



# THE UNIVERSITY *of* EDINBURGH

## Edinburgh Research Explorer

### The changing environment of conservation conflict: geese and farming in Scotland

**Citation for published version:**

Mason, THE, Keane, A, Redpath, SM & Bunnefeld, N 2017, 'The changing environment of conservation conflict: geese and farming in Scotland', *Journal of Applied Ecology*. <https://doi.org/10.1111/1365-2664.12969>

**Digital Object Identifier (DOI):**

[10.1111/1365-2664.12969](https://doi.org/10.1111/1365-2664.12969)

**Link:**

[Link to publication record in Edinburgh Research Explorer](#)

**Document Version:**

Peer reviewed version

**Published In:**

Journal of Applied Ecology

**General rights**

Copyright for the publications made accessible via the Edinburgh Research Explorer is retained by the author(s) and / or other copyright owners and it is a condition of accessing these publications that users recognise and abide by the legal requirements associated with these rights.

**Take down policy**

The University of Edinburgh has made every reasonable effort to ensure that Edinburgh Research Explorer content complies with UK legislation. If you believe that the public display of this file breaches copyright please contact [openaccess@ed.ac.uk](mailto:openaccess@ed.ac.uk) providing details, and we will remove access to the work immediately and investigate your claim.



1 **The changing environment of conservation conflict: geese and farming in Scotland**

2 **Authors:** Tom H.E. Mason<sup>1</sup>, Aidan Keane<sup>2</sup>, Stephen M. Redpath<sup>3</sup> and Nils Bunnefeld<sup>1</sup>.

3 **Affiliations:** <sup>1</sup>Biological and Environmental Sciences, Faculty of Natural Sciences, University of  
4 Stirling, Stirling, FK9 4LA, UK; <sup>2</sup>School of Geosciences, University of Edinburgh, Edinburgh, EH9  
5 3FF, UK; <sup>3</sup>Institute of Biological and Environmental Sciences, University of Aberdeen, Tillydrone  
6 Avenue, Aberdeen AB24 2TZ, UK.

7 **Corresponding author:** Tom H.E. Mason, Conservation Ecology Group, Department of  
8 Biosciences, Durham University, South Road, Durham, DH1 3LE, UK. Email:  
9 [tom.h.e.mason@gmail.com](mailto:tom.h.e.mason@gmail.com)

10 **Running title:** Environmental change and conservation conflict

11 **Word count:** 7,500

12 **Number of tables:** 2

13 **Number of figures:** 7

14 **Number of references:** 48

15 **ABSTRACT**

- 16 1. Conflict between conservation objectives and human livelihoods is ubiquitous and can be  
17 highly damaging, but the processes generating it are poorly understood. Ecological elements  
18 are central to conservation conflict, and changes in their dynamics – for instance due to  
19 anthropogenic environmental change – are likely to influence the emergence of serious  
20 human-wildlife impacts and, consequently, social conflict.
- 21 2. We used mixed-effects models to examine the drivers of historic spatio-temporal dynamics in  
22 numbers of Greenland barnacle geese (*Branta leucopsis*) on the Scottish island of Islay to  
23 identify the ecological processes that have shaped the environment in which conflict between  
24 goose conservation and agriculture has been triggered.
- 25 3. Barnacle goose numbers on Islay increased from 20,000 to 43,000 between 1987 and 2016.  
26 Over the same period, the area of improved grassland increased, the number of sheep  
27 decreased and the climate warmed.
- 28 4. Goose population growth was strongly linked to the increasing area of improved grassland,  
29 which provided geese with more high quality forage. Changing climatic conditions,  
30 particularly warming temperatures on Islay and breeding grounds in Greenland, have also  
31 boosted goose numbers.
- 32 5. As the goose population has grown, farms have supported geese more frequently and in larger  
33 numbers, with subsequent damaging effects. The creation of high-quality grassland appears to  
34 have largely driven damage by geese. Our analysis also reveals the drivers of spatial variation  
35 in goose impacts: geese were more likely to occur on farms closer to roosts and those with  
36 more improved grassland. However, as geese numbers have increased they have spread to  
37 previously less favoured farms.
- 38 6. *Synthesis and applications.* Our study demonstrates the primary role of habitat modification  
39 in the emergence of conflict between goose conservation and agriculture, alongside a  
40 secondary role of climate change. Our research illustrates the value of exploring socio-  
41 ecological history to understand the processes leading to conservation conflict. In doing so,  
42 we identify those elements that are more controllable, such as local habitat management, and

43 less controllable, such as climate change, but which both need to be taken into account when  
44 managing conservation conflict.

45

46 **Keywords:** barnacle geese, climate change, conservation conflict, goose conservation conflict, grass  
47 damage, habitat modification, human-wildlife conflict, Islay, population dynamics, spatial ecology

48

## 49 INTRODUCTION

50 Conservation conflict – conflict between stakeholders representing biodiversity conservation and  
51 those representing other interests (e.g., food production) – is widespread globally (Redpath *et al.*  
52 2013, 2015). Such conflict can be highly damaging to both biodiversity and livelihoods, so represents  
53 a key challenge for society (Sillero-Zubiri, Sukumar & Treves 2007). Human-wildlife conflict  
54 researchers have often focused on quantifying the negative impacts of wildlife on humans and vice-  
55 versa (Woodroffe, Thirgood & Rabinowitz 2005). In contrast, research into the processes leading to  
56 the emergence of serious impacts and, in turn, conflict between stakeholders, is currently scarce  
57 (Young *et al.* 2010). Such research could provide new insight into why conflict emerges and how it  
58 can be managed.

59 While conflict is clearly a social phenomenon, it emerges from environments comprising both  
60 socio-economic and natural elements, and can be triggered by change in any of these, such as wildlife  
61 population growth or decreases in the market values of crops, if they result in impacts perceived to be  
62 unacceptable by one or more parties (Young *et al.* 2010). In particular, ecological elements (e.g.,  
63 species, ecosystems) are central to conflicts, but such ecological temporal dynamics tend to be studied  
64 in isolation rather than in interaction with human activities (Redpath & Sutherland 2015).  
65 Encouragingly, conflict studies are starting to combine ecological and human dynamics over short  
66 time-scales (e.g., Simonsen *et al.* 2016). Historic applied ecological data represents a potentially  
67 valuable resource for studying how environmental change has contributed to the development of  
68 conservation conflicts, by revealing how historic management and natural resource use by humans  
69 have shaped the ecological context of conflict (Lambert 2015).

70           The analysis of spatial historic data could additionally reveal why conflict is more likely to  
71 emerge in certain areas. The potential for conflict varies considerably due to spatial variation in social,  
72 economic and ecological factors (White *et al.* 2009). The latter can play a prominent role, for instance  
73 by influencing the severity of negative impacts of wildlife experienced by humans. For example,  
74 livestock depredation by wild carnivores can be more frequent in areas with more favourable habitat  
75 for wild prey, leading to a greater potential for conflict (Treves *et al.* 2004). Such spatial variation is  
76 often highly skewed, with only a small proportion of stakeholders experiencing serious negative  
77 consequences (Naughton-Treves 1998; Michalski *et al.* 2006). In this case, only farms located within  
78 large wilderness areas may experience high rates of livestock depredation (Michalski *et al.* 2006).  
79 Approaches based on spatial historic data could reveal how these skewed spatial patterns have  
80 evolved, and how they may lead to conflict in the future.

81           Here, we used 29-year and 18-year ecological time-series to examine how environmental  
82 change has contributed to the emergence of conflict over the conservation of Greenland barnacle  
83 geese (*Branta leucopsis*) and agriculture on the Scottish island of Islay. Migratory waterbird  
84 populations are regarded as a high conservation priority due to their strong reliance on restricted sites  
85 along their migration routes; environmental change at a single site can negatively impact an entire  
86 population (Kirby *et al.* 2008). Indeed, Greenland barnacle geese are an Annex I species on the  
87 European Union (EU) Birds Directive. Islay is an important site for this species, supporting more than  
88 half of the world's population during the non-breeding season (56% of 81,000 in 2013; Mitchell &  
89 Hall 2013). Birds arrive in early October from breeding grounds in eastern Greenland, via staging  
90 grounds in Iceland, and leave Islay by mid-April (Fig. 1a). Many goose populations are growing  
91 throughout the northern hemisphere, and are feeding increasingly in agricultural rather than natural  
92 habitats (e.g., Gauthier *et al.* 2005; Van Eerden *et al.* 2005), causing substantial economic damage to  
93 grassland and arable crops (Owen 1990). In such areas, conflict between conservationists and farming  
94 bodies is common (Fox *et al.* 2016). This is the case on Islay, where barnacle geese feed  
95 predominantly on farmed grassland and form large flocks that cause substantial damage to grass  
96 yields (Percival & Houston 1992). Barnacle goose numbers on Islay more than doubled from around

97 20,000 in 1987/88 to 43,000 in 2015/16 (Fig. 2a), contributing to growing conflict among  
98 stakeholders, including conservation groups, farmers and the governmental organisation in charge of  
99 goose management, Scottish Natural Heritage (SNH; McKenzie & Shaw 2017). To date, management  
100 of goose conservation-agriculture conflict on Islay and elsewhere has generally focused on reducing  
101 agricultural damage caused by geese. Coordinated approaches combining habitat management of  
102 goose refuges, scaring geese from agricultural areas, and payment of compensation to farmers  
103 experiencing grass and crop damage have seen some success in areas such as the Netherlands,  
104 Norway and Sweden (Cope, Vickery & Rowcliffe 2005; Fox *et al.* 2016). However, increasing goose  
105 numbers can outstrip both the size of refuges and the level of funding for compensation, necessitating  
106 population regulation through sport hunting (Madsen *et al.* 2017) or, more controversially, culling, as  
107 has been applied on Islay (McKenzie & Shaw 2017).

