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

2 **Scotland**

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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 the 1987/88 and
26 2015/16 seasons. Over the same period, the area of improved grassland increased, the number
27 of sheep 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. As geese numbers have increased they have spread to previously
37 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.* 2013,
52 2015). Such conflict can be highly damaging to both biodiversity and livelihoods, so represents a key
53 challenge for society (Sillero-Zubiri, Sukumar & Treves 2007). Human-wildlife conflict researchers
54 have often focused on quantifying the negative impacts of wildlife on humans and vice-versa
55 (Woodroffe, Thirgood & Rabinowitz 2005). In contrast, research into the processes leading to the
56 emergence of serious impacts and, in turn, conflict between stakeholders, is currently scarce (Young
57 *et al.* 2010). Such research could provide new insight into why conflict emerges and how it can be
58 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. Warming and drying climate on Islay
- 122 4. Warming and drying climate at 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 more reliable estimate of total
155 barnacle goose abundance. They were carried out by five pairs of trained surveyors in vehicles around
156 five pre-defined routes of sub-areas of Islay and were conducted simultaneously on each route, with
157 care taken to avoid double counting both within and among sub-areas by monitoring the movements
158 of flocks during surveys. Geese were counted from vehicles using binoculars and spotting scopes, at
159 distances of 20m-2km. The farms occupied by geese were recorded according to a system of unique
160 field codes, using maps of the study 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 $r(x|other\ predictors)$
205 against $r(y|other\ predictors)$, where $r(x|others)$ are residuals of a model regressing predictor x against
206 all other predictors (but not response y) and $r(y|others)$ 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 year 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 exploring the
239 effects of improved grassland area and distance to roost on variation among farms in i) goose
240 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 20th 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 wet 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 would only acted during the latter part of the study period – when sheep
355 numbers decreased dramatically – and was not detected as a result. Prior to 1998, there was an
356 increasing trend in sheep numbers, largely matching the trend in improved grassland. Another
357 potential driver of abundance increases is the implementation of stricter population protection and
358 subsequent reductions in hunting. However, the protection of barnacle geese by the EU's 1979 Bird's
359 Directive and the UK's 1981 Wildlife and Countryside Act occurred a number of years prior to this
360 study's time-period. Any population recovery would likely be evident for only a short period

361 following cessation of hunting, as has been shown for other goose species (Fox *et al.* 2005; Gauthier
362 *et al.* 2005).

363 ***Drivers of farm-scale goose dynamics***

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

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

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

388 farms further from roosts and those with less improved grassland. As a result, a wider range of farms
389 may have experienced goose damage as the population has grown.

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

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

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

415 climate, for example if reductions in goose numbers from culling were offset by increases in
416 recruitment due to milder breeding conditions. Using MSE it would be possible to take into account
417 the influence of climate change on the effectiveness of these competing management strategies.

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

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434 **AUTHORS' CONTRIBUTIONS**

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

437 **DATA ACCESSIBILITY**

438 The data used in this study are available from Dryad Digital Repository.

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560

561 **Tables**

562 **Table 1.** Summary of model predictors, including the time-lags considered, the hypotheses they relate
 563 to and their hypothesised effects on goose numbers.

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

564

565

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

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

| | Occurrence | | Count | |
|-------------------------------|-----------------|---------|---------|---------|
| | Best | Null | Best | Null |
| Grass_{Farm} | $3.25x^{0.66}$ | | 1.28 | |
| Roost_{Farm} | $-5.34x^{0.09}$ | | -0.89 | |
| K | 5 | 2 | 4 | 2 |
| LL | -158.36 | -219.58 | -263.80 | -268.34 |
| ΔAIC | 0.00 | 116.44 | 0.00 | 5.09 |
| R^2 | 0.69 | - | 0.09 | - |

