards (5.14 cm, 4.66 - 5.67 95% CI) mainly comprising acidiphilous plant  
156 species (see Appendix S1 for details).

157         Across both sites, 64 experimental ground-disturbance plots (32 deep-  
158 cultivated and 32 shallow-cultivated; see Hawkes *et al.*, 2019a for details) were  
159 established in early 2015 and subsequently disturbed annually to create: (i) 25 2 ha  
160 'homogenous' plots (13 deep- and 12 shallow-cultivated, repeated annually in the  
161 same location), and (ii) 39 4 ha 'complex-mosaic' plots (19 deep- and 20 shallow-  
162 cultivated) cultivating half-overlapping and half freshly-disturbed sections building up  
163 a mosaic of 1 ha subplots varying in fallow age and disturbance frequency. Potential  
164 for unexploded ordnance excluded ground-disturbance plots in the central 'impact  
165 area' of STANTA (1,180 ha), restricting treatment plots to Brettenham Heath and outer  
166 areas of STANTA (Fig. 1). In analyses, ground-disturbance treatments were combined  
167 as a single 'disturbed grassland' category, with aggregate area of 206 ha in both years  
168 of study, comprising ~5.6% of the available grassland extent (~8.2% of available  
169 grassland outside the impact area). We did not attempt to model relative preference  
170 for deep- or shallow-cultivation, homogenous or complex-mosaic owing to limited  
171 statistical power and also as different treatments were not available in each Curlew  
172 home range.



173 Tests of wader nest placement and nest survival frequently consider landscape  
174 context (Bertholdt *et al.*, 2017; Laidlaw *et al.*, 2015), however this is problematic in this  
175 study. Although woodland may harbour mammalian predators, Foxes also den in  
176 rabbit warrens, bracken, scrub and hedgerows, so that distance to woodland is not a  
177 reliable proxy for their activity. Woodland may offer perches but Crows also perched  
178 on individual trees that were scattered throughout the entire landscape. Arable  
179 farmland may also be a source of predators (Roos *et al.*, 2019) and cause  
180 disturbances that affect the distribution of nests. However, exploratory modelling  
181 showed no effects on nest placement or survival of either distance to woodland or  
182 arable farmland; these variables were therefore omitted from subsequent analysis to  
183 avoid over-fit models.

184

### 185 **Nest searching and monitoring**

186 Our approach to locating Curlew territories differed between 2017 and 2018. In  
187 2017, territory-searches focused initially on the 64 ground-disturbance plots, plus 38  
188 4 ha untreated grassland control plots (Hawkes *et al.*, 2019a; see Fig. 1), with at least  
189 three 40-minute visits to each plot between 14 March and 26 June (days between  
190 visits: mean  $27 \pm 7$  SD) during still, dry mornings (Beaufort wind force  $<4$ ) between  
191 dawn and 11:00. Additional opportunistic searches were made in 2017 on any  
192 grassland areas where Curlew were detected. We are confident that detectability of  
193 territories was comprehensive on both Brettenham Heath and outer areas of STANTA.  
194 As unexploded ordinance precluded ground-disturbance treatments from the STANTA  
195 'impact area' (Fig. 1) and furthermore, in 2017 searches in this area were largely  
196 restricted to 20 control plots and were not comprehensive; impact area nests were  
197 excluded from analyses of nest placement relative to random points (see below). In

198 contrast, in 2018 we conducted systematic searches for Curlew territories across the  
199 entire grassland extent (including the impact area), conducted by one observer  
200 walking linear transects spaced 250 m apart (following Brown and Shepherd, 1993)  
201 repeated three times between 1 April and 8 June (days between visits:  $18 \pm 6$  SD),  
202 between dawn and dusk. In both years, the location and behaviour of any detected  
203 Curlew was recorded.

