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**Licensed control does not reduce local Cormorant *Phalacrocorax carbo* population size in winter**

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# UNIVERSITÀ DEGLI STUDI DI TORINO

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18 **Licensed control does not reduce local Cormorant *Phalacrocorax***  
19 ***carbo* population size in winter**

20

21 **D.E. Chamberlain · G. E. Austin · S.E. Newson · A. Johnston · N.H.K Burton**

22

23 *D Chamberlain ([dan.chamberlain99@gmail.com](mailto:dan.chamberlain99@gmail.com)) DBIOS, University of Turin, Via Accademia Albertina*  
24 *13, Turin 10123, Italy*

25 *G Austin, S Newson, A Johnston, N Burton, British Trust for Ornithology, The Nunnery, Thetford,*  
26 *Norfolk IP24 2PU, UK.*

27

28 **Abstract** Cormorants *Phalacrocorax carbo* have increased on European freshwaters, creating  
29 conflicts with fishing interests. As a result, control measures have been implemented in several  
30 countries, although their effect on the English population has yet to be determined. Wetland Bird  
31 Survey data was used to derive population growth rates (PGR) of non-coastal Cormorant populations  
32 in England. PGR was analysed in relation to control intensity at different scales (5km to 30km radius)  
33 from 2001 to 2009 in order to determine (i) the extent to which control intensity (proportion of the  
34 local population shot per winter) was associated with site-level population change, and (ii) whether  
35 potential effects of control intensity were evident on Special Protection Areas (SPAs). There were no  
36 clear differences in PGR when comparing sites which had experienced control versus sites where  
37 control had never been carried out. The few significant relationships between control intensity and  
38 Cormorant PGR detected were mostly positive, i.e. population growth was associated with higher  
39 control intensity. Control intensity was not related to Cormorant numbers in SPAs. Positive  
40 associations with control may arise because control is reactive, or because non-lethal effects cause  
41 greater dispersal of Cormorants. These results provide no evidence that Cormorant removal at local  
42 scales is having an effect on longer term (i.e. year-to-year) population size at a site level. They also  
43 suggest that control measures have not affected national population trends, although a better  
44 understanding of site use and movements of individual Cormorants needs to be developed at  
45 smaller scales (including those due to disturbance caused by control measures) to more fully  
46 understand processes at larger scales. Further research is also needed into the extent to which lethal  
47 and non-lethal effects of control on Cormorants are having the desired impact on predation rates of  
48 fish, and so help resolve the conflict between Cormorants and fisheries.

49

50 **Keywords** Culling · disturbance · fisheries · human-wildlife conflict · population growth rate · SPA ·  
51 Wetland Bird Survey.

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54

## 55 **Introduction**

56

57 Human-wildlife conflicts are at the root of many current conservation problems and occur when  
58 requirements of wildlife overlap with those of human interests. The source of the conflict is often  
59 the consumption of resources of value to humans by wildlife, for example predation of livestock  
60 (Musiani et al. 2003; Patterson et al. 2004) or game species (Redpath and Thirgood 1997; Valkama et  
61 al. 2005), or damage to crops (Naughton-Treves 1997; Weladji and Tchamba 2003). The underlying  
62 causes may be increase and expansion in either human or wildlife populations, the latter often  
63 arising after conservation interventions (e.g. Vijayan and Pati 2002) or cessation of human activities  
64 which formerly limited populations, especially hunting (e.g. Musiani et al. 2003). Measures to  
65 resolve such conflicts may include both lethal and non-lethal control of wildlife, but any such  
66 measures should take into account potential consequences for the animal populations in question,  
67 ideally through thorough *a priori* research. In addition, monitoring programmes to assess effects of  
68 management measures both on the animal population and on the resource that is the source of the  
69 conflict are necessary to ensure the goals of such measures are being met in a cost-effective way  
70 without unintended effects on the target animals.

71 Cormorants *Phalacrocorax* spp are the source of human-wildlife conflicts in a number of  
72 regions where their populations are increasing (e.g. Europe – Lindell et al. 1995; Japan – Kameda et  
73 al. 2003; North America – Hebert et al. 2005; Ridgway et al. 2011), both due to damage to trees from  
74 guano and potential impacts on fish populations. Within Europe, the Great Cormorant  
75 *Phalacrocorax carbo* (hereafter Cormorant) population has shown steep increases over the past few  
76 decades. This is particularly true of the subspecies *Phalacrocorax carbo sinensis* which is most  
77 numerous in the northern parts of continental Europe and has expanded its range and population  
78 rapidly (Lindell et al. 1995, van Eerden and Gregersen 1995, Bregnballe et al. 2011, Keller et al.  
79 2012), partly as a result of reduced persecution in breeding colonies and bans on hunting in the  
80 major staging and wintering areas. In addition, the coastal breeding subspecies *P.c. carbo* has also  
81 shown a tendency to increasingly winter on inland freshwaters in the UK (Rehfisch et al. 1999;  
82 Newson et al. 2004). Consequently the Cormorant population expansion has created conflicts with  
83 inland fisheries (Feltham et al. 1999) in the UK but also continental Europe. As a result, control

84 measures to limit the expansion of the Cormorant population and to minimise impacts on inland fish  
85 stocks have been implemented in several European countries, although in most, no attempt has  
86 been made to assess the impact of such control measures on Cormorant populations (Smith et al.  
87 2008). Attempts at controlling populations of double-crested Cormorant *P. auritus* in North America  
88 have, however, had mixed results (e.g. Ridgway et al. 2011), although population reduction has been  
89 achieved through combined measures of shooting adults and intensive reductions in breeding  
90 success (Bédard et al. 1995).

91 In the UK, in order to prevent serious damage to fisheries, licences have been made  
92 available for limited control of Cormorant populations by shooting since autumn 1996. Initially, the  
93 numbers involved were small (up to 517 nationally per year), and shooting was considered largely a  
94 technique to aid scaring, rather than as a means of population control (Central Science Laboratory  
95 2005), and at a local level, shooting was shown to have affected Cormorant numbers (Parrott et al.  
96 2003). However, in 2004, there was an increase in the number of birds that could be controlled per  
97 year, with an upper limit of 3000 individuals in the first two years, and up to 2000 birds annually  
98 thereafter. Modelling of the likely consequences of such levels of control predicted a slightly lower,  
99 and more-or-less stable national population (CSL 2005; Smith et al. 2008), although the modelling  
100 approach was later criticised, casting doubt on the predictions (Green 2008).

101 The UK holds internationally important waterbird populations (*sensu* Rose and Scott 1997),  
102 particularly in winter, and many Special Protection Areas (SPAs) have been designated under the EC  
103 Birds Directive (2009/147/EC) on the basis of the numbers of waterbirds that they support, including  
104 Cormorants. There is therefore a risk that control measures carried out to protect fishing interests  
105 could negatively impact on SPAs. Indeed, of 20 UK SPAs for which Cormorant is a designated  
106 feature, Thaxter et al. (2010) reported a sharp decline in Cormorant numbers on three, and for three  
107 more a possible increase in the rate of decline, coincident with increased control under the current  
108 control licensing scheme. However, the extent to which such changes on SPAs are statistically linked  
109 to control intensity at a site level has yet to be determined. In the view of Natural England (the  
110 relevant competent authority) “Cormorant control under licence which might affect a SPA would  
111 usually be subject to a site-based appropriate assessment by Natural England if likely significant  
112 effects on that SPA could not be ruled out”.

113 In this paper, we consider statistical associations between the number of Cormorants  
114 controlled and the year-to-year change in the numbers of non-coastal winter Cormorants at a site  
115 level in England, using data from the Wetland Bird Survey (WeBS; Pollitt et al. 2003), which is the  
116 main source of data used for deriving the annual population estimates of the national winter  
117 Cormorant population (henceforth termed the ‘Cormorant index’; Chamberlain et al. 2012). The

118 introduction of control measures has created a natural experiment, with some sites not experiencing  
119 any control throughout the period considered, whilst others have been subject to control for some  
120 or all of the time period, which enables a thorough assessment of possible impacts on site-level  
121 populations. Specifically, we test whether Cormorant control in or around sites has affected the  
122 magnitude of apparent population changes at these sites, and whether associations with control  
123 intensity are related to the scale at which they are considered. In addition, we also consider whether  
124 the number of Cormorants on SPAs is associated with control intensity and over what spatial scale  
125 such an effect may be apparent. Finally, we compare the results against national-level population  
126 trends and discuss the extent to which inferences can be drawn on effects of control from the local  
127 to the national scale.