108 To understand how the environment has shaped the conflict over time, we investigated the  
109 drivers of increasing goose numbers on Islay, at two spatial scales. First, we examined the factors that  
110 have driven increases in total barnacle goose abundance on Islay (hereafter, ‘population-scale  
111 analysis’), relating goose numbers to historic land-use and climate data for Islay and breeding grounds  
112 in Greenland. Increasing goose numbers across North America and western Europe are thought to  
113 have been caused by a combination of agricultural intensification (e.g., Van Eerden *et al.* 2005),  
114 release from hunting pressure (Menu, Gauthier & Reed 2002) and climate change, such as warming  
115 temperatures (e.g., Gauthier *et al.* 2005), though the relative importance of these drivers is unclear and  
116 likely to vary among species and regions. Here, we tested four non-mutually exclusive hypotheses for  
117 population increases, assuming that effects would act primarily via increasing forage availability  
118 and/or quality. We tested whether population increases resulted from:

- 119 1. Increases in improved grassland availability on Islay following agricultural improvements
- 120 2. Increases in improved grassland availability on Islay due to reductions in sheep densities
- 121 3. The climate becoming warmer and drier on Islay
- 122 4. The climate becoming warmer and drier on breeding grounds in Greenland

123 We then examined how changes in goose abundance have influenced the distribution of geese across  
124 different farms, (hereafter, ‘farm-scale analysis’), testing three hypotheses. We tested whether geese  
125 occurred more frequently and in greater numbers:

126 5. When the population was larger

127 6. On farms with more improved grassland

128 7. On farms closer to roosting sites

129

## 130 **MATERIALS AND METHODS**

### 131 *Study area*

132 Islay is an island of 62,000ha situated in the Inner Hebrides of western Scotland (Fig. 1). Islay’s  
133 landscape is dominated by agriculture (56,000ha), predominantly rough grazing and farmed grassland  
134 supporting sheep and cattle. In 1992, a government-funded goose management scheme was initiated  
135 on Islay, partially compensating farmers for economic losses from goose damage. From 2000, farmers  
136 were also allowed to protect parts of their farm by scaring geese, which in certain cases included  
137 licensed shooting of geese. However, steep increases in goose numbers during the early 2000s,  
138 combined with growing costs of farming and reductions in funding for compensation, resulted in  
139 geese causing serious economic damage to Islay’s agricultural economy (currently estimated at £1.6  
140 million per annum). In 2014, a new goose management strategy was implemented by SNH and the  
141 Scottish Government, which aimed to reduce goose damage by 25-30% by reducing barnacle goose  
142 numbers (SNH 2014). Since 2014, between 1,000 and 2,700 barnacle geese have been culled on Islay  
143 each year. This has contributed to an escalation in conflict between SNH, farmers and conservation  
144 organisations on Islay, with the Royal Society for the Protection of Birds and Wildfowl and Wetlands  
145 Trust lodging a formal complaint to the European Commission in 2015 over the culling programme.

146 *Data collection and statistical analysis*

147 *Goose abundance data*

148 Population censuses across the wintering range of Greenland barnacle geese are undertaken every five  
149 years, using ground and aerial surveys (Mitchell & Hall 2013). More frequent surveys are undertaken  
150 at a number of key wintering sites, including Islay. We used data from island-wide ground surveys of  
151 Islay's overwintering barnacle geese, carried out by SNH multiple times each year, generally in  
152 November, December, January and March ( $n=101$ ). These provided estimates of total goose numbers  
153 on Islay for the period 1987-2016 and farm-specific goose numbers for the period 1998-2016. Surveys  
154 were conducted twice over consecutive days and averaged to produce a reliable estimate of total  
155 barnacle goose abundance. They were carried out simultaneously by five pairs of trained surveyors in  
156 vehicles around five pre-defined routes of sub-areas of Islay, with care taken to avoid double counting  
157 within and among sub-areas by monitoring the movements of flocks during surveys. Geese were  
158 counted from vehicles using binoculars and spotting scopes, at distances of 20m-2km. The farms  
159 occupied by geese were recorded according to a system of unique field codes, using maps of the study  
160 area.

161 *Population-scale analysis*

162 To test hypotheses 1-4, we acquired land-use and climate data for the period 1985-2015. We obtained  
163 Islay land-use data from the Scottish Government  
164 (<http://www.gov.scot/Topics/Statistics/Browse/Agriculture-Fisheries/Datasets>). We used data on  
165 annual variation in sheep numbers on Islay, collected by the annual June Scottish Agricultural census,  
166 and in the area of improved grassland on Islay (defined as grassland that has previously been  
167 reseeded), collected by the Agricultural census (1985-2008) and from Single Farm Application forms  
168 (2009-2015). We used monthly climate data for the West Scotland from the Met Office to represent  
169 Islay's climate (<http://www.metoffice.gov.uk/climate/uk/summaries/datasets>), calculating mean daily  
170 temperature and total precipitation during the barnacle goose non-breeding season (October-March).  
171 We used monthly climate data from Danmarkshavn meteorological station, which lies within the  
172 barnacle goose breeding range in eastern Greenland (74.48°N; 18.98°W), to represent breeding



173 ground climate (<http://research.dmi.dk/publications/other-publications/reports/>). We calculated mean  
174 daily temperature and total precipitation for two important periods during breeding for arctic goose  
175 reproduction and post-fledging survival (e.g., Dickey, Gauthier & Cadieux 2008): in early spring  
176 (May) when geese have recently arrived and are egg laying, and late summer (August) when geese are  
177 brood rearing and preparing to leave. We considered predictors at time-lags of 1-3 years, assuming  
178 that predictors would influence abundance via lagged, and possibly additive, effects on survival and  
179 recruitment. Time-lags of  $t-1$  represent, for Greenland, the climate during the breeding season directly  
180 preceding abundance surveys on Islay and, for Islay, the climate/land-use during the previous year's  
181 non-breeding season on Islay.  $Greenland_{t-3}$  and  $Islay_{t-2}$  predictors allow for delayed cohort effects on  
182 the future reproduction of juveniles, which reach sexual maturity at 2 years (Forslund & Larsson  
183 1992; see Fig. S1 in Supporting Information for an illustration of the timing of predictors).  
184 Environmental conditions experienced in early life by arctic-breeding geese can influence survival  
185 (van der Jeugd & Larsson 1998) and reproduction in later life (Sedinger, Flint & Lindberg 1995). See  
186 Table 1 for a summary of all predictors and their hypothesised effects.

187 We fitted linear mixed-effects regressions between barnacle goose abundance and predictors,  
188 including a random intercept for survey month, using the 'lme' function in R (Pinheiro *et al.* 2016; R  
189 Core Team 2016). We fitted models with maximum likelihood and scaled variables to produce  
190 standardised coefficients. We considered separate improved grassland coefficients for pre-2009 and  
191 post-2009 time-periods, using an interaction with a categorical variable representing time-period. This  
192 was because, whilst improved grassland is defined in the same way on the data collection forms for  
193 these periods, more guidance on differences between improved grassland and rough grazing is  
194 provided on Single Farm Application Forms (post-2009), resulting in slightly different classifications  
195 of improved grassland between the two periods (Fig. 2b). We fitted models with 'AR-1'  
196 autocorrelation structures to account for temporal autocorrelation in model residuals. We considered  
197 models of increasing complexity, fitting models containing all possible combinations of predictors for  
198 Islay land-use, Islay climate and Greenland climate (Table 1) for a given number of predictors, until  
199 the addition of an extra predictor did not produce a parsimonious model according to Akaike's

200 Information Criterion (AIC). We assessed models with  $\Delta AIC \leq 6$  and lower than simpler nested  
201 models to have some support (Richards 2015), and considered predictors occurring in all these ‘top  
202 models’ to have strong support. We visualised relationships between goose abundance and these  
203 predictors using partial-effect plots, which display response-predictor relationships while accounting  
204 statistically for the effects of other predictors in a model. This is done by plotting  $r(x|\text{other predictors})$   
205 against  $r(y|\text{other predictors})$ , where  $r(x|\text{others})$  are residuals of a model regressing predictor  $x$  against  
206 all other predictors (but not response  $y$ ) and  $r(y|\text{others})$  are residuals of a model regressing  $y$  against  
207 all predictors except for  $x$ .

### 208 *Farm-scale analysis*

209 To test hypotheses 5-7, we fitted models exploring the influences of Islay goose abundance, farm-  
210 specific improved grassland area and farm-specific distance to nearest roost on barnacle goose  
211 numbers on farms. To test the effect of abundance, we used the total abundance estimates  
212 corresponding to farm-scale goose numbers. We calculated distance to roost as the Euclidean distance  
213 between a farm’s centroid and the nearest barnacle goose roost. There are three main night-time  
214 roosting sites on Islay, composed predominantly of saltmarsh and inter-tidal mudflats, used by the  
215 majority of barnacle geese (see Fig. 1b). We calculated mean area of improved grassland (grassland  
216 reseeded within the past seven years) on farms using data provided by the Islay goose management  
217 scheme. See Table 1 for a summary of these predictors.