204 In both years, nests were located between mid-April and late June, visiting any  
205 area where Curlew had been seen and looking for adults sitting on, or walking back  
206 to, the nest. To determine the date and timing of nest failure, temperature sensors  
207 were placed under nests (iButtons thermocrons, Maxim Integrated Products Ltd, CA,  
208 USA; set to record the temperature every 10 minutes, following Berg, 1992). Nests  
209 were remotely checked every three-to-seven days to confirm adults were still  
210 incubating, and the scrape was visited once a week to record any predation events  
211 (e.g. partial clutch predation). To avoid leaving tracks that could lead predators to  
212 nests, observers adopted a different meandering path during subsequent nest visits.  
213 It is also important to note that, particularly at STANTA, our activity was superimposed  
214 on ubiquitous tracks and scent trails from frequent ground troop and shepherd  
215 movements, further reducing the likelihood that Foxes would follow our tracks. From  
216 three days before the predicted hatch date (calculated from egg measurements at  
217 STANTA only in 2018, following Grant, 1996) nests were remotely monitored daily to  
218 accurately determine their fate.

219 Nest outcome was inferred from visits and temperature sensor data.  
220 Successfully hatched nests were characterised by the presence of small shell  
221 fragments within the nest cup and the presence of chicks or alarming adults in the  
222 area. Nest failure was assumed if nests were found empty before the predicted

223 hatching date and if no adult birds or chicks were seen around the nest site. Failure  
224 was attributed to predation if the nest contained shell remains or no eggs (larger  
225 predators, particularly Foxes, remove intact eggs, Guilherme *et al.*, 2018) and a sharp  
226 permanent decline in temperature (when temperature sensor data were available).  
227 Destroyed nests were identified by obvious signs of sheep trampling or freshly cut  
228 grass. When temperature sensor data were not available, due to the sensor being  
229 removed from the nest (5/28 cases), failure date was calculated as the mid-point  
230 between the final two visits (Johnson, 1979). After hatching, the nest site was visited  
231 every three-to-five days to observe adults and chicks from a vehicle at a distance,  
232 continuing until the chicks fledged (determined by observing chicks flying or their  
233 survival to 35 days post-hatching), or the breeding attempt had failed.

234 Laying date of the first egg (hereafter 'lay date') was estimated in one of three  
235 ways. For successful nests with known hatch date, or when expected hatch date of a  
236 failed nest was available from egg measurement, lay date was back-estimated  
237 allowing for a 29-day incubation (Berg, 1992) and  $n \times 1.5$ -day laying period (where  $n$   
238 = number of eggs in the clutch). When the nest was found during-laying (with clutch  
239 size incrementing by the second nest visit), lay date was estimated allowing 1.5 days  
240 per egg present at the find date. In remaining cases ( $n = 16$ , 33%), when the nest was  
241 found after incubation commenced, eggs were not measured and the clutch failed prior  
242 to hatching, the lay date was estimated as the mid-point of the earliest and latest  
243 possible lay dates, based on find and failure dates (following Mallord *et al.*, 2007;  
244 Koshkin *et al.*, 2016).

245 Where available, temperature sensor data informed classification of diurnal  
246 (after sunrise, before sunset), crepuscular (between dawn and sunrise, and between  
247 sunset and dusk) and nocturnal (between dusk and dawn) predation events, with

248 nocturnal and crepuscular events attributable to mammalian predators (most likely Fox  
249 or Badger *Meles meles*, but potentially also European Hedgehog *Erinaceus*  
250 *europaeus*, as found by Jackson 2001) and diurnal events unattributable (MacDonald  
251 & Bolton, 2008). To further validate predator identity, in 2018 infra-red nest cameras  
252 were placed at 10 nests on STANTA (as 2017 monitoring indicated a higher incidence  
253 of nest predation at STANTA than at Brettenham Heath) following Bolton *et al.*  
254 (2007a). The camera (~3.6mm lens, ~30x20x20mm camera head including the hood  
255 and infrared array) was placed about a meter from the nest and c. 15 cm above the  
256 ground within vegetation (to help concealment), with the battery (between  
257 180x76x167mm and 269x174x225mm) and recording unit buried seven-to-ten meters  
258 away to reduce disturbance, trampling or scent in the vicinity of the nest (that could  
259 potentially attract a predator) whilst changing batteries. Cameras triggered by  
260 movement were set to save five consecutive images within two seconds, with one  
261 image before triggering (the device continuously records and temporarily stores  
262 frames, but only saves these frames if triggered), and four after, with a five-second  
263 pause before it could be triggered again.