128

## 129 **Methods**

130

### 131 **Bird data**

132

133 Bird data were derived from WeBS Core Count data, and were available for Cormorant from 1988 to  
134 2009. WeBS provides the principal source of data for deriving population estimates of the UK's non-  
135 breeding waterbirds, for assessing the international importance of UK wetland sites and for  
136 monitoring long-term trends and waterbird distributions (Pollitt et al. 2003). WeBS Core Counts are  
137 made using the so-called 'look-see' methodology (Bibby et al. 2000), whereby the observer, familiar  
138 with the species involved, surveys the whole of a predefined area, which may vary considerably from  
139 site-to-site (for the sites used in this analysis, mean area  $\pm$  SE = 114.5  $\pm$  20.0 ha, range 0.93 to 5815  
140 ha, n = 466 sites with data available). Counts are made at all wetland habitats, including lakes,  
141 lochs/loughs, ponds, reservoirs, gravel pits, rivers, freshwater marshes, canals, sections of open  
142 coast and estuaries. Numbers of all waterbird species, as defined by Wetlands International (Rose  
143 and Scott 1997), are recorded. Counts are made once per month, ideally on predetermined priority  
144 dates. This enables counts across the whole country to be synchronised, thus reducing the likelihood  
145 of birds being double counted or missed. For this analysis, Cormorant count was taken as the  
146 maximum of December to February counts. It is thus assumed that maximum count is representative  
147 of the local site-level winter population ('population' here is used in a broad sense to indicate the  
148 number of birds in a defined area). This measure is the most relevant to Cormorant monitoring as it  
149 is used in deriving the population index (e.g. Chamberlain et al. 2012). Furthermore, peak counts are  
150 used as the basis for SPA site designation (Stroud et al. 2001). The vast majority of conflicts are with

151 inland freshwater fisheries, so only non-coastal sites were considered. The analyses are based  
152 around winter counts, and control measures in the non-breeding period (September-April), and  
153 throughout the paper 'year' is used to refer to the earlier year of a given non-breeding period, as per  
154 WeBS protocol (e.g. 2005 indicates autumn and winter 2005/06).

155

156 Licensed control data

157

158 The first Cormorant control licences were issued in autumn 1996, although only annual totals were  
159 available for analysis prior to autumn 2001. A database of the number of Cormorants killed under  
160 licence in England was available from 2001 onwards. This included data for each individual licence  
161 application and so was site-specific and spatially referenced. Licences usually ran overwinter from  
162 September to mid-April of the following year, although there were exceptions (fisheries with salmon  
163 or trout were allowed an extension until 1 May, and there was also scope for licences to be granted  
164 outside the normal period under exceptional circumstances). The number of Cormorants killed was  
165 known for any given licence period. However, the precise timing of control activity was unknown  
166 (i.e. the dates on which any kills took place) which necessarily restricts the analysis to temporally  
167 broad scales (i.e. winter-to-winter). This has important implications for the estimation of concurrent  
168 control intensity (see below).

169 Although control was usually allowed only outside of the Cormorant breeding season,  
170 licences were sometimes granted for longer periods (i.e. over a year), especially between 2004 and  
171 2005. As it was not possible to assign numbers controlled to a given year in these cases, mean  
172 values of total Cormorants killed were used when considering overall trends at the national scale  
173 (i.e. England), and any such licences (from any year) were not included in any subsequent site-level  
174 analyses (see below). Furthermore, the data were for England only, and no information was  
175 available on control measures in neighbouring Wales or Scotland. In order to minimise any potential  
176 effects of unknown control measures, only sites that were at least 50km distant from the borders of  
177 Wales or Scotland were included.

178

179 Environmental data

180

181 A number of variables have been shown to influence Cormorant winter population growth rates,  
182 including the cover of water bodies, the cover of urban land, whether the site is classed as upland or  
183 lowland, and the broad geographical location. Following previous work (Jackson et al. 2006,  
184 Chamberlain et al. 2012), categories of urban habitat cover and water cover (high, medium or low),

185 habitat class (upland or lowland) and region of England (southwest, southeast, London, East Anglia,  
186 midlands, northwest and northeast) were assigned according to the principal 1-km squares of each  
187 WeBS site. In addition, winter severity has been shown to be an important determinant of adult  
188 survival (Frederiksen and Bregnballe 2000) and is therefore likely to influence Cormorant population  
189 growth. Monthly temperature data were available from 2001 to 2006 at a 5x5-km scale from UKCIP.  
190 Mean temperature was calculated per winter (Dec-Feb) and assigned to WeBS sites within each  
191 5x5km square.

192

### 193 Statistical analysis

194

195 Year-to-year change in Cormorant count (hereafter termed population growth rate, PGR) per site  
196 was modelled in relation to Cormorant control within fixed radii of each WeBS site. Licenses were  
197 usually granted for relatively small water bodies, and very few of these were WeBS sites (see below).  
198 Cormorant control was therefore determined within set radii of each WeBS site, and Cormorant PGR  
199 on the WeBS sites was analysed in relation to control intensity in the surrounding landscape,  
200 considering scales of 5km, 10km, 20km and 30km radius around each counted site. The goal was to  
201 determine if the presence of control activity and its intensity within the surrounding landscape had  
202 any effect on the numbers of Cormorants on a given site in the following year. Cormorant control  
203 was expressed as an index between 0 and 1, derived from the proportion of the local population that  
204 was culled each winter. The local population was the estimated annual winter population in each  
205 set radius within which a given WeBS site was situated. This estimate is that developed by  
206 Chamberlain et al. (2012) for derivation of the standard Cormorant population index and is based on  
207 the total WeBS count for a given 1-km square plus a model-derived estimate based on Dispersed  
208 Waterbird Survey data (Jackson et al. 2006). The control index was therefore the number killed  
209 under licence for a given radius divided by the estimated population for the same area. In the few  
210 cases ( $n = 57$  out of 5753 observations) where the estimated population was lower than the  
211 numbers controlled, the index was set at 1.

212 The data were analysed following the methods of Freeman and Newson (2008), which uses a  
213 recursive relationship to allow the expected count at a site to be dependent upon the expected  
214 count at the previous year. We expect some temporal autocorrelation in the data, as Cormorants  
215 tend to be site faithful in successive winters (e.g. 85-90% site fidelity – Frederiksen et al. 2002). This  
216 approach makes better use of the data than conventional modelling approaches, as a count can still  
217 be modelled if the previous count at the same site is missing or zero (cf Thomson et al. 1998),  
218 resulting in this study in a sample size which is c. 25% larger, and consequently greater precision and



219 power in the analysis. In addition to allowing easy estimation and inference about annual growth  
 220 rates, the Freeman and Newson (2008) approach allows us to model the effects of covariates on  
 221 population growth, which may themselves vary in space and time. Here we adopted a similar model  
 222 structure to Newson et al. (2012), but modelling the rate of change in winter Cormorant count from  
 223 year t-1 to year t in relation to control intensity and environmental variables, with site identity fitted  
 224 as a fixed effect (Eqn 1).

225

$$226 \quad \ln(E[N_{i,t}]) = \sum_{j=1}^t R_j + S_i + \beta_1 \cdot control_t + \beta_2 \cdot control_{t-1} + \beta_3 \cdot env \quad (\text{Eqn 1})$$

227

228 Where  $N_{i,t}$  is the winter Cormorant count at site  $i$  and time  $t$ ,  $R_t$  defines the recursion parameters  
 229 denoting years,  $S_i$  are site effects,  $\beta_1$ ,  $\beta_2$  and  $\beta_3$  are vectors of fitted parameters for matrices of the  
 230 control values in year  $t$ , the control values in the previous year, and environmental variables,  
 231 respectively. The control values and environmental variables are matrices of several variables at  
 232 different radii, and are cumulative variables, so each represents all values at a site up to year  $t$ .

233 Initially, Poisson models suggested overdispersion in the data, and subsequently, models  
 234 were fitted specifying a negative binomial error structure using the `glm.nb` command in R 2.12 (R  
 235 Development Core Team 2010). Effects of control were considered in two separate analyses. First,  
 236 sites were classified as control (control had taken place in at least one year), versus non-control sites  
 237 (control never undertaken), within a given radius. This involved fitting rates of change separately for  
 238 control and non-control sites within the model. This analysis was not dependent on using sites  
 239 where the period of control could be identified to a fixed period within a given winter (see below),  
 240 hence it maximised the sample size ( $n = 5753$  observations from 917 sites).