218 We used a hurdle modelling procedure, first fitting models exploring drivers of probability of  
219 goose occurrence during a survey on farms, using presence-absence data (hereafter, ‘occurrence  
220 models’), and second fitting models exploring the drivers of their numbers when they were present,  
221 using presence-only count data (hereafter, ‘count models’). This procedure allowed us to investigate  
222 the processes generating goose occurrence and numbers separately. We fitted models using linear  
223 mixed-effects regressions, including random intercepts for survey year and farm ID ( $n=103$ ) using the  
224 ‘glmer’ function in R (Bates *et al.* 2015). We fitted models with maximum likelihood, using binomial  
225 and Poisson error structures for occurrence and count models, respectively. We tested for spatial  
226 autocorrelation per survey in the responses and residuals by calculating Moran’s  $I$  statistic, to

227 determine the ability of models to explain any spatial autocorrelation in the responses. There were low  
228 levels of autocorrelation in the data, with significant spatial autocorrelation in farm-specific  
229 occurrences and counts, respectively, on only 18% (21/120) and 5% (6/120) of surveys. There were  
230 similarly low levels of autocorrelation in the residuals of the best occurrence (16%) and count models  
231 (4%).

232 To test hypothesis 5, we first fitted models with total barnacle goose abundance as a fixed  
233 effect. We included farm ID random coefficients for the effect of abundance, to account for variation  
234 in this effect among farms. We included linear and quadratic effects of day of season to account for  
235 seasonal changes in goose spatial aggregation potentially resulting from depletion in grass  
236 availability. We fitted models with the scaled predictors together, separately and both absent,  
237 identifying the best model using AIC. Next, to test hypotheses 6 and 7, we extracted the farm-specific  
238 intercepts/coefficients (i.e.,  $\beta_{\text{Population}} + \gamma_{\text{Farm}}$ ) from the best models, and fitted post-hoc models  
239 exploring the effects of improved grassland area and distance to roost on variation among farms in i)  
240 goose occurrence/number (farm-specific intercepts) and ii) the effect of Islay abundance on  
241 occurrence/number (farm-specific coefficients). We used non-linear regression, implemented with the  
242 ‘nlsLM’ function in R (Elzhov *et al.* 2013), considering linear and curvilinear effects of the form  $ax^b$   
243 for each scaled predictor. As before, we selected the best models using AIC.

244 For all models, we assessed model fit using  $R^2$  (Nakagawa & Schielzeth 2013) and  
245 collinearity using variance inflation factors, accepting those  $<3$  (Zuur, Ieno & Elphick 2010).

246

## 247 **RESULTS**

### 248 *Population-scale analysis*

249 The best model of barnacle goose abundance ( $R^2=0.86$ ) showed that population increases were linked  
250 primarily to changes in land-use on Islay, but were also associated with climate variation on Islay and  
251 Greenland (Fig. 3-4). All top models contained predictors of Islay land-use, Islay climate and  
252 Greenland climate (Fig. 3; Table S1). The area of improved grassland on Islay two years previously  
253 was by far the strongest predictor of goose abundance (Fig. 3 & 4a); this predictor was selected in all

254 top models and its partial effect ( $R^2=0.67$ ) was more than four times stronger than any other. This  
255 supports hypothesis 1, suggesting that the area of improved grassland on Islay – which increased by  
256 45% between 1987 and 2004 (Fig. 2b) – has boosted goose numbers by roughly 6,000 per 1,000ha  
257 increase in grassland. In contrast, there was no evidence for hypothesis 2 – a negative effect of sheep  
258 numbers – despite a 40% decrease in sheep numbers on Islay from 78,500 to 47,000 between 1998  
259 and 2011 (Fig. 2c).

260 We found strong evidence for a positive effect of Islay temperature on abundance, operating  
261 at both one and two year time-lags, thus supporting hypothesis 3 (Fig. 3 & 4b). Both time-lags were  
262 present in all top models (Fig. 3), with a 1°C increase at a one year time-lag boosting goose numbers  
263 by roughly 3,000. We also detected weaker, negative effects of Islay precipitation at one and two year  
264 time-lags, with goose numbers decreasing by 700 ( $t_1$ ) and 900 ( $t_2$ ) per 100mm increase in  
265 precipitation. Both time-lags featured in the best model, but not all top models (Fig. 3; Table S1).  
266 Islay's October-March temperature and precipitation exhibited increasing, though non-significant,  
267 trends during the study period (see Fig. S2). Spring and late summer climatic conditions at breeding  
268 grounds were also associated with goose abundance, providing some support for hypothesis 4,  
269 although effect sizes were generally weaker than for Islay climate (Fig. 3 & 4c). There was evidence  
270 for a moderate positive effect of August temperature (2,300 more geese per 1°C increase) and a  
271 weaker negative effect of August precipitation (1,100 fewer geese per 10mm increase) during the  
272 breeding season directly preceding goose surveys; these effects are present in all top models. A weak  
273 negative effect of precipitation at a two year time-lag was also present in all top models. These effects  
274 indicate that warmer and drier periods preceding migration from breeding grounds influenced  
275 recruitment positively. August breeding ground temperatures have become significantly warmer, from  
276 an average of 2.2°C in 1985 to 3.6°C in 2015, but there has been no significant change in precipitation  
277 (see Fig. S2). There was some evidence of positive effects of spring breeding ground precipitation and  
278 temperature on goose abundance (Fig. 3; Table S1), in particular suggesting delayed positive effects  
279 of wet springs on recruitment. However these effects were not present in all top models (Fig. 3; Table  
280 S1).

281 *Farm-scale analysis*

282 The best models describing the number and occurrence probability of geese at a farm level contained  
283 positive effects of goose abundance, thus supporting hypothesis 5 (Fig. 5; Table S2). Our models  
284 estimated that, for a 10% growth in the population, probability of occurrence and abundance on an  
285 average farm increased by 5% and 9%, respectively. The best models also contained quadratic effects  
286 of day (Table S2). The probability of goose occurrence on farms increased from the start of the  
287 season, peaking in February-March before declining later in the season (see Fig. S3). In contrast, the  
288 number of geese recorded per farm showed a slight decline during the season, suggesting that geese  
289 spread out over more farms.

290 Variation in farm-specific intercepts from both occurrence and count models was linked  
291 primarily to the area of improved grassland on farms, thus supporting hypothesis 6. Geese were more  
292 likely to occur and to do so in greater numbers on farms with more improved grassland (Fig. 6a & c;  
293 Table 2a). For example, geese were present on farms with 10ha and 100ha of improved grassland,  
294 respectively, during 7% and 79% of surveys, at average abundances of 160 and 1,400. There was also  
295 evidence for negative effects of distance to roost in both models, indicating that geese were more  
296 likely to occur and to do so in greater numbers on farms nearer roosts, thus supporting hypothesis 7  
297 (Fig. 6b & d; Table 2a). For example, geese were present on farms 1km and 8km from roosts,  
298 respectively, during 43% and 23% of surveys, at average abundances of 580 and 190.

299 While the effect of Islay goose abundance on farm-scale goose occurrence and number was  
300 positive on average, it varied in strength and direction among different farms when random effects are  
301 considered (Fig. 7). In the best occurrence model, 2 out of the 104 farms had negative abundance  
302 coefficients – indicating decreasing occurrence probability as total abundance has increased – whilst  
303 for the remaining 98%, positive coefficients varied considerably, between 0.12 and 2.47 (mean, 1.16).  
304 Even greater variation was present in the count model, where 21% of farms have negative abundance  
305 coefficients and the remaining 79% vary by several orders of magnitude, between 0.09 and 11.65  
306 (mean, 2.00). We were able to identify the drivers of farm-specific variation for occurrence models,  
307 but not count models. We detected a negative effect of improved grassland area and a positive

308 curvilinear effect of distance to roost on farm-specific abundance coefficients for occurrence  
309 probability (Table 2b). This suggests that goose occurrence became more likely on farms with less  
310 improved grassland and those further from roosts, as goose abundance increased (Fig. 7).

311

## 312 **DISCUSSION**

313 This study illustrates how environmental change can shape the ecological dynamics underlying the  
314 emergence of conservation conflict. The growth of Islay's barnacle goose population was strongly  
315 linked to changing farming practice, specifically improvements to grassland, and was also associated  
316 with climate warming. As goose abundance increased, farmers experienced geese on their farms with  
317 greater frequency and in larger numbers, and geese spread to previously less favoured farms. By  
318 revealing the drivers of goose numbers experienced by farmers, our analysis explained how spatial  
319 patterns of human-wildlife impacts can evolve.

### 320 *Drivers of goose population dynamics*

321 Increases in the number of barnacle geese on Islay were associated with environmental conditions at  
322 different stages of this species' annual cycle. We identified lagged effects of land-cover and climate  
323 experienced during the non-breeding season on Islay and of climate experienced during the breeding  
324 season on Greenland. Of these, the strongest driver of abundance was the area of improved grassland  
325 on Islay. This concurs with other studies implicating agricultural intensification as a likely driver of  
326 increasing goose populations (e.g., Abraham, Jefferies & Alisauskas 2005; Fox *et al.* 2005). Increased  
327 application of Nitrogen-based fertilisers during the 20<sup>th</sup> century, in Europe encouraged by production  
328 subsidies paid through the Common Agricultural Policy until 2003, has created areas of pasture  
329 significantly higher in protein and digestibility than natural goose foraging areas (van Eerden *et al.*  
330 2005). On Islay, some of the increases in high-quality grassland were driven by the EU funded  
331 Agricultural Development Programme for the Scottish islands, which commenced in 1987 (McKenzie  
332 & Shaw 2017). The increase in improved grassland has probably increased Islay's goose carrying  
333 capacity, providing geese with 'escape' from density-dependent survival. Density-dependence may  
334 have acted in recent years, with goose numbers fluctuating around 40,000 and increases in improved

335 grassland slowing. Goose abundance correlated most strongly with improved grassland at a two-year  
336 time-lag, suggesting that cohort effects may also be acting on survival and reproduction. Cohorts born  
337 prior to non-breeding seasons when improved grassland is abundant may produce more offspring  
338 when they breed for the first time two years later. Increased immigration from neighbouring non-  
339 breeding sites could also be playing a role in population growth in Islay. However, populations have  
340 also increased at neighbouring sites and the total population overwintering on Islay has remained  
341 constant during the period of population increase (WWT range-wide surveys: 1999, 0.65; 2003, 0.65;  
342 2008, 0.64; Mitchell & Hall 2013), suggesting that a strong role of immigration is unlikely.