264

## 265 **Data analysis**

266 To examine nest placement in relation to ground-disturbance treatments and  
267 vegetation strata, we compared characteristics of nest locations to those of random  
268 points sampled in ArcGIS 10.3 (ESRI, 2014; 'used-available' design), using  
269 Generalised Linear Models (GLMs) with binomial error and log-link, conducted in R (R  
270 Core Team 2017). We excluded nests within the STANTA central 'impact area',  
271 thereby restricting analyses to areas with both disturbed and undisturbed grassland  
272 available (Fig. 1), and that were comprehensively surveyed in both years. Analyses

273 were conducted separately at the 'study-area' scale, considering the entire grassland  
274 area, and the 'home-range' scale, considering grassland with a 164 m radius of each  
275 nest site (the distance within which >85% of breeding adults or broods were observed  
276 foraging; threshold follows Odum & Kuenzler 1955, see Appendix S2). At both scales,  
277 we sampled three times as many random points as nests. At the study-area scale, the  
278 placement of control points was restricted to outside the STANTA impact area, and  
279 GLMs examined fixed effects of treatment (two levels: disturbed vs. undisturbed  
280 grassland) and vegetation strata (two levels: calcareous/young grassland vs older  
281 acidic grassland). We did not examine the effects of site on nest placement as the two  
282 study sites both contained experimental ground-disturbance plots and were  
283 comparable in terms of vegetation structure (Hawkes *et al.*, 2019b). For the home-  
284 range scale, we sampled three random points within a 164 m radius (of each nest)  
285 and GLMs examined fixed effects of treatment (two levels) but not vegetation strata,  
286 as most (38/41) home ranges contained only a single stratum.

287 To examine factors influencing daily nest survival, GLMs were performed with  
288 the number of binomial trials of each nest determined by the number of 'nest days' it  
289 was active and monitored, incorporating fixed effects of year (two levels), treatment  
290 (two levels), vegetation strata (two levels), site (two levels, reflecting differing predator  
291 control effort across sites) and lay date (following Dinsmore *et al.*, 2002), using the  
292 RMark 2.2.5 package (Dinsmore & Dinsmore, 2007). Analysis considered all  
293 monitored nests as independent observations, as: (i) lack of treatment plots within the  
294 impact area affects settlement options but does not bias failure relative to nest-site  
295 characteristics; (ii) failure was assumed to be largely caused by stochastic factors  
296 independent of parental quality, and (iii) within each year most nests were from  
297 different pairs (90% in 2017; 92% in 2018) with few re-nesting attempts. The mean

298 probability of nest success (hatching at least one egg) per nesting attempt was  
299 calculated from the product of daily clutch survival rates across the 29-day incubation  
300 period. Breeding productivity was quantified as the number of fledglings per nesting  
301 attempt, including any re-nesting attempt, as independent observations; it was not  
302 possible to estimate productivity per pair per year as adults were unmarked and we  
303 could not reliably allocate re-nests to individual pairs. For analysis of nest placement  
304 and nest survival, candidate model sets comprising all possible variable combinations  
305 were examined using the 'lme4' package. The model with the lowest value of Akaike  
306 Information Criterion adjusted for small sample size (AICc) was accepted as 'best' if  
307 the difference ( $\Delta\text{AICc}$ ) relative to all other candidate models was  $>2$ . When multiple  
308 models were within two AICc units of the 'best' model, multimodal inference was  
309 conducted to estimate model-averaged coefficients across these competing models  
310 (following Burnham & Anderson, 2002), using the MuMIn package (Barton, 2019).  
311 Candidate variables were considered to be supported where their 95% CI did not span  
312 zero (following Burnham & Anderson, 2002; Boughey *et al.*, 2011). Where the fixed  
313 effect of treatment was supported in nest placement models, we quantified the  
314 probability of selection of disturbed grassland relative to undisturbed grassland (model  
315 intercept) using odds ratios derived from the model coefficients. For each analysis,  
316 spatial autocorrelation of residuals (from the best or averaged model, as appropriate)  
317 was examined, calculating Moran's I in the 'Ape' package (Paradis *et al.*, 2004).