241 Second, a more detailed analysis was undertaken considering effects of control intensity, i.e.  
 242 the proportion of the wider population controlled per site per year. Cormorant control could have  
 243 effects on PGR from year t-1 to year t through delayed effects, i.e. the population growth is affected  
 244 by the proportion killed in the previous winter, or through concurrent effects, i.e. by the proportion  
 245 killed in the same winter as the counts. In considering the former, the number killed and the  
 246 estimated local population within a set radius of each site was simply summed over the duration of  
 247 the licence and the control index calculated as described above. For the latter, however, there was a  
 248 problem in that the count period (December-February) was almost always within the licence period,  
 249 but it was unknown precisely when control was carried out (i.e. the licence period was known, and  
 250 the number killed, but the control could have been carried out anytime within that period). The  
 251 effects of concurrent control were therefore analysed by adjusting the numbers controlled by the

252 number of months prior to the WeBS count. First, the month of the maximum count for each WeBS  
253 site was determined. Then, the difference between the date of maximum count and the start of the  
254 licence duration was determined, and this was then divided by the duration of the licence to give a  
255 correction factor between 0 and 1 (in the few cases where the licence began after the count date,  
256 the correction factor was set to zero). This was then multiplied by the total killed, making the  
257 assumption that control effort was constant across the duration of the licence. Control intensity was  
258 then calculated as previously. Cormorant control intensity in year t-1 is termed delayed control, and  
259 the adjusted control index in year t as concurrent control.

260 All WeBS sites and licence locations were spatially referenced in GIS, and the control  
261 intensity within different radii of each site in each year were determined, at 5km, 10km, 20km and  
262 30km (sample sizes were very small ( $n < 20$ ) at larger radii). Data for some licences were not used,  
263 either due to evident errors or because licences ran for long periods, hence it was not possible to  
264 assign numbers controlled to a given year (see above). These were not included in the analysis,  
265 hence any radii that contained such data were excluded. For each WeBS site, the probability that  
266 unsuitable control data contributed to the calculation of the numbers controlled increased as the  
267 radius around the site increased, hence sample sizes become progressively smaller as radii increase.  
268 The sample size for the 5km radius (i.e. the maximum sample size) was 4354 observations from 695  
269 WeBS sites, 167 of which had been subject to licensed control.

270 In common with previous uses of the Freeman and Newson (2008) model (e.g. Chamberlain  
271 et al. 2009; Newson et al. 2012), a statistical hypothesis testing approach was adopted in order to  
272 assess whether control had a significant effect on Cormorant PGR in the WeBS sites considered. For  
273 control measures, both linear and quadratic effects were fitted to the models, but quadratic effects  
274 were only retained if significant. There was a relatively strong correlation between concurrent  
275 control and delayed control in most years (mean  $r = 0.55$ ,  $n = 8$  years and 525-592 sites per year).  
276 Furthermore, Variance Inflation Factors were high ( $>5.0$ ) when both variables were considered  
277 simultaneously in a given model. Therefore, control measures were modelled separately, with a  
278 focus on delayed control, as this measure represented a known total for a given site, and was not  
279 reliant on assumptions about the seasonal distributions of control measures.

280 All models included land class, urban cover class, water cover class and region as categorical  
281 variables. The mean winter temperature of each 5x5km square that contained WeBS sites was  
282 available for winter 2001/02 to 2005/06, so effects of temperature were considered in a separate  
283 analysis ( $n = 613$  sites 2746 observations). Temperature in year t-1 (i.e. the preceding winter,  
284 concurrent with delayed control) was considered in the analysis, although temperature in year t (i.e.

285 concurrent with the bird survey data) and in year t-1 were very highly correlated ( $r > 0.85$  in all  
286 years).

287 In order to determine whether control measures may impact on Cormorant numbers on SPA  
288 sites, and hence have implications for SPA designation, the site-level analyses were re-run on the  
289 subset of 16 non-coastal WeBS sites in the analysis which were SPAs. The majority of licences for  
290 Cormorant control were granted for relatively small commercial fishing enterprises on small water  
291 bodies which are not included in WeBS and so do not directly contribute to the Cormorant index  
292 (although correction factors are included for the population outside WeBS sites – see Chamberlain *et al.*  
293 *al.* 2012). There were only 14 WeBS sites where control measures were carried out. The site-level  
294 analyses were repeated, but only these 14 sites were considered for the control sites in order to  
295 assess whether patterns on these sites were consistent with results from the whole sample.

296 Spatial autocorrelation was assessed by examining the spatial distribution of the residuals by  
297 considering variograms. In neither case was there any strong suggestion of spatial autocorrelation in  
298 the data (e.g. Fig S1). Similarly, temporal correlation was examined using the ACF command in R,  
299 and was found to be low.

300

## 301 **Results**

302

303 The annual totals of Cormorants controlled under licence in England is shown in Fig. 1, along with  
304 the Cormorant index for inland sites in winter (from Chamberlain *et al.* 2012). The Cormorant index  
305 showed high variability from year-to-year, but there was a general increasing trend in the late 1980s  
306 and the 1990s (Fig. 1). The index stabilised and even showed some declines in more recent years, a  
307 pattern also reflected in the trends in mean numbers per site for data considered in the site-level  
308 analysis (Fig. 2).

309 Legal control was initiated in 1996/97, initially at fairly low levels, but there was a sharp rise  
310 in 2004/05 which followed a change in the licensing policy (note that due to difficulties in assigning  
311 numbers controlled to a given year, mean values are assigned to 2004 and 2005 –nevertheless, the  
312 increase in numbers controlled is evident; Fig. 1). There was no evidence that trends in Cormorant  
313 populations at the national level from year-to-year were linked in any way to trends in control  
314 intensity in that there was no correlation between the Cormorant index and either concurrent  
315 control (considering only years where control took place,  $r_{12} = -0.03$ ,  $P = 0.91$ ) or delayed control ( $r_{11}$   
316  $= 0.02$ ,  $P = 0.94$ ). For the site-level analysis, the numbers controlled were expressed as an annual  
317 rate per site. The trend suggested that there had been some increase in control rate since 2001, but  
318 there was a very large rate of control in 2004, the year the new licensing policy was introduced (Fig.

319 2). There was no significant correlation between the mean number of Cormorants per site per year  
320 for the analysis and concurrent control ( $r_7 = 0.25$ ,  $P = 0.52$ ), or delayed control ( $r_6 = -0.14$ ,  $P = 0.74$ ).

321

322 Control versus non-control sites

323

324 The model fitting separate trends to sites with and without control over the period considered  
325 showed relatively little difference in trends between the two (Fig. 3). The majority of confidence  
326 intervals overlapped 1.0, suggesting no significant increases or decreases in the rate of population  
327 change over this period, with a few exceptions – there was a significant ( $P = 0.0004$ ) positive change  
328 from 2002 to 2003, and an almost significant ( $P = 0.053$ ) positive change from 2005 to 2006, both in  
329 non-control sites, and a significant ( $P = 0.009$ ) positive change from 2001 to 2002 in control sites.  
330 Similar patterns were evident at larger scales (Fig. S2).

331

332 Control intensity

333

334 For the site-level control intensity analysis, of the 167 sites where control took place (out of a total  
335 of 695 sites), an average of  $5.30 \pm 4.71$  sd Cormorants were controlled per year ( $n = 420$   
336 observations), equating to an average control intensity of  $0.34 \pm 0.34$  sd. There were no significant  
337 relationships between delayed control nor concurrent control at the 5km radius and Cormorant PGR  
338 (Table 1; full model details are given in Table S1). For delayed control at larger scales, significant  
339 non-linear relationships were found at the 10km radius, whilst there was a positive linear  
340 relationship at 30km, and no significant relationship at 20km. For concurrent control, there were  
341 significant non-linear relationships at the 20km scale (Table 1). The annual rates of population  
342 change for the significant relationships between control intensity and PGR at different scales derived  
343 from Table 1 are shown in Fig. 4. In each case, a higher proportion of control of the local population  
344 was generally associated with population growth, although at the 20km scale, negative growth rate  
345 was predicted when less than c. 20% of the local population was controlled.

346 Repeat analyses were carried out only considering cases where control was actually carried  
347 out on a given WeBS site at the 5km scale. Positive relationships between PGR and both delayed  
348 control (parameter estimate =  $0.363 \pm 0.124$ ,  $z = 2.919$ ,  $P = 0.004$ ) and concurrent control  
349 (parameter estimate =  $0.522 \pm 0.240$ ,  $z = 2.177$ ,  $P = 0.029$ ) were evident, although only 14 control  
350 sites were available for analysis (out a total of 542 sites and 3584 observations).

351

352 Effects of temperature

353

354 When also including temperature in the models with a reduced data set ( $n = 613$  sites, 2746  
355 observations), there was a negative relationship with delayed control that approached significance  
356 ( $P = 0.053$ ), and a significant negative relationship concurrent control at the 5km scale (Table 2). At  
357 larger scales, there was a significant non-linear relationship with concurrent control at 20km radius,  
358 which in common with non-linear associations from the whole data set (Fig. 4), predicted positive a  
359 trajectory in PGR above a control intensity of *c.* 0.20. There were no other relationships with control  
360 intensity at any scale (Table 2). Temperature was not significant in either of these models, and  
361 dropping temperature did not affect the significance of the control intensity measures, indicating  
362 that the reduced sample, rather than effects of temperature *per se*, were affecting the results  
363 relative to those from the full data set.