343 We identified secondary climatic effects on goose abundance. In particular, abundance was  
344 higher following warmer and drier non-breeding seasons. This is probably linked to effects on forage  
345 quality: during colder winters grass protein content can be lower (Therkildsen & Madsen 2000), while  
346 during wetter winters, grass availability may be lower due the combined effects of waterlogging and  
347 trampling by geese damaging grass (Kahl & Samson 1984). We detected positive effects of warm and  
348 dry weather during the early and late breeding season on Greenland. In particular, abundance was  
349 higher following warmer, drier Augusts. Cold, potentially snowy, periods late in the breeding season  
350 can result in brood losses due to hypothermia (Dickey, Gauthier & Cadieux 2008). The presence of  
351 climate effects reveals that external, uncontrollable, factors can play a role in shaping the  
352 environmental context of conflicts.

353 We detected no effect of decreasing competition with sheep on goose abundance, though it is  
354 possible that such an effect only acted during the latter part of the study period – when sheep numbers  
355 decreased dramatically – and was not detected as a result. Prior to 1998, there was an increasing trend  
356 in sheep numbers, largely matching the trend in improved grassland. Another potential driver of  
357 abundance increases is the implementation of stricter population protection and subsequent reductions  
358 in hunting. However, the protection of barnacle geese by the EU's 1979 Bird's Directive and the  
359 UK's 1981 Wildlife and Countryside Act occurred a number of years prior to this study's time-period.  
360 Any population recovery would likely be evident for only a short period following cessation of  
361 hunting, as has been shown for other goose species (Fox *et al.* 2005; Gauthier *et al.* 2005).

362 *Drivers of farm-scale goose dynamics*

363 As the population has grown, goose numbers on farms have increased and their distribution has  
364 spread over a wider area. These relationships provide a link between the drivers of goose population  
365 dynamics and their spatial dynamics at a scale experienced by stakeholders. The creation of high-  
366 quality grassland was the principal driver of goose population growth and was thus likely to be  
367 responsible for the problem of serious grass damage by geese (relationships between local goose  
368 abundance and damage are probably simple; Fox *et al.* 2016).

369 The farm-specific intercept models also reveal that farms with more improved grassland were  
370 more likely to support large numbers of geese, supporting the population-scale results. Such farms are  
371 likely to have larger carrying capacities. Additionally, geese are known to graze more intensely on  
372 more productive pasture (e.g., Ydenberg & Prins 1981). Geese were also more likely to occur on  
373 farms closer to roosts. In order to minimize energy expenditure, geese preferentially forage closest to  
374 roosts and only move further afield when these resources become depleted, as has been identified in a  
375 range of goose species including barnacle geese (Si *et al.* 2011). These results go some way in  
376 explaining why goose impacts vary between farmers and illustrate how skewed impacts on  
377 stakeholders – a common feature of conservation conflicts (e.g., Naughton-Treves 1998; Cope,  
378 Vickery & Rowcliffe 2005) – can emerge. It should be noted that, while the occurrence model  
379 explained a large proportion of variation in farm-specific intercepts ( $R^2=0.69$ ), the count model  
380 explained much less ( $R^2=0.09$ ). There are likely to be a range of other factors contributing to variation  
381 in goose numbers among farms, such as scaring intensity and quality of grassland.

382 Our analysis also shows how the Islay case-study has evolved over time; the effects of  
383 abundance on farm-scale goose occurrence and number were highly variable. Interestingly, farms  
384 with less improved grassland and further from roosts – which were less likely to support geese on  
385 average – became more likely to harbour geese as the population increased. This could be because  
386 forage is becoming more depleted on preferred farms, forcing geese to forage more frequently on  
387 farms further from roosts and those with less improved grassland. As a result, a wider range of farms  
388 may have experienced goose damage as the population has grown.



389 *Linking drivers of ecological dynamics to management of conflict*

390 By exploring the socio-ecological history of this conflict, we identified that the contemporary problem  
391 of damage to grass by geese on Islay is largely an unforeseen consequence of historic improvements  
392 in grass productivity. This illustrates that changes in land management by humans can be a key driver  
393 of environmental change contributing to the emergence of conflict. While conservationists have often  
394 expressed concern over the negative impacts of agricultural intensification on biodiversity and  
395 wildlife populations (e.g., Donald, Green & Heath 2001), our study illustrates how inadvertent  
396 positive impacts of agricultural management on wildlife populations can ultimately be damaging for  
397 conservation interests. Proactive responses to initial population increases could prevent human-  
398 wildlife impacts from reaching conflict levels and be more cost-effective than reactive interventions  
399 (Drechsler, Eppink & Wätzold 2011). Managers need to tackle emerging conflicts early not only to  
400 prevent stakeholders positions from becoming entrenched, for example by working closely with  
401 stakeholders to find shared solutions as carried out for geese in Norway and Denmark (Tombre,  
402 Eythórsson & Madsen 2013), but also to prevent impacts from wildlife reaching levels that are  
403 challenging and costly to manage.

404 We found that uncontrollable external processes such as climate change can influence the  
405 environmental context underlying conservation conflict. Managers should consider such processes  
406 when planning interventions. This could be achieved using predictive modelling frameworks such as  
407 management strategy evaluation (MSE), an approach gaining popularity in conservation (Bunnefeld,  
408 Hoshino & Milner-Gulland 2011). MSE combines models of natural dynamics with those for  
409 monitoring and management, incorporating the various uncertainties of complex socio-ecological  
410 systems. The use of shooting as a population-reduction tool on Islay has resulted in the escalation in  
411 conflict between stakeholder groups. An alternative strategy could be coordinated reductions in  
412 grassland productivity, through decreased reseeding frequencies and fertiliser application, in order to  
413 reduce the carrying capacity of the island. The effectiveness of these strategies could depend on  
414 climate, for example if reductions in goose numbers from culling were offset by increases in

415 recruitment due to milder breeding conditions. Using MSE it would be possible to take into account  
416 the influence of climate change on the effectiveness of these competing management strategies.

417 The gathering of ecological and social evidence is recognised as an important step along the  
418 roadmap to conflict management (Redpath *et al.* 2013). However, in many cases, management  
419 interventions are put in place before the drivers of conflict are fully understood. The suitability of  
420 different management options will depend on the unique ecological and socio-economic  
421 characteristics of a particular region (Henle *et al.* 2008), including historic changes in these  
422 characteristics (Lambert 2015). As such, studies like ours provide an important step in understanding  
423 how conflict emerges and how to manage it. For waterbird populations, such studies can inform how  
424 to manage populations at the centre of conflicts sustainably, in order to pursue the African-Eurasian  
425 Waterbird Agreement (AEWA 2015). It is uncertain how the Islay case-study will develop in the  
426 future following the UK's decision to leave the EU. Brexit could potentially lead to change in the  
427 protection status of barnacle geese in the UK, however this could open up new options for the  
428 management of this conflict.

#### 429 **ACKNOWLEDGEMENTS**

430 We are indebted to Rae McKenzie and others at SNH Islay for providing the survey data and fruitful  
431 discussions about the conflict. TM was supported by a Carnegie Trust for the Universities of Scotland  
432 grant awarded to NB, AK and SR (grant 50197).

#### 433 **AUTHORS' CONTRIBUTIONS**

434 NB, AK, SR and TM formulated the question. TM conducted the analysis and wrote the paper. All  
435 authors contributed to revisions.

#### 436 **DATA ACCESSIBILITY**

437 The data used in this study are available from Dryad Digital Repository  
438 <http://dx.doi.org/10.5061/dryad.pj59h> (Mason *et al.* 2017).

439 **REFERENCES**

- 440 Abraham, K.F., Jefferies, R.L. & Alisauskas, R.T. (2005) The dynamics of landscape change and  
441 snow geese in mid-continent North America. *Global Change Biology*, **11**, 841–855.
- 442 AEWA. (2015) *Guidelines on Sustainable Harvest of Migratory Waterbirds*. AEWA Conservation  
443 *Guidelines No. 5, AEWA Technical Series No. 62*. Bonn, Germany.
- 444 Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015) Fitting Linear Mixed-Effects Models Using  
445 lme4. *Journal of Statistical Software*, **67**, 1–48.
- 446 Bunnefeld, N., Hoshino, E. & Milner-Gulland, E.J. (2011) Management strategy evaluation: a  
447 powerful tool for conservation? *Trends in Ecology & Evolution*, **26**, 441–447.
- 448 Cope, D., Vickery, J. & Rowcliffe, M. (2005) From conflict to coexistence: a case study of geese and  
449 agriculture in Scotland. *People and wildlife, conflict or co-existence?* (eds R. Woodroffe, S.  
450 Thirgood, & A. Rabinowitz), pp. 176–191. Cambridge University Press, Cambridge, UK.
- 451 Dickey, M.-H., Gauthier, G. & Cadieux, M.-C. (2008) Climatic effects on the breeding phenology and  
452 reproductive success of an arctic-nesting goose species. *Global Change Biology*, **14**, 1973–1985.
- 453 Donald, P.F., Green, R.E. & Heath, M.F. (2001) Agricultural intensification and the collapse of  
454 Europe's farmland bird populations. *Proceedings of the Royal Society of London B: Biological*  
455 *Sciences*, **268**, 25–29.
- 456 Drechsler, M., Eppink, F. V. & Wätzold, F. (2011) Does proactive biodiversity conservation save  
457 costs? *Biodiversity and Conservation*, **20**, 1045–1055.
- 458 van Eerden, M.R., Drent, R.H., Stahl, J. & Bakker, J.P. (2005) Connecting seas: western Palaearctic  
459 continental flyway for water birds in the perspective of changing land use and climate. *Global*  
460 *Change Biology*, **11**, 894–908.
- 461 Elzhov, T., Mullen, K., Spiess, A.-N. & Bolker, B. (2013) minpack.lm: R Interface to the Levenberg-  
462 Marquardt Nonlinear Least-Squares Algorithm Found in MINPACK. R package version 1.1-8.