318 For nests where the timing of nest predation failure was known (through  
319 temperature logger or nest camera data) we examined whether predation events were  
320 more likely during the night (nocturnal and crepuscular) or day, relating the ratio of  
321 observed night/day predation events to the numbers of night/day hours summed

322 across all monitored nest-days (as day length varies through the season), using a 2x2  
323 Fisher Exact test.

324 Finally, considering all predated nests for which the date and time of failure  
325 were known, we used a Fishers Exact test to determine whether nest predation was  
326 more likely during the 24 hours following a direct monitoring visit (2x2 Fishers Exact:  
327 the number of predation events in relation to the number of nights within 24 hours of  
328 a disturbance event, against the numbers of predation events in relation to the number  
329 of other nights monitored).

330 **Results**

331 **Nest placement**

332           Across the two years of study 46 Curlew nests were located (2017, 20 including  
333 two re-nests; 2018, 26 including two re-nests). Of these, 41 were outside the impact  
334 area (2017, 17 nests; 2018, 24 nests), with 20 (49%) on disturbed grassland (17 on  
335 shallow-cultivated and three on deep-cultivated treatments) and 21 (51%) on  
336 undisturbed grassland.

337           For models of nest placement, at the study-area scale multi-model inference  
338 was undertaken across two candidate models within <2 AICc units (Table S2) and at  
339 the home-range scale the best-supported model was >2 AICc relative to all other  
340 models. At both spatial scales, Curlew were five- to six-times more likely to select  
341 disturbed than undisturbed grassland as nesting habitat (Fig. 2; study-area scale, odds  
342 ratio = 5.16, 95% CI: 2.0 – 13.3; home-range scale, odds ratio = 6.3, 95% CI: 2.8 –  
343 14.6). No effect of vegetation strata was found in the study-area scale averaged model  
344 (vegetation strata was not considered in the home-range scale analysis). Modelled  
345 residuals from nest placement analyses were not spatially autocorrelated.

346

347 **Nest survival**

348           Excluding two nests with zero observation days (found at or after failure or  
349 hatching), 44 nests were monitored (for 557 nest-days) of which 32 failed (Brettenham  
350 Heath: 3 of 11, STANTA 29 of 33), with 29 predated (Brettenham Heath: 3, STANTA:  
351 26), one trampled by livestock (STANTA), one destroyed by grass cutting (STANTA)  
352 and one deserted (a single-egg re-nest late in the season at STANTA). Mean overall  
353 nest survival probability from start of incubation to hatching was  $0.24 \pm 0.07$  SE



354 (Brettenham Heath:  $0.70 \pm 0.18$  SE, STANTA:  $0.16 \pm 0.06$ ). Overall breeding  
355 productivity was  $0.16 \pm 0.01$  SE fledged chicks per nesting attempt.

356 For analysis of daily nest survival rate, multi-model inference was undertaken  
357 across four candidate models within  $<2$  AICc units (Table S2). The effects of lay date  
358 and site were supported; daily nest survival rate decreased through the nesting season  
359 and was greater at Brettenham Heath than at STANTA (Fig. 2, Fig. 3). No support was  
360 found for effects of treatment, vegetation strata or year (Fig. 2). Residuals of the  
361 averaged-model were not spatially autocorrelated.