364

365 Effects of control on SPAs

366

367 The analysis was repeated for the subset of SPA sites (a maximum of  $n = 16$  sites and 137  
368 observations), up to a radius of 20km (there were not enough sites in the sample to consider larger  
369 radii). Due to the small sample size, land class was not considered (all sites were lowland) and only  
370 three regions were included (southeast, northeast and East Anglia). There were no significant  
371 relationships between delayed control, nor concurrent control and PGR at any scale (Table 3).

372

## 373 Discussion

374

375 Based on the results here, there is no evidence that Cormorant removal at local scales (5km to 30km  
376 radius) has had an effect on longer term (i.e. year-to-year) population size at a site level – put simply,  
377 killing Cormorants in one winter did not appear to impact upon numbers at a site level in the next  
378 winter. Furthermore, there were no significant relationships between control intensity and  
379 Cormorant PGR on SPAs, and therefore control measures did not have an adverse effect on the  
380 objectives under the designation of these sites, although the small sample sizes should be noted.  
381 The lack of evidence for negative effects of control, despite a national-level decrease in population  
382 growth (Fig. 1), may imply that other factors are influencing the wider population trend, including  
383 density-dependent effects (i.e. the population has reached carrying capacity), which have been  
384 detected in other populations (Frederiksen et al. 2001), changes in factors affecting reproductive

385 success and/or survival, or changes in immigration (although annual immigration rate is thought to  
386 be low anyway – Wernham et al. 1999).

387

388 Apparent positive effects of control

389

390 A number of models considering different measures of control at different scales showed significant  
391 positive relationships between control and PGR, or where the trend was non-linear, showed positive  
392 relationships over the greater part of the distribution of control intensity measures, e.g. predicted  
393 positive relationships from a control intensity of c. 0.20 onwards (Fig. 3), which is well below the  
394 mean of 0.33. There was a single model where there was a significant negative relationship  
395 between control and Cormorant population growth, that of concurrent control at a 5km radius when  
396 considering the subset with temperature data (Table 2). However, given that this result was based  
397 on a restricted number of years, that most analyses indicated either positive relationships or no  
398 relationship with control, and that the magnitude of this negative relationship with population  
399 growth was effectively balanced by positive relationships at larger scales, these results must be  
400 considered at best weak evidence of negative impacts of control on winter Cormorant populations.  
401 It should also be noted that that this and several other results were only weakly significant – if  
402 applications for multiple testing were applied, then the evidence for relationships between control  
403 intensity and Cormorant PGR would be even weaker (although we concur with criticisms of formal  
404 adjustments for multiple testing (e.g. Moran 2003) and do not apply them here).

405 The general pattern of results suggested more Cormorants controlled at a site level was  
406 associated with higher rates of population growth. There are four mechanisms by which positive  
407 relationships with control intensity may arise. First, the removal of residents may simply result in  
408 replacement of more birds via a density-dependent response, which seems plausible in an  
409 expanding population. However, if numbers at a site level are limited by density-dependent  
410 processes, then the expectation would be that birds replacing those controlled would re-colonise up  
411 to the level of the previous population, but results here suggest they may exceed it. Second, there  
412 may be significant disturbance caused by control measures which may alter birds' behaviour, for  
413 example by making them more dispersive, which may lead to apparent population increases. It is  
414 possible that short-term disturbance effects of control carried out in the autumn and early winter  
415 could have immediate effects on bird behaviour in the January and February of the following year, as  
416 suggested by results using concurrent control. However, similar results were also evident for delayed  
417 control, and such disturbance effects seem implausible given the long time span between controls  
418 and counts. Third, as control was typically not carried out on WeBS sites, a positive association may

419 arise if control measures force birds to move into WeBS sites, which act as refuges. Although sample  
420 sizes were small, this seems unlikely given that on the few WeBS sites that were also subject to  
421 control measures, there were also significant positive relationships detected. Fourth, licensed  
422 control may be sought in anticipation of increased Cormorant predation prior to enhanced fish  
423 stocking or other management changes that increase local fish populations, and which therefore  
424 subsequently attract more Cormorants. Fifth, the positive results may arise as control measures  
425 may be reactive, i.e. licences are granted at short notice (which is commonplace – Natural England  
426 2012) in response to local increases in Cormorant numbers. This would suggest that control  
427 measures are undertaken on the sites with the greatest growth rates, but also that such measures  
428 do not have significant impacts on the increasing local population.

429

430 Caveats on the analysis

431

432 The analytical approach adopted was based on year-to-year change in numbers at the site level in  
433 relation to control intensity, thus there is an underlying assumption that populations are linked from  
434 one winter to the next. This was supported by previous research which has shown high site fidelity  
435 from winter-to-winter (Reymond and Zuchuat 1995; Lekuona and Campos 2000; Frederiksen et al.  
436 2002), and to some extent by the lack of strong spatial autocorrelation (Fig. S1). Nevertheless,  
437 wintering Cormorants do sometimes make long distance movements (Schifferli et al. 2011), and are  
438 able to respond to locally abundant food supplies (Richner 1995). In order to determine if the  
439 statistical approach was in effect too conservative in detecting effects of control on local  
440 populations, a further simpler analysis was undertaken where no year-to-year dependence was  
441 assumed – a Poisson model considering the effects of numbers controlled on numbers at a given  
442 site. The results were qualitatively similar in that all parameter estimates were positive, although  
443 there was only a single significant effect (Table S2). Therefore we conclude that the assumption of  
444 year-to-year dependence did not affect our main conclusion that there was no negative effect of  
445 control on local Cormorant population size.

446 The analyses used maximum count per winter as the response variable. This was chosen in  
447 part because maximum count is the ‘currency’ for Cormorant monitoring in England, being used to  
448 derive the Cormorant index (Chamberlain et al. 2012) and also being the basis for SPA designation  
449 (which uses the mean of five-year peak counts per site, Stroud et al. 2001). The analysis is therefore  
450 underpinned by the assumption that the maximum count is representative of the population using a  
451 given site. Using the mean is a possible alternative that would incorporate more the variability in  
452 counts, but in fact the mean and maximum counts across sites were very highly correlated (e.g.  $r =$

453 0.967 across all 5017 sites/years) suggesting a degree of consistency in counts across visits within  
454 sites. The use of maximum count was also appropriate for the temporal resolution of the control  
455 data, which could only be summarised at the level of the whole winter at best. The approach  
456 therefore may detect relatively strong effects of control which affect the year-to-year change in  
457 maximum count, but more subtle effects of control would not be detected by this method. For  
458 example, there may be short-term effects of mortality followed by rapid recovery by new colonists  
459 within a given winter, or numbers may be temporarily reduced at a given site through disturbance  
460 effects. Interestingly, Parrott et al. (2003) found an effect of shooting on local Cormorant  
461 populations in a relatively small-scale study (13 sites), but there was no difference between lethal  
462 and non-lethal shooting, suggesting that disturbance effects may occur. However, from a policy  
463 perspective, the effect of the control measures undertaken in England is explicitly linked to year-to-  
464 year change in terms of Cormorant monitoring (i.e. through the Cormorant index; Chamberlain et al.  
465 2012) and SPA designation (Stroud et al. 2001). Nevertheless, it would be interesting to develop  
466 analytical techniques that can assess potentially more subtle within-winter effects, although the  
467 temporal resolution of the control data should ideally be higher for such an approach.

468

469 Future research needs

470

471 The positive relationships with control intensity detected may suggest more subtle effects involving  
472 the part of the population outside of the monitored WeBS sites (usually small water bodies). The  
473 Cormorant index is largely based on WeBS sites, although an estimate of the numbers outside of  
474 these sites is also included, derived from the Dispersed Waterbird Survey (DWS; Jackson et al. 2006):  
475 between 64% and 70% of numbers contributing to the index per year (2001-2009) are from WeBS  
476 sites. Furthermore, it should be noted that DWS was from a single year, 2003, and that  
477 extrapolations of PGR for DWS estimates are also derived from WeBS trends. We therefore conclude  
478 that the English winter Cormorant population as measured by the Cormorant index is not negatively  
479 influenced by control measures, but we need to add the caveat that not enough is known about the  
480 population outside of WeBS sites (i.e. those not contributing to the national index) which are poorly  
481 monitored, but which may nevertheless be crucial in understanding potential responses to control  
482 measures. A further survey of Cormorants in the wider countryside, following DWS methods, is  
483 needed to understand the effects of control intensity not included in the Cormorant index, and how  
484 these interact with those that are (e.g. through disturbance, and non-control sites acting as refugia),  
485 is needed before firmer conclusions can be drawn on effects of control on the national population  
486 trend.