- 463 Forslund, P. & Larsson, K. (1992) Age-Related Reproductive Success in the Barnacle Goose. *Journal*  
464 *of Animal Ecology*, **61**, 195.
- 465 Fox, A.D., Elmberg, J., Tombre, I.M. & Hessel, R. (2016) Agriculture and herbivorous waterfowl: a  
466 review of the scientific basis for improved management. *Biological Reviews*, **92**, 854–877.
- 467 Fox, A.D., Madsen, J., Boyd, H., Kuijken, E., Norriss, D.W., Tombre, I.M. & Stroud, D.A. (2005)  
468 Effects of agricultural change on abundance, fitness components and distribution of two arctic-  
469 nesting goose populations. *Global Change Biology*, **11**, 881–893.
- 470 Gauthier, G., Giroux, J.-F., Reed, A., Bechet, A. & Belanger, L. (2005) Interactions between land use,  
471 habitat use, and population increase in greater snow geese: what are the consequences for natural  
472 wetlands? *Global Change Biology*, **11**, 856–868.
- 473 Henle, K., Alard, D., Clitherow, J., Cobb, P., Firbank, L., Kull, T., McCracken, D., Moritz, R.F.A.,  
474 Niemelä, J., Rebane, M., Wascher, D., Watt, A. & Young, J. (2008) Identifying and managing  
475 the conflicts between agriculture and biodiversity conservation in Europe—A review.  
476 *Agriculture, Ecosystems & Environment*, **124**, 60–71.
- 477 van der Jeugd, H.P. & Larsson, K. (1998) Pre-breeding survival of barnacle geese *Branta leucopsis* in  
478 relation to fledgling characteristics. *Journal of Animal Ecology*, **67**, 953–966.
- 479 Kahl, R. & Samson, F. (1984) Factors affecting yield of winter wheat grazed by geese. *Wildlife*  
480 *Society Bulletin*, **12**, 256–262.
- 481 Kirby, J.S., Stattersfield, A.J., Butchart, S.H.M., Evans, M.I., Grimmett, R.F.A., Jones, V.R.,  
482 O’Sullivan, J., Tucker, G.M. & Newton, I. (2008) Key conservation issues for migratory land-  
483 and waterbird species on the world’s major flyways. *Bird Conservation International*, **18**, S49–  
484 S73.
- 485 Lambert, R.A. (2015) Environmental history and conservation conflicts. *Conflicts in conservation:*  
486 *Navigating towards solutions* (eds S. Redpath, R. Gutiérrez, K. Wood, & J. Young), pp. 49–60.  
487 Cambridge University Press, Cambridge, UK.

- 488 Madsen, J., Williams, J.H., Johnson, F.A., Tombre, I.M., Dereliev, S. & Kuijken, E. (2017)  
489 Implementation of the first adaptive management plan for a European migratory waterbird  
490 population: The case of the Svalbard pink-footed goose *Anser brachyrhynchus*. *Ambio*, **46**, 275–  
491 289.
- 492 Mason, T.H.E., Keane, A., Redpath, S.M. & Bunnefeld, N. (2017) Data from: The changing  
493 environment of conservation conflict: geese and farming in Scotland. *Dryad Digital Repository*,  
494 <http://dx.doi.org/10.5061/dryad.pj59h>.
- 495 McKenzie, R. & Shaw, J.M. (2017) Reconciling competing values placed upon goose populations:  
496 The evolution of and experiences from the Islay Sustainable Goose Management Strategy.  
497 *Ambio*, **46**, 198–209.
- 498 Menu, S., Gauthier, G. & Reed, A. (2002) Changes in survival rates and population dynamics of  
499 greater snow geese over a 30-year period: implications for hunting regulations. *Journal of*  
500 *Applied Ecology*, **39**, 91–102.
- 501 Michalski, F., Boulhosa, R.L.P., Faria, A. & Peres, C.A. (2006) Human-wildlife conflicts in a  
502 fragmented Amazonian forest landscape: determinants of large felid depredation on livestock.  
503 *Animal Conservation*, **9**, 179–188.
- 504 Mitchell, C. & Hall, C. (2013) *Greenland Barnacle Geese Branta Leucopsis in Britain and Ireland:*  
505 *Results of the International Census, Spring 2013*. Wildfowl and Wetlands Trust, Slimbridge,  
506 UK.
- 507 Nakagawa, S. & Schielzeth, H. (2013) A general and simple method for obtaining  $R^2$  from  
508 generalized linear mixed-effects models. *Methods in Ecology and Evolution*, **4**, 133–142.
- 509 Naughton-Treves, L. (1998) Predicting Patterns of Crop Damage by Wildlife around Kibale National  
510 Park, Uganda. *Conservation Biology*, **12**, 156–168.
- 511 Owen, M. (1990) The damage-conservation interface illustrated by geese. *Ibis*, **132**, 238–252.
- 512 Percival, S.M. & Houston, D.C. (1992) The Effect of Winter Grazing by Barnacle Geese on Grassland

513 Yields on Islay. *Journal of Applied Ecology*, **29**, 35–40.

514 Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team. (2016) Linear and Nonlinear Mixed  
515 Effects Models. R package version 3.1-125.

516 R Core Team. (2016) *R: A Language and Environment for Statistical Computing*. R Foundation for  
517 Statistical Computing, Vienna, Austria.

518 Redpath, S., Gutiérrez, R., Wood, K. & Young, J. (2015) *Conflicts in Conservation: Navigating  
519 towards Solutions*. Cambridge University Press, Cambridge, UK.

520 Redpath, S. & Sutherland, W. (2015) The value of ecological information in conservation conflict.  
521 *Conflicts in conservation: Navigating towards solutions* (eds S. Redpath, R. Gutiérrez, K. Wood,  
522 & J. Young), pp. 35–45. Cambridge University Press, Cambridge, UK.

523 Redpath, S.M., Young, J., Evely, A., Adams, W.M., Sutherland, W.J., Whitehouse, A., Amar, A.,  
524 Lambert, R.A., Linnell, J.D.C., Watt, A. & Gutiérrez, R.J. (2013) Understanding and managing  
525 conservation conflicts. *Trends in Ecology and Evolution*, **28**, 100–109.

526 Richards, S.A. (2015) Likelihood and model selection. *Ecological statistics: Contemporary theory  
527 and application* (eds G. Fox, S. Negrete-Yankelevich, & V. Sosa), pp. 58–78. Oxford University  
528 Press, Oxford, UK.

529 Sedinger, J.S., Flint, P.L. & Lindberg, M.S. (1995) Environmental Influence on Life-History Traits:  
530 Growth, Survival, and Fecundity in Black Brant (*Branta Bernicla*). *Ecology*, **76**, 2404–2414.

531 Si, Y., Skidmore, A.K., Wang, T., De Boer, W.F., Toxopeus, A.G., Schlerf, M., Oudshoorn, M.,  
532 Zwerver, S., Van der Jeugd, H.P., Exo, K.-M. & Prins, H.H.T. (2011) Distribution of Barnacle  
533 Geese *Branta leucopsis* in relation to food resources distance to roosts and the location of  
534 refuges. *Ardea*, **99**, 217–226.

535 Sillero-Zubiri, C., Sukumar, R. & Treves, A. (2007) Living with wildlife: the roots of conflict and the  
536 solutions. *Key Topics in Conservation Biology* (eds D.W. Macdonald & K. Service), pp. 253–  
537 270. Blackwell Publishing Ltd, Oxford, UK.

538 Simonsen, C.E., Madsen, J., Tombre, I.M. & Nabe-Nielsen, J. (2016) Is it worthwhile scaring geese to  
539 alleviate damage to crops? – An experimental study. *Journal of Applied Ecology*, **53**, 916–924.

540 SNH. (2014) *Islay Sustainable Goose Management Strategy 2014-2024*.

541 Therkildsen, O.R. & Madsen, J. (2000) Energetics of Feeding on Winter Wheat Versus Pasture  
542 Grasses: A Window of Opportunity for Winter Range Expansion in the pink-footed Goose *Anser*  
543 *brachyrhynchus*. *Wildlife Biology*, **6**, 65–74.

544 Tombre, I.M., Eythórsson, E. & Madsen, J. (2013) Towards a solution to the goose-agriculture  
545 conflict in North Norway, 1988-2012: the interplay between policy, stakeholder influence and  
546 goose population dynamics. *PloS one*, **8**, e71912.

547 Treves, A., Naughton-Treves, L., Harper, E.K., Mladenoff, D.J., Rose, R.A., Sickley, T.A. &  
548 Wydeven, A.P. (2004) Predicting Human-Carnivore Conflict: a Spatial Model Derived from 25  
549 Years of Data on Wolf Predation on Livestock. *Conservation Biology*, **18**, 114–125.

550 White, R.M., Fischer, A., Marshall, K., Travis, J.M.J., Webb, T.J., di Falco, S., Redpath, S.M. & van  
551 der Wal, R. (2009) Developing an integrated conceptual framework to understand biodiversity  
552 conflicts. *Land Use Policy*, **26**, 242–253.