362

### 363 **Timing of nest failure and predator identity**

364 Of the ten 2018 nests with nest cameras: three survived to hatching; four were  
365 predated by Fox (one diurnal and three nocturnal; Fig. 4, Digital material 1); one was  
366 predated by an unknown predator (following camera malfunction); one was predated  
367 by a Sheep *Ovis aries* (two out of four eggs remained but incubation was not resumed  
368 and the clutch was classified as failed; Digital material 2) and a single-egg late-season  
369 re-nesting attempt was abandoned three days after camera deployment (with failure  
370 therefore not directly attributable to the installation). For all four confirmed fox-  
371 predation events, the scrapes were undisturbed, and no shell fragments remained. In  
372 one predated nest without a camera, large shell fragments were found with teeth  
373 marks, which suggested a further predation event attributable to a Fox (following  
374 Green *et al.*, 1987). Cameras also recorded an unsuccessful predation attempt by a  
375 Crow, fended off by the incubating Curlew (Digital material 3), and two instances of  
376 Crows scavenging abandoned clutches; one 29 hours after the partial-predation by a  
377 sheep (that had already resulted in complete clutch failure), the second five hours after

378 the late-season desertion of a re-nesting attempt. There was no effect of nest cameras  
379 on daily nest survival rate (see Appendix S3).

380 The timing of failure was known for 23 predated nests (28/29 predated nests  
381 were fitted with temperature loggers but five were removed from the nest by the bird)  
382 of which 17 events were during the night (13 nocturnal, four crepuscular) and six during  
383 the day (Fig. 4). Relative to the ratio of night/day hours monitored (pooled across each  
384 nest-day monitored, ratio 0.50) predation more often occurred at night (night/day ratio,  
385 2.83) than expected by chance (Fisher Exact test,  $p < 0.001$ ). Nest predation did not  
386 occur more frequently during the 24 hours following a disturbance event caused by  
387 monitoring (three predation events  $< 24$  hours after a disturbance event,  $n = 52$ , 20  
388 predation events  $> 24$  hours after disturbance,  $n = 164$ ; Fisher Exact test,  $p = 0.303$ ).

389 **Discussion**

390 Through a two-year study on one of the UK's largest remaining semi-natural  
391 grassland sites, we have demonstrated that breeding Curlew selectively placed nests  
392 on physically-disturbed grassland (deep-cultivated by ploughing, or shallow-  
393 cultivated by rotovation) over undisturbed grassland. Overall breeding productivity  
394 was low due to high rates of nest predation, primarily attributed to Foxes. While nest  
395 survival was not influenced by ground-disturbance treatment, it decreased with lay  
396 date and was substantially lower at STANTA than at Brettenham Heath; probably  
397 due to differences in Fox activity between these two sites (though this was not  
398 directly measured). As far as we are aware, this is the first study to simultaneously  
399 investigate Curlew nest placement, survival and predator identity within a lowland  
400 system.

401

402 **Nest placement**

403 Contrary to our predictions, Curlew were five- to six-times more likely to select  
404 nest-sites on physically-disturbed than undisturbed grassland, with 48.7% of nests  
405 located on disturbed grassland across both years, which only occupied ~8.2% of the  
406 grassland area. Curlew are long-lived and site-faithful (Currie *et al.*, 2001); as ground-  
407 disturbance was first applied two years prior to this study, treated plots may have been  
408 created within already-established breeding territories, rather than influencing territory  
409 settlement. However, analysis of nest placement relative to random locations within  
410 home-ranges showed nests were more frequently placed on disturbed than  
411 undisturbed grassland relative to availability.

412 Disturbed grassland is characteristically bare and short compared to  
413 uncultivated grassland (Dolman & Sutherland, 1994; Hawkes *et al.*, 2019b). Curlew

414 may have placed nests on this habitat because it allows greater vigilance (to facilitate  
415 and evade predator detection, Amat & Masero, 2004) and a greater abundance of  
416 some important prey (confirmed experimentally by Hawkes *et al.*, 2019b) than the  
417 surrounding grassland. Although we did not examine whether ground-disturbance  
418 detail matters (to avoid overparameterizing the models), most nests were on shallow-  
419 cultivated plots (n = 17, 41.5%), with few on deep-cultivated plots (n = 3, 7.3%). It is  
420 possible that the likelihood of attracting nest placement is greater on shallow-cultivated  
421 grassland, though further work is needed to establish this.