487 Lethal control measures undertaken to resolve human-wildlife conflicts often have mixed  
488 results (e.g. Donnelly et al. 2006; Ridgway et al. 2011), and may only be successful when intensive  
489 measures cause very high mortality rates (e.g. Bédard et al. 1995). In order to maximise the chances  
490 of success, such approaches need to be underpinned by sound science. Modelling potential effects  
491 of such interventions is a potentially useful tool, although assumptions underlying such approaches  
492 need careful consideration. Behavioural responses may be particularly difficult to anticipate. For  
493 example, badger *Meles meles* culls to reduce their population and hence reduce transmission of  
494 badger-borne tuberculosis to cattle have sometimes had the opposite effect, due to unexpected  
495 disruption to territorial behaviour which caused badgers to disperse more widely than they would  
496 otherwise have done (Carter et al. 2007). In the light of this, we suggest that a better understanding  
497 is developed of site use and movements of individual Cormorants (including those due to  
498 disturbance caused by control measures) at smaller scales through more intensive research using  
499 mark-resighting or remote tracking of individuals. Furthermore, although control measures do not  
500 have any apparent effect on local Cormorant populations, we cannot conclude that there is no effect  
501 on Cormorant behaviour (including foraging efficiency) at these sites.

502 Given that ultimately the goal of the control measures is to reduce conflicts with fishing  
503 interests, we suggest that a greater priority is needed for research into assessing whether control  
504 has the desired impact on predation rates of fish (e.g. either directly through mortality or indirectly  
505 through disturbance), and the extent to which the cost of control measures compares against other  
506 measures to reduce Cormorant predation, e.g. scaring techniques including non-lethal effects of  
507 shooting (Parrott et al. 2003) and providing better fish refuges (Russell *et al.* 2008), and so help  
508 resolve the conflict between Cormorants and fisheries.

509

510

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520 for the Protection of Birds (RSPB) and Joint Nature Conservation Committee (JNCC), in association  
521 with Wildfowl & Wetlands Trust (WWT), that aims to monitor non-breeding waterbirds in the UK.

522

523

## 524 **Supplementary Material**

525 *Cormorant control manuscript supplementary material Oct2012.doc* – this file contains additional  
526 details and results to support the main analysis and is intended for review.

527

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644

645

646 **Table 1.** Relationships between the proportion of local population of Cormorants controlled at  
647 different radii around the count sites and Cormorant PGR. Models also included urban habitat  
648 category, water cover, landscape class, and region (further details in Table S1) of the central 1-km  
649 square of each WeBS site. Models assumed negative binomial errors and included fixed site effects.  
650 (a) Relationships with control intensity in the previous winter (delayed control -  $CONTROL_{t-1}$ ). (b)  
651 Relationships with control intensity in the winter concurrent with the Cormorant counts (concurrent  
652 control -  $CONTROL_t$ ).  $N_{sites}$  is the number of sites in the model,  $N_{obs}$  is the number of observations (i.e.  
653 site/years).

654

| Scale | Variable          | $N_{sites}$ | $N_{obs}$ | Parameter estimate | SE    | $z$    | $P$   |
|-------|-------------------|-------------|-----------|--------------------|-------|--------|-------|
| (a)   |                   |             |           |                    |       |        |       |
| 5km   | $CONTROL_{t-1}$   | 695         | 4354      | -0.030             | 0.068 | -0.445 | 0.657 |
| 10km  | $CONTROL_{t-1}$   | 506         | 3225      | 0.384              | 0.184 | 2.090  | 0.037 |
|       | $CONTROL_{t-1}^2$ |             |           | -0.190             | 0.077 | -2.469 | 0.014 |
| 20km  | $CONTROL_{t-1}$   | 211         | 1406      | -0.103             | 0.394 | -0.261 | 0.794 |
| 30km  | $CONTROL_{t-1}^2$ | 57          | 417       | 5.071              | 2.112 | 2.401  | 0.016 |
| (b)   |                   |             |           |                    |       |        |       |
| 5km   | $CONTROL_t$       | 695         | 4354      | -0.071             | 0.091 | -0.777 | 0.437 |
| 10km  | $CONTROL_t$       | 506         | 3225      | -0.094             | 0.118 | -0.796 | 0.426 |
| 20km  | $CONTROL_t$       | 211         | 1406      | -3.335             | 1.419 | -2.351 | 0.019 |
|       | $CONTROL_t^2$     |             |           | 7.462              | 3.373 | 2.212  | 0.027 |
| 30km  | $CONTROL_t$       | 57          | 417       | 1.114              | 1.465 | 0.761  | 0.447 |

655

656

657 **Table 2.** Relationships between the proportion of local population of Cormorants controlled at  
 658 different radii around the count sites and Cormorant PGR, when including temperature of the  
 659 previous winter. (a) Relationships with control intensity in the previous winter (delayed control -  
 660  $CONTROL_{t-1}$ ). (b) Relationships with control intensity in the winter concurrent with the Cormorant  
 661 counts (concurrent control -  $CONTROL_t$ ).  $N_{sites}$  is the number of sites in the model,  $N_{obs}$  is the number  
 662 of observations (i.e. site/years). Other details as per Table 1.

663

| Scale      | Variable          | $N_{sites}$ | $N_{obs}$ | Parameter estimate | SE    | $z$    | $P$   |
|------------|-------------------|-------------|-----------|--------------------|-------|--------|-------|
| <b>(a)</b> |                   |             |           |                    |       |        |       |
| 5km        | $CONTROL_{t-1}$   | 613         | 2746      | -0.388             | 0.200 | -1.938 | 0.053 |
| 10km       | $CONTROL_{t-1}$   | 448         | 2044      | 0.312              | 0.229 | 1.357  | 0.175 |
| 20km       | $CONTROL_{t-1}$   | 184         | 874       | -0.480             | 1.113 | -0.426 | 0.670 |
| 30km       | $CONTROL_{t-1}^2$ | 55          | 265       | -0.623             | 1.860 | -0.335 | 0.738 |
| <b>(b)</b> |                   |             |           |                    |       |        |       |
| 5km        | $CONTROL_t$       | 613         | 2746      | -0.428             | 0.213 | -2.012 | 0.044 |
| 10km       | $CONTROL_t$       | 448         | 2044      | 0.017              | 0.236 | 0.073  | 0.941 |
| 20km       | $CONTROL_t$       | 184         | 874       | -5.689             | 2.325 | -2.447 | 0.014 |
|            | $CONTROL_t^2$     |             |           | 13.430             | 6.282 | 2.138  | 0.032 |
| 30km       | $CONTROL_t$       | 55          | 265       | -0.696             | 1.799 | -0.387 | 0.699 |

664

665

666

667 **Table 3.** Relationships between numbers of Cormorants controlled at different radii around count  
668 sites designated as SPAs and Cormorant PGR(a) Relationships with control intensity in the previous  
669 winter (delayed control -  $CONTROL_{t-1}$ ). (b) Relationships with control intensity in the winter  
670 concurrent with the Cormorant counts (concurrent control -  $CONTROL_t$ ). Due to the small sample  
671 size, some categories used in other models were redundant. Models included region (southeast,  
672 northeast and East Anglia), urban cover class (high or medium), and water cover class (high, medium  
673 or low).

674

| Scale | Variable        | $N_{sites}$ | $N_{obs}$ | Parameter estimate | SE    | $z$    | $P$   |
|-------|-----------------|-------------|-----------|--------------------|-------|--------|-------|
| (a)   |                 |             |           |                    |       |        |       |
| 5km   | $CONTROL_{t-1}$ | 16          | 137       | 0.599              | 2.432 | 0.246  | 0.805 |
| 10km  | $CONTROL_{t-1}$ | 13          | 112       | 2.660              | 1.916 | 1.390  | 0.164 |
| 20km  | $CONTROL_{t-1}$ | 8           | 67        | 1.184              | 1.474 | 0.804  | 0.422 |
| (b)   |                 |             |           |                    |       |        |       |
| 5km   | $CONTROL_t$     | 16          | 137       | -0.419             | 2.811 | -0.149 | 0.881 |
| 10km  | $CONTROL_t$     | 13          | 112       | -1.423             | 3.119 | -0.456 | 0.648 |
| 20km  | $CONTROL_t$     | 8           | 67        | -1.927             | 2.990 | -0.644 | 0.519 |