553 Woodroffe, R., Thirgood, S. & Rabinowitz, A. (2005) *People and Wildlife, Conflict or Co-Existence?*  
554 Cambridge University Press, Cambridge, UK.

555 Ydenberg, R.C. & Prins, H.H.T. (1981) Spring Grazing and the Manipulation of Food Quality by  
556 Barnacle Geese. *The Journal of Applied Ecology*, **18**, 443.

557 Young, J.C., Marzano, M., White, R.M., McCracken, D.I., Redpath, S.M., Carss, D.N., Quine, C.P. &  
558 Watt, A.D. (2010) The emergence of biodiversity conflicts from biodiversity impacts:  
559 characteristics and management strategies. *Biodiversity and Conservation*, **19**, 3973–3990.

560 Zuur, A.F., Ieno, E.N. & Elphick, C.S. (2010) A protocol for data exploration to avoid common  
561 statistical problems. *Methods in Ecology and Evolution*, **1**, 3–14.





563 **Tables**

564 **Table 1.** Summary of model predictors, including the time-lags considered, the hypotheses they relate

565 to and their hypothesised effects on goose numbers.

<b>Analysis</b>	<b>Name</b>	<b>Description</b>	<b>Mean (range)</b>	<b>Time-lags</b>	<b>Hypothesis</b>	<b>Effect</b>
Population-scale	Grass <sub>Islay</sub>	Area of improved grassland on Islay	7,040ha (5,331-8,331)	<i>t</i> -1; <i>t</i> -2	1	+
	Sheep <sub>Islay</sub>	Number of sheep on Islay	65,913 (47,040-78,537)	<i>t</i> -1; <i>t</i> -2	2	-
	Temp <sub>Islay</sub>	Mean Islay October-March temperature	5.0°C (3.5-6.5)	<i>t</i> -1; <i>t</i> -2	3	+
	Precip <sub>Islay</sub>	Total Islay October-March precipitation	1,105mm (829-1,462)	<i>t</i> -1; <i>t</i> -2	3	-
	Temp <sub>Aug</sub>	Mean August Greenland temperature	2.9°C (1.1-5.2)	<i>t</i> -1; <i>t</i> -2; <i>t</i> -3	4	+
	Precip <sub>Aug</sub>	Total August Greenland precipitation	16.6mm (0.2-63.7)	<i>t</i> -1; <i>t</i> -2; <i>t</i> -3	4	-
	Temp <sub>May</sub>	Mean May Greenland temperature	-6.4°C (-8.8- -3.3)	<i>t</i> -1; <i>t</i> -2; <i>t</i> -3	4	+
	Precip <sub>May</sub>	Total May Greenland precipitation	6.2mm (0-19.8)	<i>t</i> -1; <i>t</i> -2; <i>t</i> -3	4	-
Farm-scale	Abund <sub>Islay</sub>	Islay barnacle goose abundance	41,400 (28,500-53,000)	None	5	+
	Grass <sub>Farm</sub>	Area of improved grassland on farm	39.7ha (0-152.5ha)	None	6	+
	Roost <sub>Farm</sub>	Distance to roost from farm	4.6km (0.2-13.9)	None	7	-

566

567

568 **Table 2.** Best models of farm-specific intercepts (a) and coefficients for the effect of Islay barnacle  
 569 goose abundance (b). Standardised coefficients, numbers of parameters ( $K$ ), log-likelihoods (LL),  
 570  $\Delta$ AIC and  $R^2$  are displayed. Null models are displayed for comparison, or in the case that they are the  
 571 most parsimonious. See Table 1 for descriptions of predictors.

572 a) **Farm-specific intercept models**

	Occurrence		Count	
	Best	Null	Best	Null
<b>Grass<sub>Farm</sub></b>	$3.25x^{0.66}$		1.28	
<b>Roost<sub>Farm</sub></b>	$-5.34x^{0.09}$		-0.89	
<b>K</b>	5	2	4	2
<b>LL</b>	-158.36	-219.58	-263.80	-268.34
<b><math>\Delta</math>AIC</b>	0.00	116.44	0.00	5.09
<b><math>R^2</math></b>	0.69	-	0.09	-

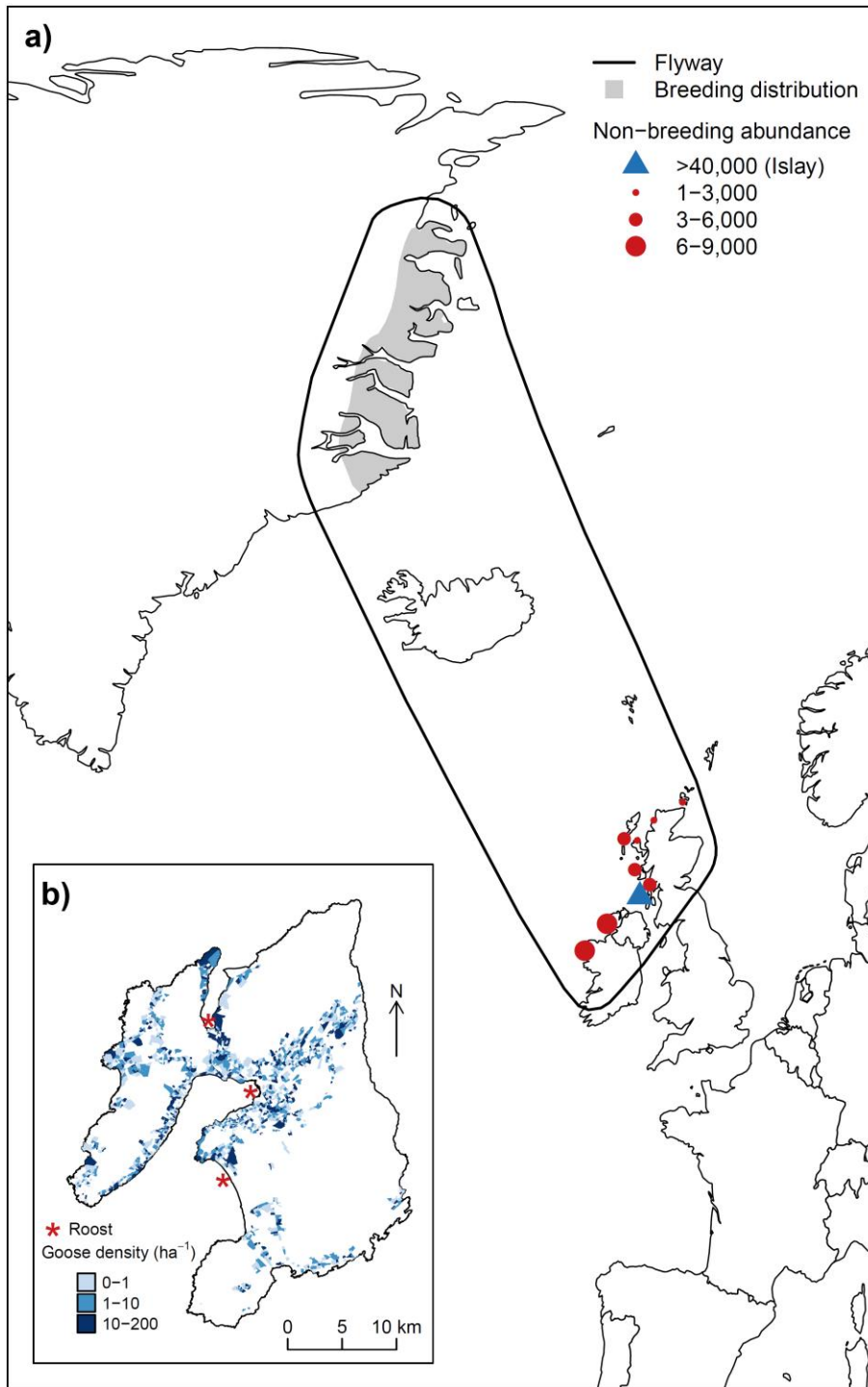
573

574 b) **Farm-specific abundance coefficient models**

	Occurrence		Count
	Best	Null	Null
<b>Grass<sub>Farm</sub></b>	-0.15		
<b>Roost<sub>Farm</sub></b>	$1.34x^{0.16}$		
<b>K</b>	4	2	2
<b>LL</b>	-61.02	-72.28	-251.18
<b><math>\Delta</math>AIC</b>	0.00	18.52	0.00
<b><math>R^2</math></b>	0.19	-	-