422

### 423 **Nest survival**

424 Nest survival was low and re-nesting following failure appeared infrequent.  
425 Annual productivity was lower than found in other lowland UK Curlew populations (Call  
426 of the Curlew 2017, Table S1), and is likely to be substantially below that required to  
427 maintain a stable population. Consistent with other passerine and non-passerine  
428 species (Gunnarsson *et al.*, 2006), daily nest survival rate decreased during the  
429 breeding season (by 39% from start to end). For Lapwing and Common Redshank,  
430 this is related to predator phenology, particularly as Foxes become more active once  
431 their cubs require more prey (Kentie *et al.*, 2015; Mason *et al.*, 2017). Seasonal  
432 declines in nest survival may also be attributable to decreasing visibility of predators  
433 as vegetation grows taller (Whittingham & Evans, 2004; MacDonald & Bolton, 2008).  
434 Importantly, nest survival was not influenced by ground-disturbance, which suggests  
435 that this management intervention (which positively influenced nest placement) did not  
436 increase nest exposure to predators.

437

### 438 **Predator identity**

439 Predation accounted for most nest failures in this study, similar to predation  
440 rates reported in other Curlew (Grant *et al.*, 1999) and wader populations (MacDonald  
441 & Bolton, 2008). Timing of nest predation was disproportionately higher during the  
442 night (nocturnal or crepuscular), consistent with mammalian rather than avian  
443 predators. Although predator identity was confirmed by camera for only five nest  
444 predation events, Foxes were responsible for all three nocturnal and one of two  
445 diurnal events, with the other confirmed diurnal nest predator a Sheep. In all cases but  
446 one, where predator identity was not certain, scrapes were undisturbed and had no  
447 shell remains, consistent with confirmed Fox predation events in this and other studies  
448 (e.g. Koshkin *et al.*, 2016). We found no evidence of activity by other predators; for  
449 example, nests predated by Badgers are usually characterised by trampled vegetation  
450 and disturbed nest scrapes (Draycott *et al.*, 2008). It is notable that, although Crows  
451 were not scared off by cameras and were recorded at nests, they were not found to  
452 be predators of Curlew nests and in one instance the sitting adult successfully  
453 defended the clutch against a Crow (see Digital material 3); this is unlike other smaller  
454 wader species where Crows are frequent nest predators (Teunissen *et al.*, 2008;  
455 Ausden *et al.*, 2009). The combined evidence of cameras and timing of predation  
456 therefore implicated Fox as the primary nest predator of Curlew in this landscape,  
457 consistent with studies that have identified Fox as the major predator of lowland nests  
458 of other wader species in the UK (Teunissen *et al.*, 2008; Ausden *et al.*, 2009).

459 Monitoring protocols were designed to minimise disturbance to the nest site,  
460 but in any nest monitoring study there remains a concern as to whether the study has  
461 itself affected the fate of nests. However, we found no difference in nest survival rate  
462 within the 24 hour periods immediately following direct nest visits, or between nest  
463 days with and without nest cameras, consistent with other studies that found no effect

464 of nest cameras on survival of ground-nesting Lapwing (Bolton *et al.*, 2007a) or Asian  
465 Houbara *Chlamydotis macqueenii* (Koshkin *et al.*, 2016). We are therefore confident  
466 that reported outcomes were not affected by the study protocols.

467 In agreement with our *a priori* predictions, nest survival was lower at STANTA  
468 than Brettenham Heath. Although this is a quasi-anecdotal contrast between only two  
469 sites, it is consistent with greater predator control effort and lower apparent Fox  
470 densities at Brettenham Heath. In the UK uplands, predator control can reduce  
471 generalist predator abundance and increase Curlew breeding success (Fletcher *et al.*,  
472 2010). However, predator control may be more effective at high initial predator  
473 densities (Bolton *et al.*, 2007b), and its effectiveness may be compounded by meso-  
474 predator release (Bodey *et al.*, 2011) and replacement of culled individuals by inward  
475 dispersal from surrounding habitat. Supplementing lethal control with predator-  
476 exclusion fencing along a site boundary reduces the need for shooting (important for  
477 ethical reasons) and their combination could reduce Fox activity within the fences  
478 towards zero (P. Merrick, pers. comm.). Site-fencing reduces Fox predation of  
479 Lapwing clutches (Malpas *et al.*, 2013) and chicks (Rickenback *et al.*, 2011) and in our  
480 study, Brettenham Heath, which was both fenced and subject to lethal Fox control,  
481 had a breeding productivity well above that considered necessary for replacement  
482 (Grant *et al.*, 1999). We recommend further experimental evaluation of whether  
483 combined fencing and lethal Fox control consistently increases Curlew productivity in  
484 lowland contexts.