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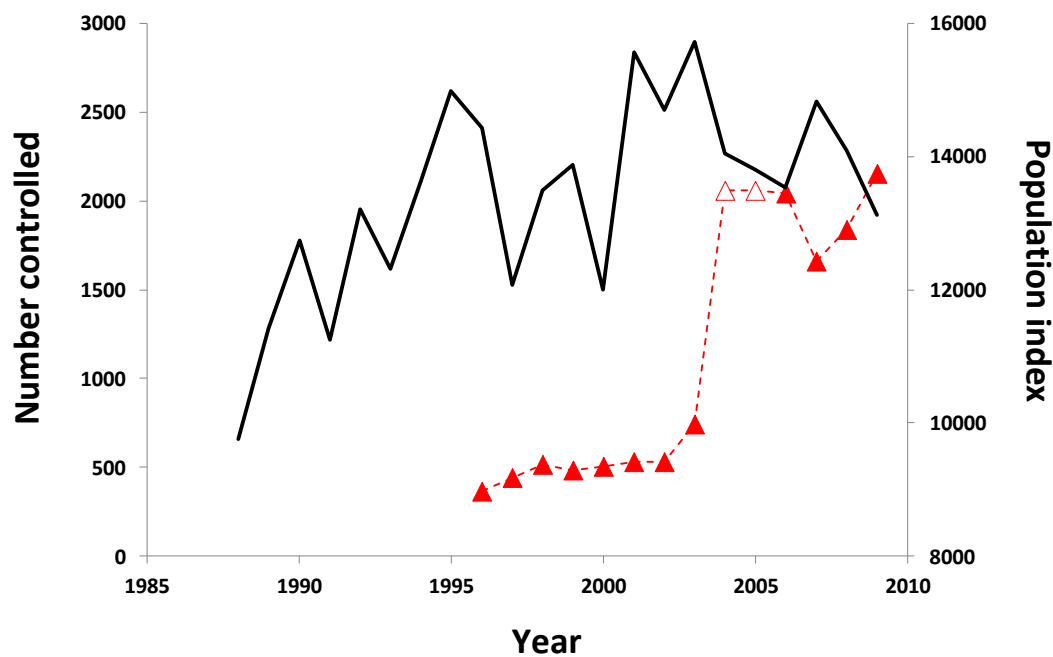
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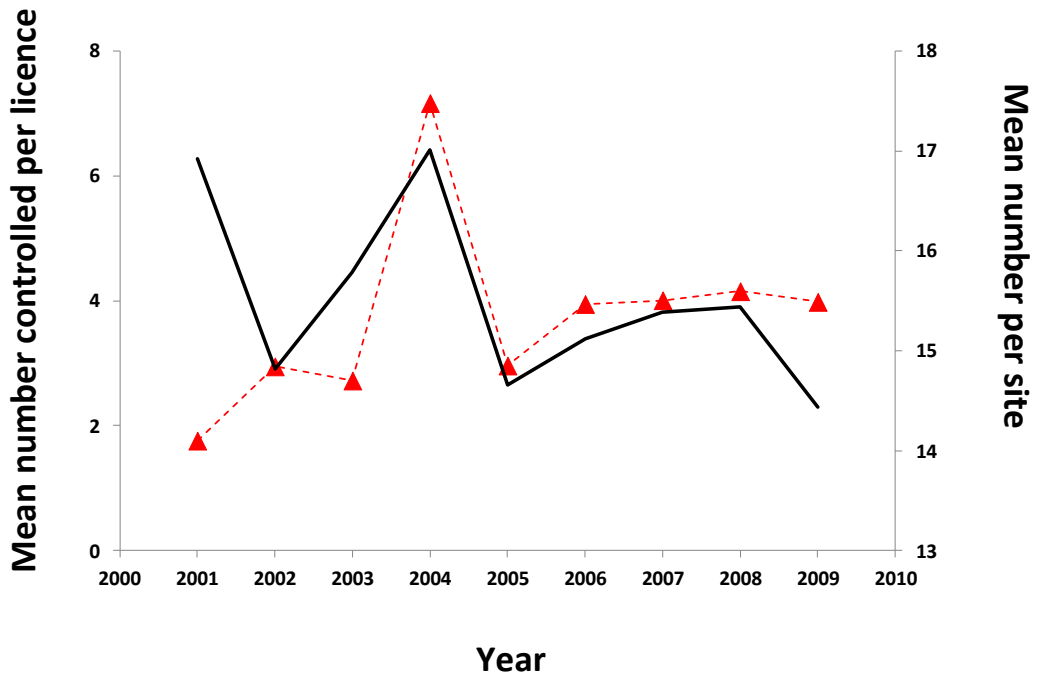
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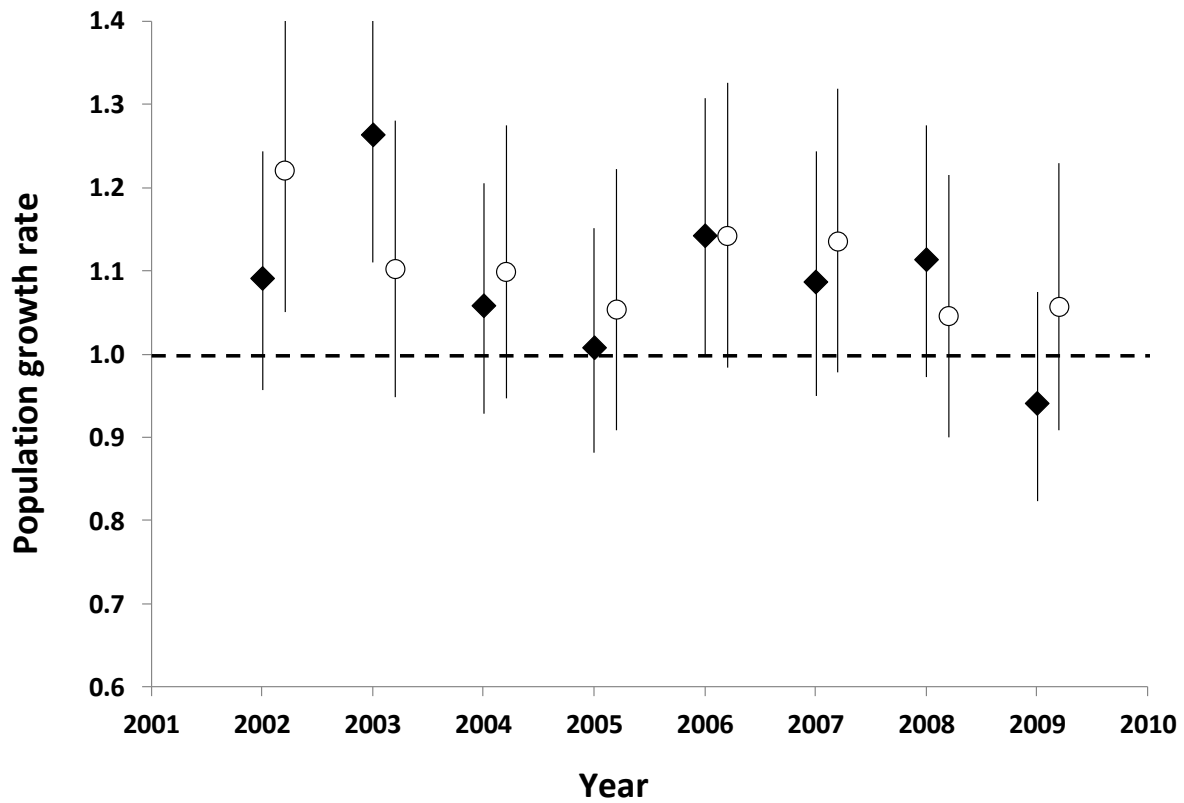
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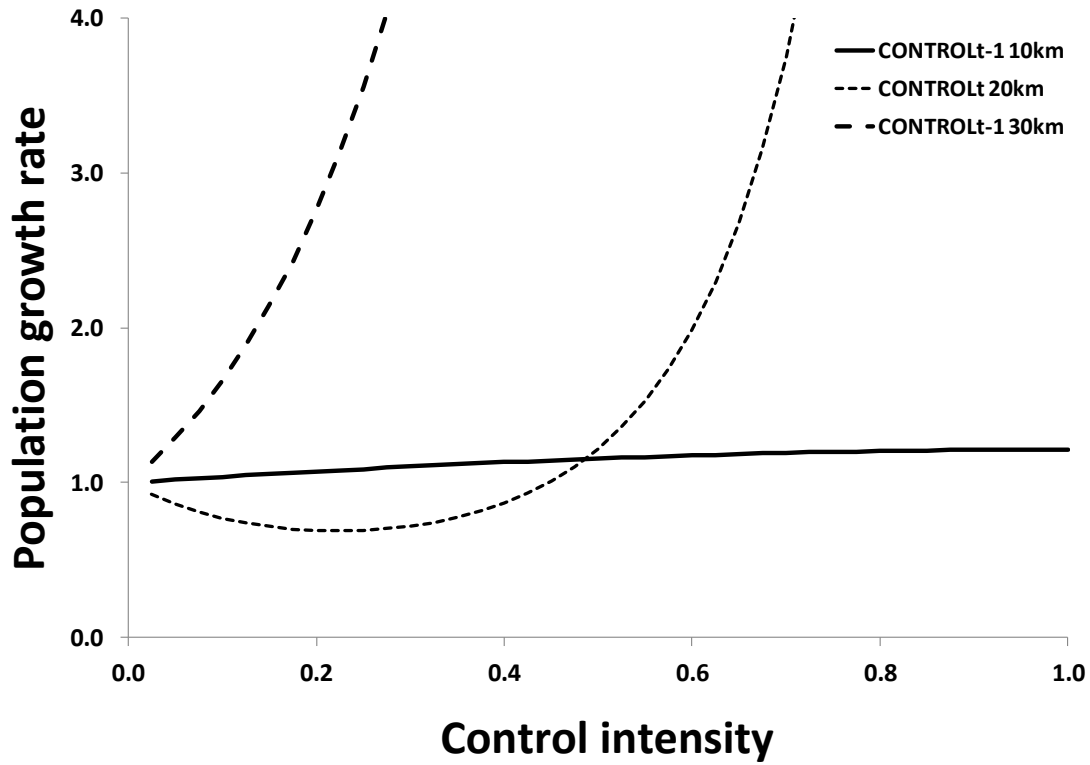
**Fig. 1.** Total annual inland winter Cormorant population index (solid line) and the annual number of Cormorants controlled under licence (dashed line). Note that due to difficulties in assigning numbers controlled to a given year in 2004 and 2005, the mean value over the two years is presented for each (open triangles). The Cormorant population index is taken from Chamberlain et al. (2012).