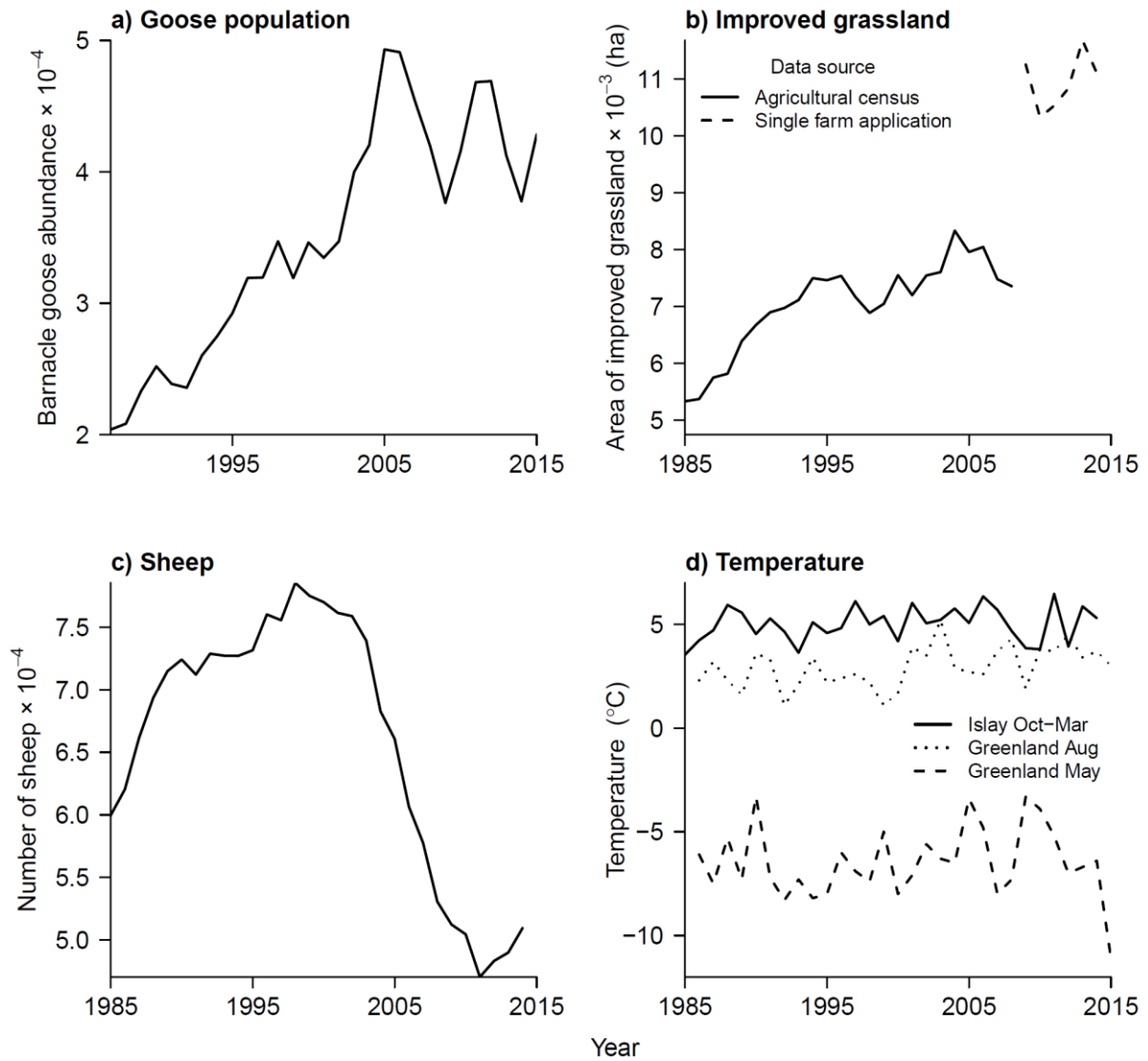
575

576



578

579 **Figure 1.** The distribution and abundance of Greenland barnacle geese across their range (a) and on  
 580 Islay, including locations of roosting sites (b). Goose abundances at non-breeding sites were summed  
 581 from Wildfowl and Wetlands Trust survey data (Mitchell & Hall 2013). Goose density per hectare of  
 582 farmland on Islay was calculated using Scottish Natural Heritage survey data.

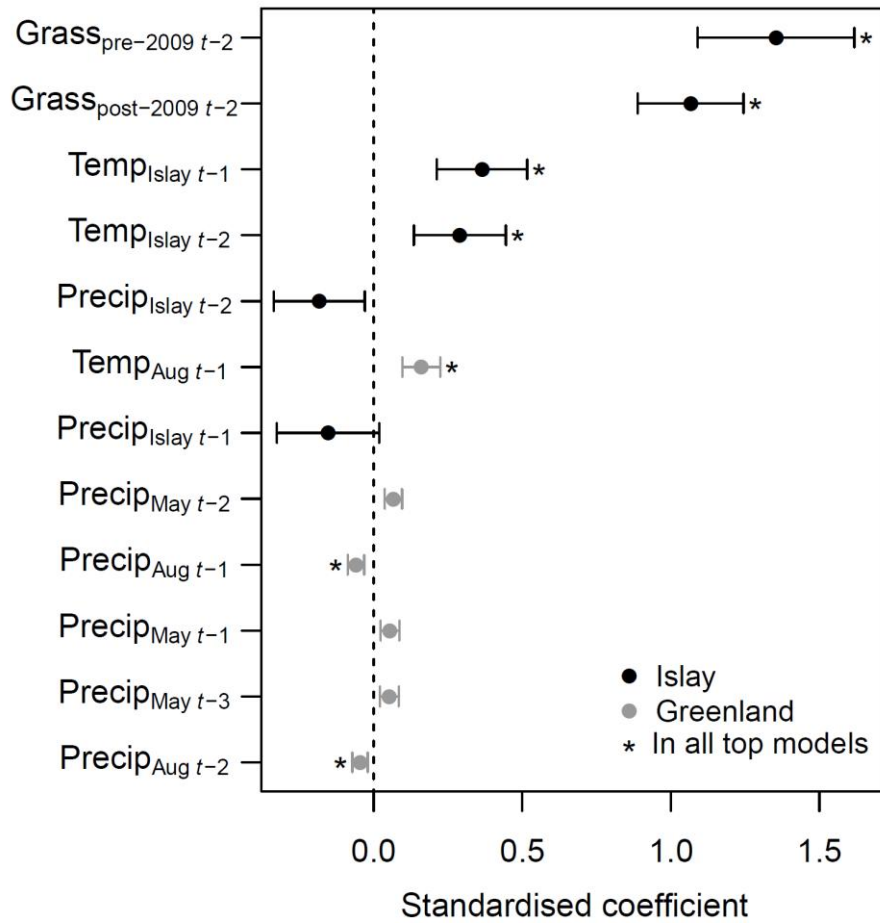


583

584 **Figure 2.** Annual variation in barnacle goose mean abundance on Islay (a), area of improved  
 585 grassland on Islay (b), number of sheep on Islay (c) and temperature on Islay and Greenland (d).

586 Where relevant, years represent the starting years of non-breeding seasons e.g., 2015 for the 2015-16  
 587 season.

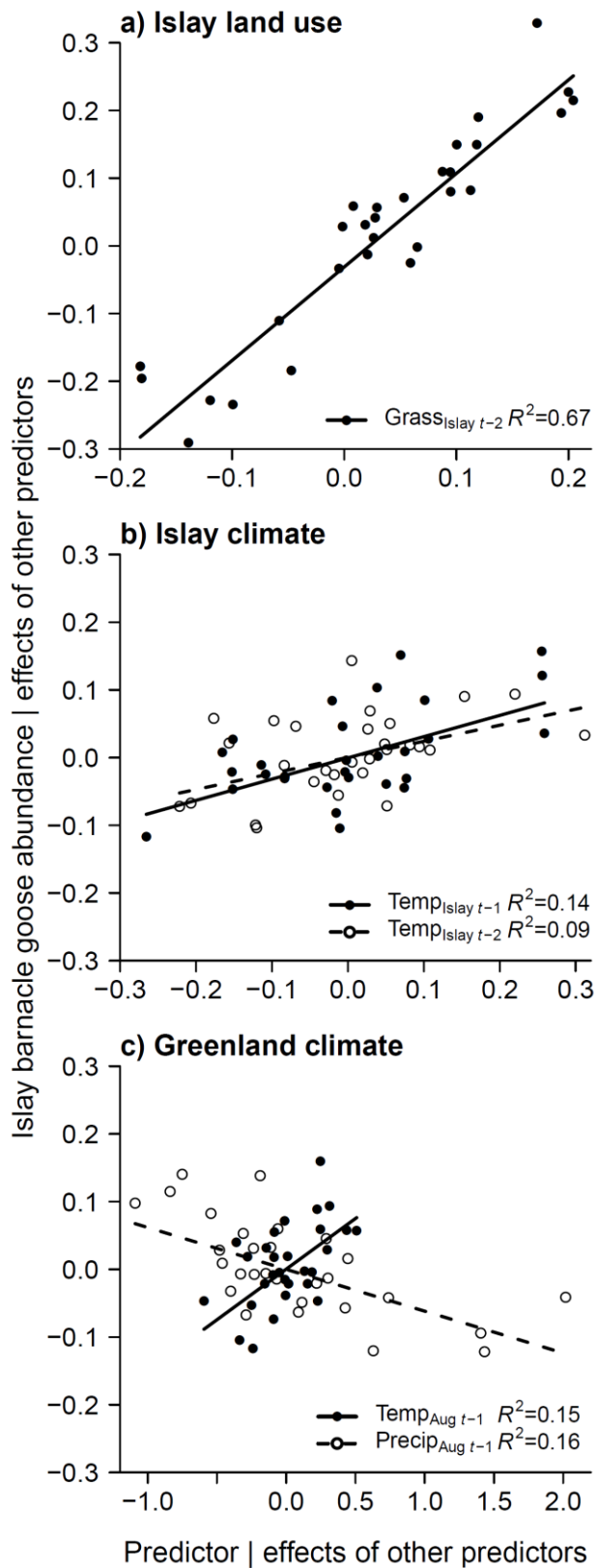
588



589

590 **Figure 3.** Standardised coefficients  $\pm$  95% confidence intervals for the best model of Islay barnacle  
 591 goose abundance, according to AIC. See Table 1 for descriptions of predictors.