485

## 486 **Conservation implications**

487 The impact of land management interventions (e.g. rotational moorland  
488 burning) on Curlew abundance has previously been studied in upland habitats

489 (Douglas *et al.*, 2014, Littlewood *et al.*, 2019). Here, for the first time, we have shown  
490 that physical ground-disturbance, which is advocated as a conservation measure  
491 within lowland dry grassland and grass-heath for many rare, scarce and threatened  
492 species (Fuller *et al.*, 2017; Hawkes *et al.*, 2019a,b), also provides suitable Curlew  
493 nesting habitat, with no reduction in nest survival. Implementing ground-disturbance,  
494 particularly through shallow-cultivating, in areas with few or no mammalian nest  
495 predators (e.g. inside anti-predator fenced sites with effective Fox control) could  
496 provide a useful management tool for attracting breeding Curlew to safer areas.

497         Here, nest predation was unsustainably high, and Foxes were the main  
498 predator. Given low breeding productivity is an issue across all UK lowland Curlew  
499 populations (Table S1), experimental tests which examine the efficacy of different anti-  
500 predator options (whether lethal or not) as a way of improving breeding success (not  
501 just clutch survival) are urgently needed.

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684 **Appendices**

685 Appendix S1 – Site management

686 Appendix S2 – Home range of nesting Curlew

687 Appendix S3 – Effect of camera monitoring on Curlew nest survival

688 Table S1 – Curlew breeding productivity across Europe

689 Table S2 – Candidate models MMI

690 Digital materials: <http://eurasiancurlewnestproductivity.simplesite.com>

691 **Figure legends**

692 **Figure 1.** Surveyed grassland (dark grey, c. 3,700 ha) across the study sites (Stanford  
693 Training Area and Brettenham Heath). Symbols (not to scale) show the location of  
694 experimental ground-disturbance plots (totalling 206 ha) and grassland controls. The  
695 dashed line shows the boundary of the Stanford Training Area 'impact area' (within  
696 which ground-disturbance was precluded). Arable farmland and woodland are also  
697 shown.

698 **Figure 2.** Coefficient estimates from models relating Eurasian Curlew *Numenius*  
699 *arquata*: i) nest placement at the study-area and home-range scale to treatment (two  
700 levels, reference level undisturbed grassland) and vegetation strata (study-area scale  
701 model only: two levels, reference level older acidic grassland); and ii) nest survival to  
702 treatment, vegetation strata, year (two levels, reference level 2017), site (two levels,  
703 reference level Brettenham Heath) and lay date (continuous), showing model  
704 coefficients (black dot), standard error (thick grey line) and 95% CI (thin grey line).  
705 Variables were deemed to be supported when their 95% CIs did not span zero (dashed  
706 line).

707 **Figure 3.** Estimated variation in the daily nest survival probability for Eurasian Curlew  
708 *Numenius arquata* within the Stanford Training Area (black) and Brettenham Heath  
709 (grey) in 2017 and 2018. Estimates are based on multi-model inference (Table S2,  
710 see Fig. 2 for included variable). Vertical bars show SE.

711 **Figure 4.** Date and time of 23 Eurasian Curlew *Numenius arquata* nest predation  
712 events across two years of study. Light shading indicates crepuscular (between dawn  
713 and sunrise, and between sunset and dusk) and darker shading indicates nocturnal  
714 (between dusk and dawn) periods. Symbols indicate predation events: crosses denote  
715 cases where the predator identity was not known, squares denote predation by Red  
716 Fox *Vulpes vulpes*, and a triangle predation by a Sheep *Ovis aries*.