**Fig. 2.** Mean number of Cormorants per site per year (solid line) and the annual number of Cormorants controlled per licence (dashed line) for the period for which there were spatially referenced control data, and for sites used in the site-level control intensity analysis where control measures could be assigned to specific years;  $n = 695$  sites overall (525-592 per year).



**Fig. 3.** Estimated population growth rates of winter Cormorant populations in sites where no control ever took place (black diamonds) and those where control took place in at least one year (open circles) within a 5-km radius of the site. Estimates were back-transformed from a negative binomial model of year-to-year change. The dashed line at 1.0 indicates zero population growth. The models included site as a fixed effect and water area within a 5km radius (set to zero in this model) as a covariate. Error bars represent 95% confidence intervals.  $n = 5753$  observations from 917 sites.



**Fig. 4.** Predicted relationships between Cormorant control intensity in the previous year (delayed control -  $CONTROL_{t-1}$ ) and in the current year concurrent control - ( $CONTROL_t$ ) within different radii of a given WeBS site, and Cormorant relative population rate of change derived from the models presented in Table 1. All other variables in the model (site effects, water, urban and landscape class, and region) have been set at zero. Relationships were significant ( $P < 0.05$ ) in each case.

684 **Supporting information**

685 Table S1. Modelled rate of cormorant winter population growth in relation to control intensity, and  
 686 urban habitat category, water cover category ('high' is the reference category for both, with  
 687 Parameter = 0), landscape class (LS; 'Upland' reference category), and region (East Anglia reference  
 688 category) of the central 1-km square of each WeBS site. Models assumed negative binomial errors  
 689 and included fixed site effects. r1 to r8 represents the estimated rate of change from year to year,  
 690 where r1 is from 2001 to 2002. (a) Effects of numbers controlled in the previous winter (delayed  
 691 control - CONTROL<sub>t-1</sub>). (b) Effects of control in the winter concurrent with the Cormorant counts  
 692 (concurrent control - CONTROL<sub>t</sub>). N = 695 sites, 4354 observations.

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|                        | Parameter estimate | SE    | z      | P     |
|------------------------|--------------------|-------|--------|-------|
| (a)                    |                    |       |        |       |
| CONTROL <sub>t-1</sub> | -0.030             | 0.068 | -0.445 | 0.657 |
| Urban(medium)          | -0.019             | 0.014 | -1.355 | 0.175 |
| Urban(low)             | -0.004             | 0.015 | -0.250 | 0.802 |
| Water(medium)          | 0.004              | 0.013 | 0.299  | 0.765 |
| Water(low)             | 0.007              | 0.012 | 0.530  | 0.596 |
| LS(lowland)            | -0.097             | 0.029 | -3.371 | 0.001 |
| r1                     | 0.125              | 0.062 | 2.000  | 0.045 |
| r2                     | 0.255              | 0.062 | 4.128  | 0.000 |
| r3                     | 0.113              | 0.062 | 1.834  | 0.067 |
| r4                     | 0.034              | 0.063 | 0.536  | 0.592 |
| r5                     | 0.178              | 0.063 | 2.808  | 0.005 |
| r6                     | 0.130              | 0.063 | 2.068  | 0.039 |
| r7                     | 0.146              | 0.063 | 2.328  | 0.020 |
| r8                     | 0.008              | 0.062 | 0.128  | 0.899 |
| London                 | -0.068             | 0.026 | -2.625 | 0.009 |
| Southeast              | -0.033             | 0.016 | -2.077 | 0.038 |
| Southwest              | -0.030             | 0.021 | -1.393 | 0.164 |
| Midlands               | -0.009             | 0.017 | -0.543 | 0.587 |
| Northeast              | -0.051             | 0.018 | -2.811 | 0.005 |
| Northwest              | 0.006              | 0.022 | 0.259  | 0.795 |
| Intercept              | -1.569             | 0.736 | -2.133 | 0.033 |

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|                      | Parameter estimate | SE    | z      | P     |
|----------------------|--------------------|-------|--------|-------|
| (b)                  |                    |       |        |       |
| CONTROL <sub>t</sub> | -0.071             | 0.091 | -0.777 | 0.437 |
| Urban(medium)        | -0.019             | 0.014 | -1.321 | 0.186 |
| Urban(low)           | -0.004             | 0.015 | -0.241 | 0.809 |
| Water(medium)        | 0.004              | 0.013 | 0.313  | 0.755 |
| Water(low)           | 0.007              | 0.012 | 0.556  | 0.578 |
| LS(lowland)          | -0.097             | 0.029 | -3.368 | 0.001 |
| r1                   | 0.124              | 0.062 | 1.980  | 0.048 |
| r2                   | 0.255              | 0.062 | 4.123  | 0.000 |
| r3                   | 0.113              | 0.062 | 1.832  | 0.067 |
| r4                   | 0.033              | 0.063 | 0.528  | 0.598 |
| r5                   | 0.177              | 0.063 | 2.801  | 0.005 |
| r6                   | 0.130              | 0.063 | 2.060  | 0.039 |
| r7                   | 0.146              | 0.063 | 2.318  | 0.020 |
| r8                   | 0.008              | 0.062 | 0.134  | 0.894 |
| London               | -0.067             | 0.026 | -2.604 | 0.009 |
| Southeast            | -0.033             | 0.016 | -2.072 | 0.038 |
| Southwest            | -0.029             | 0.021 | -1.377 | 0.169 |
| Midlands             | -0.009             | 0.017 | -0.526 | 0.599 |
| Northeast            | -0.051             | 0.018 | -2.786 | 0.005 |
| Northwest            | 0.005              | 0.022 | 0.255  | 0.799 |
| Intercept            | -0.067             | 0.026 | -2.604 | 0.009 |

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702 Table S2. Relationships between the number of local cormorants controlled at different radii around  
 703 the count sites and cormorant count per winter. Models assumed negative binomial errors and  
 704 included fixed site effects. (a) Relationships with control intensity in the previous winter (delayed  
 705 control -  $\text{CONTROL}_{t-1}$ ). (b) Relationships with control intensity in the winter concurrent with the  
 706 cormorant counts (concurrent control -  $\text{CONTROL}_t$ ).  $N_{\text{sites}}$  is the number of sites in the model,  $N_{\text{obs}}$  is  
 707 the number of observations (i.e. site/years).