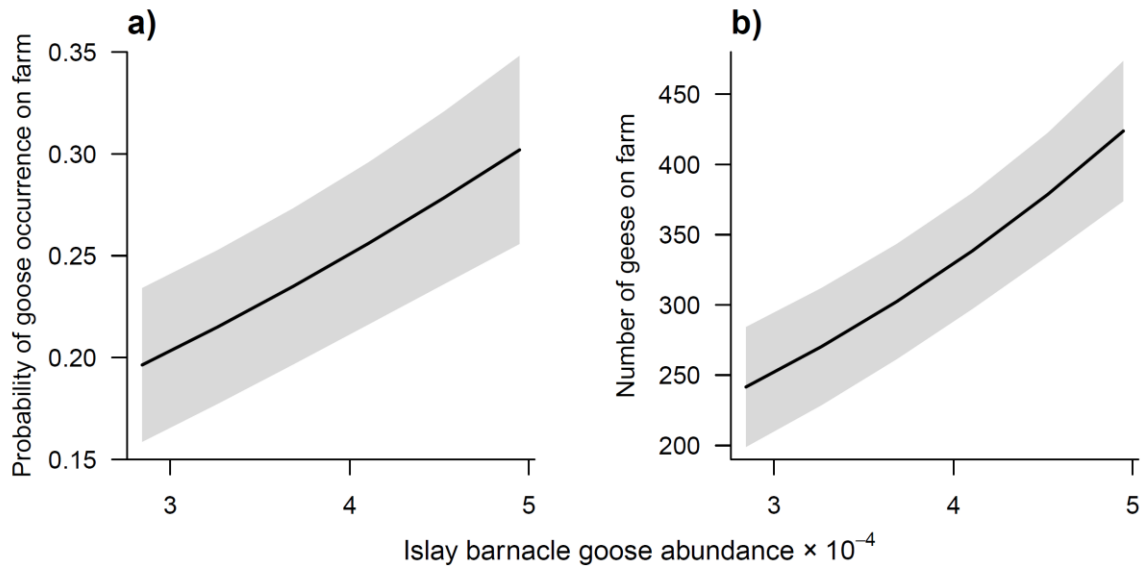
592



593

594 **Figure 4.** Partial effects of selected environmental predictors on Islay barnacle goose abundance.  $R^2$   
 595 displayed for each partial effect. See Table 1 for descriptions of predictors.

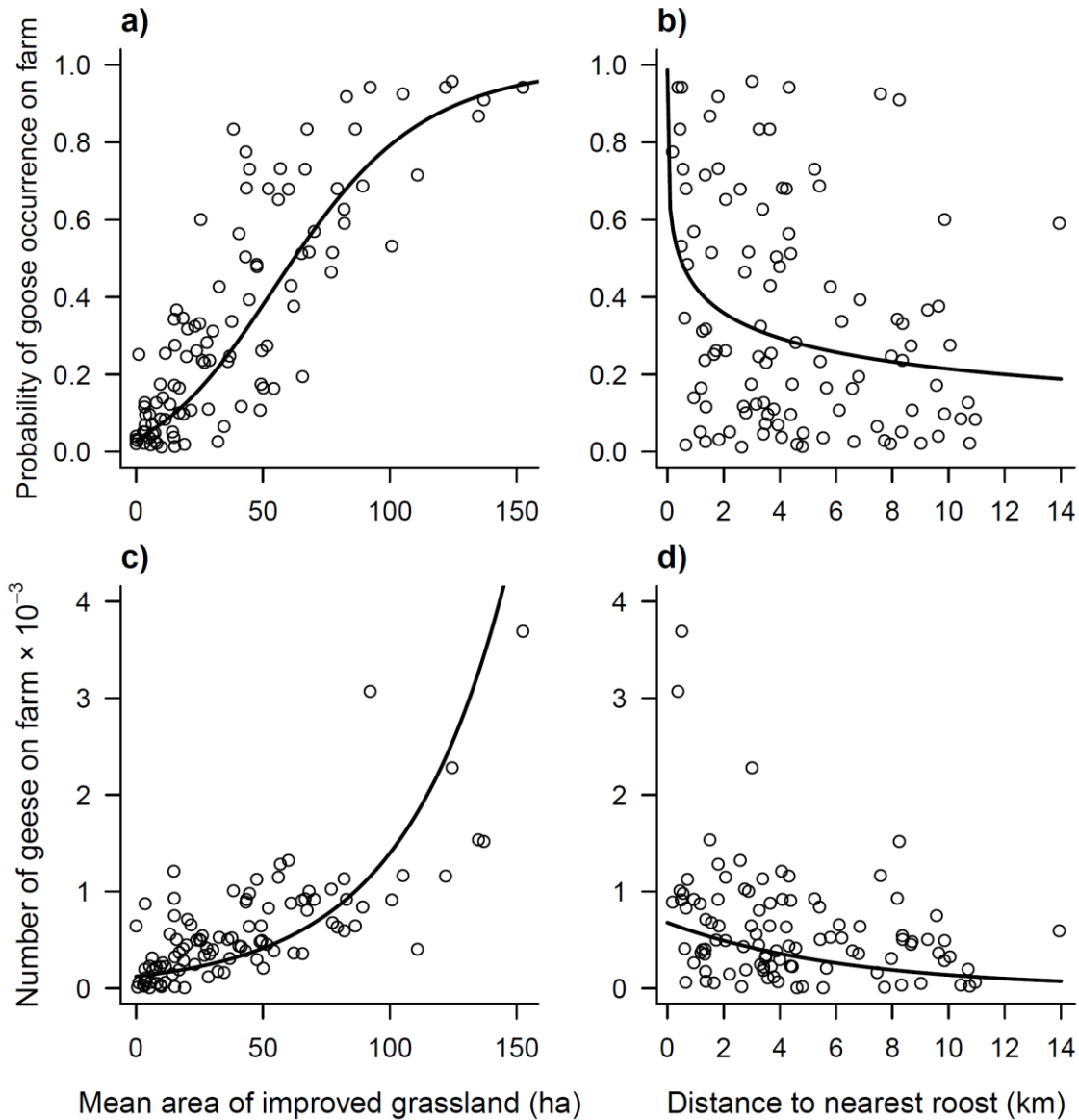
596



597

598 **Figure 5.** Fitted effects of Islay barnacle goose abundance on farm-scale barnacle goose probability of  
 599 occurrence (a) and number (b), from best occurrence and count models. Shaded areas represent fitted  
 600 values ± standard errors. Models were fitted for an average farm, with day set to an intermediate level  
 601 (5<sup>th</sup> December).

602

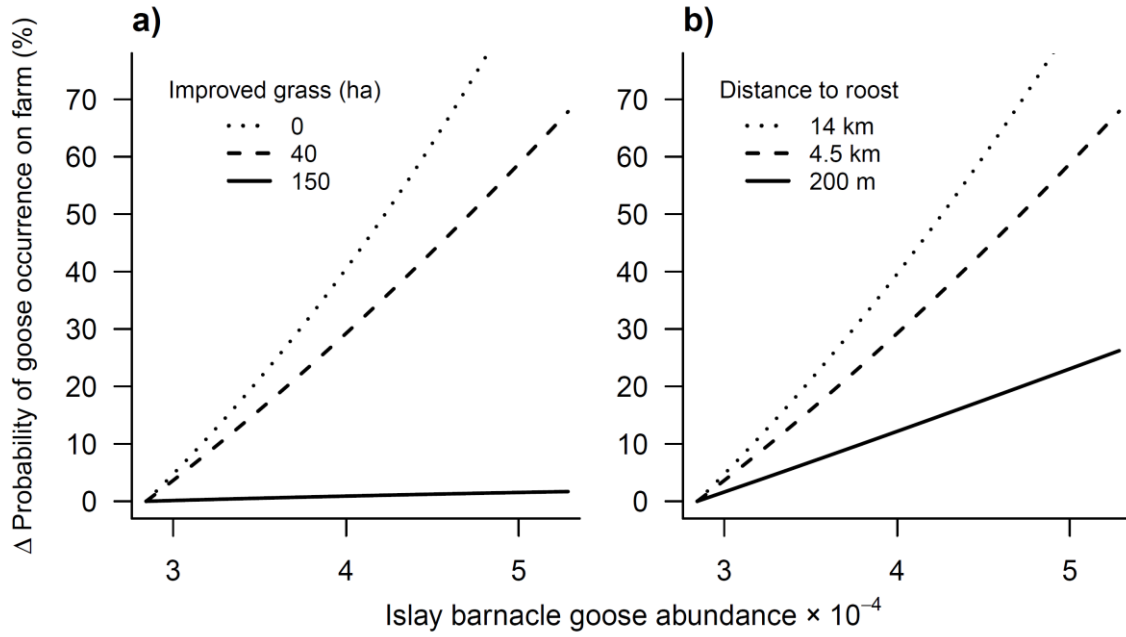


603

604 **Figure 6.** Fitted effects of mean area of improved grassland and distance to nearest roosting site on  
 605 farm-scale barnacle goose probability of occurrence (a-b) and number (c-d). Points are farm-specific  
 606 estimates from the best occurrence and count models. Lines are produced by incorporating the  
 607 relationships between farm-specific intercepts and grassland/distance to roost (see Table 2a) into the  
 608 fitted estimates. Models were fitted with Islay goose abundance and day set to intermediate levels  
 609 (4,000; 5<sup>th</sup> December).

610





611

612 **Figure 7.** Percentage change in farm-scale probability of barnacle goose occurrence with Islay goose  
 613 abundance, for farms with varying improved grassland area (a) and proximity to roosting site (b).  
 614 Fitted lines are produced by incorporating the relationships between farm-specific intercepts/slopes  
 615 and grassland/distance to roost (see Table 2) into the fitted estimates of the best occurrence model.  
 616 Models were fitted with day set to an intermediate level (5<sup>th</sup> December).

617

618 **SUPPORTING INFORMATION**

619 Additional Supporting Information may be found in the online version of this article:

620 **Table S1.** Population-scale model selection table.

621 **Table S2.** Farm-scale model selection table.

622 **Fig. S1.** Relative timings of variables.

623 **Fig. S2.** Temporal trends in climatic variables.

624 **Fig. S3.** Influence of day on farm-scale goose numbers.