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| Scale      | Variable                 | $N_{\text{sites}}$ | $N_{\text{obs}}$ | Parameter estimate | SE    | $\chi^2$ | P     |
|------------|--------------------------|--------------------|------------------|--------------------|-------|----------|-------|
| <b>(a)</b> |                          |                    |                  |                    |       |          |       |
| 5km        | $\text{CONTROL}_{t-1}$   | 695                | 4354             | 0.011              | 0.007 | 2.52     | 0.113 |
| 10km       | $\text{CONTROL}_{t-1}^2$ | 506                | 3225             | 0.009              | 0.006 | 2.43     | 0.119 |
| 20km       | $\text{CONTROL}_{t-1}$   | 211                | 1406             | 0.007              | 0.004 | 2.70     | 0.101 |
| 30km       | $\text{CONTROL}_{t-1}$   | 57                 | 417              | 0.005              | 0.005 | 1.13     | 0.289 |
| <b>(b)</b> |                          |                    |                  |                    |       |          |       |
| 5km        | $\text{CONTROL}_t$       | 695                | 4354             | 0.010              | 0.009 | 1.49     | 0.223 |
| 10km       | $\text{CONTROL}_t$       | 506                | 3225             | 0.001              | 0.006 | 0.05     | 0.820 |
| 20km       | $\text{CONTROL}_t$       | 211                | 1406             | 0.006              | 0.006 | 1.03     | 0.311 |
| 30km       | $\text{CONTROL}_t$       | 57                 | 417              | 0.003              | 0.008 | 0.10     | 0.756 |

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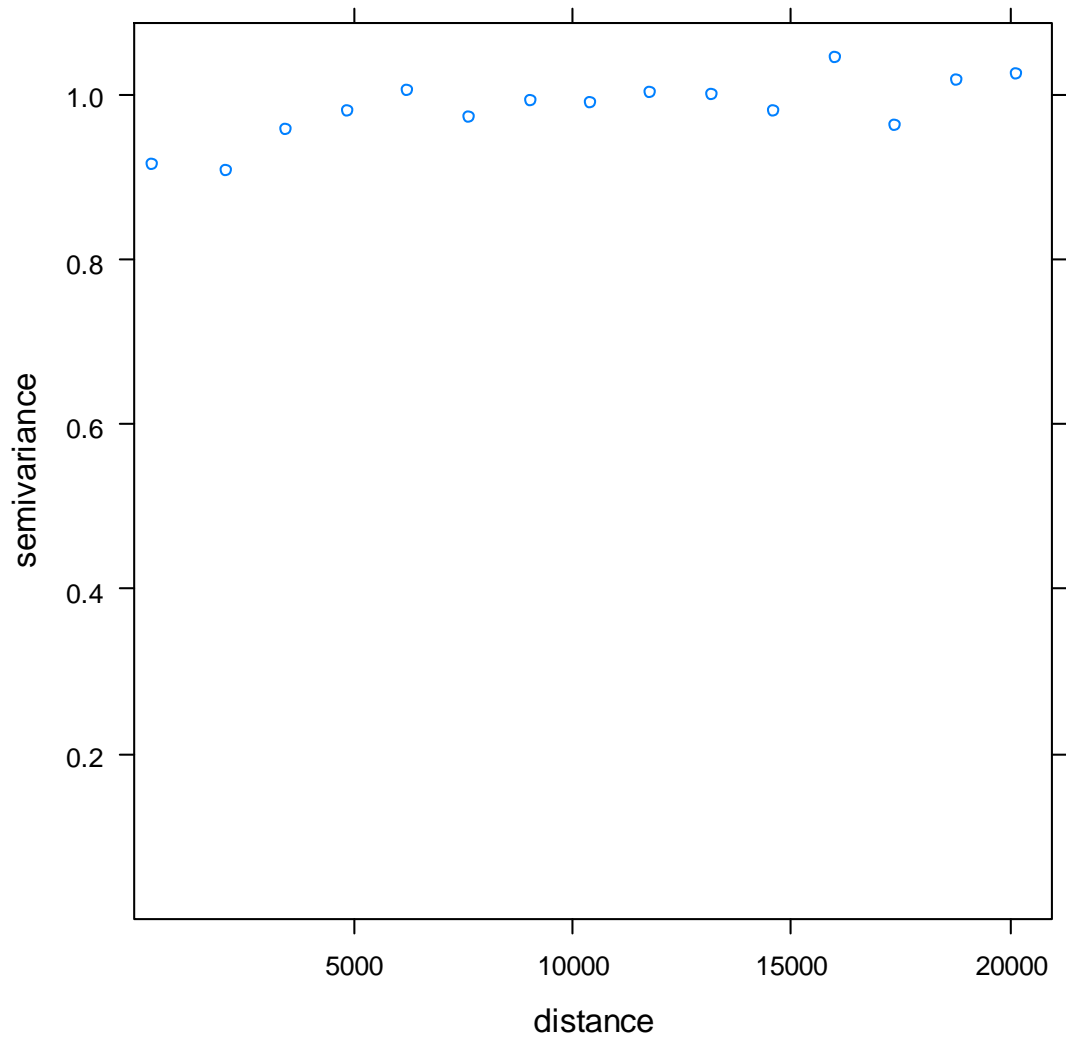


Figure S1. Variogram of residuals plotted against distance derived from the model of  $\text{CONTROL}_{t-1}$  at the 5km scale. There was some slight positive correlation at small scales and at larger scales, but overall the evidence for spatial autocorrelation was weak.



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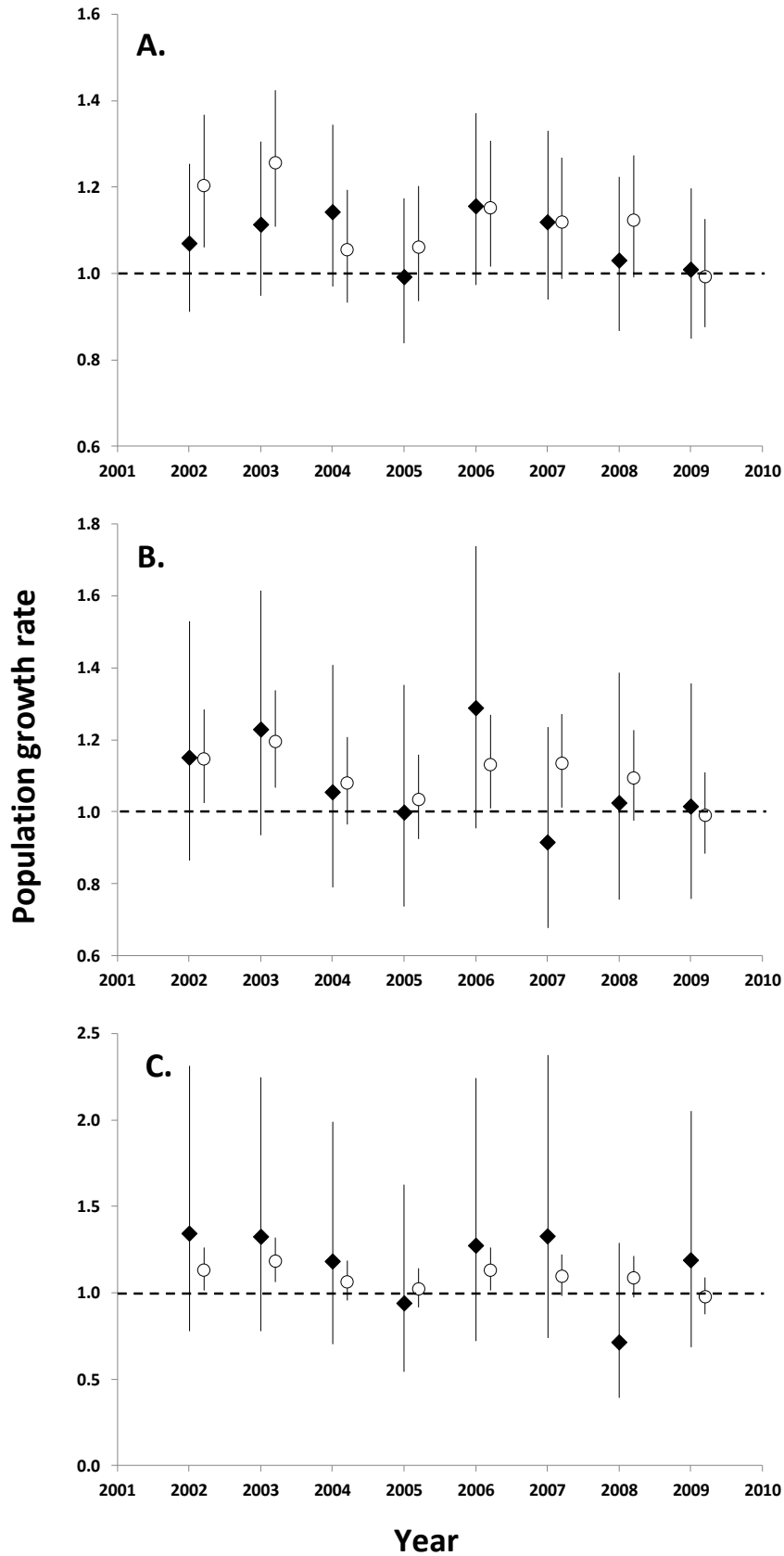


Figure S2. Estimated population growth rates of winter cormorant populations in sites where no control took place (black diamonds) and those without control (open circles at different radii around each site). A 10km, B 20km, C 30km. N = 5753 observations from 917 sites. Note that the number of no control sites decreases (and hence errors increase) as the radius increases. Other details as per Fig. 2.