571

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

| | Occurrence | | Count |
|-------------------------------|----------------|--------|---------|
| | Best | Null | Null |
| Grass_{Farm} | -0.15 | | |
| Roost_{Farm} | $1.34x^{0.16}$ | | |
| K | 4 | 2 | 2 |
| LL | -61.02 | -72.28 | -251.18 |
| ΔAIC | 0.00 | 18.52 | 0.00 |
| R^2 | 0.19 | - | - |

573

574

575 **FIGURE LEGENDS**

576 **Figure 1.** The distribution and abundance of Greenland barnacle geese across their range (a) and on
577 Islay, including distributions of roosting sites (b). Goose abundances at wintering sites were
578 calculated using Wildfowl and Wetlands Trust survey data (Mitchell & Hall 2013). Goose density per
579 hectare of farmland on Islay was calculated using Scottish Natural Heritage survey data.

580 **Figure 2.** Annual variation in barnacle goose mean abundance on Islay (a), area of improved
581 grassland on Islay (b), number of sheep on Islay (c) and temperature on Islay and Greenland (d).
582 Where relevant, years represent the starting years of wintering seasons e.g., 2015 for the 2015-16
583 season.

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

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

588 **Figure 5.** Fitted effects of Islay barnacle goose abundance on farm-scale barnacle goose probability of
589 occurrence (a) and number (b), from best occurrence and count models. Shaded areas represent fitted
590 values \pm standard errors. Models were fitted for an average farm, with day set to an intermediate level
591 (5th December).

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

598 **Figure 7.** Percentage change in farm-scale probability of barnacle goose occurrence with Islay goose
599 abundance, for farms with varying improved grassland area (a) and proximity to roosting site (b).

600 Fitted lines are produced by incorporating the relationships between farm-specific intercepts/slopes
601 and grassland/distance to roost (see Table 2) into the fitted estimates of the best occurrence model.
602 Models were fitted with day set to an intermediate level (5th December).

603

604 **SUPPORTING INFORMATION**

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

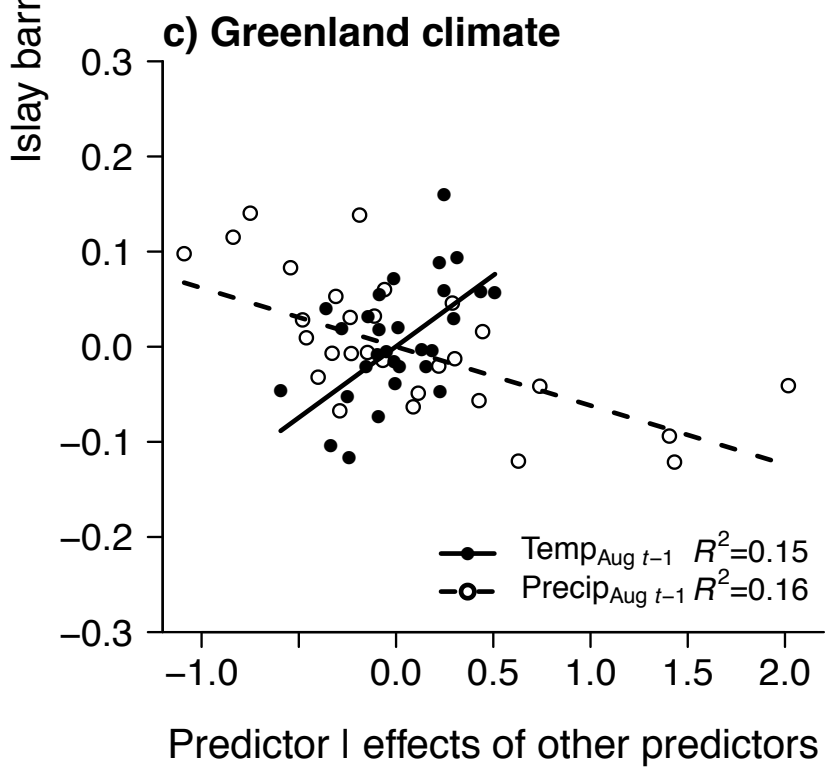
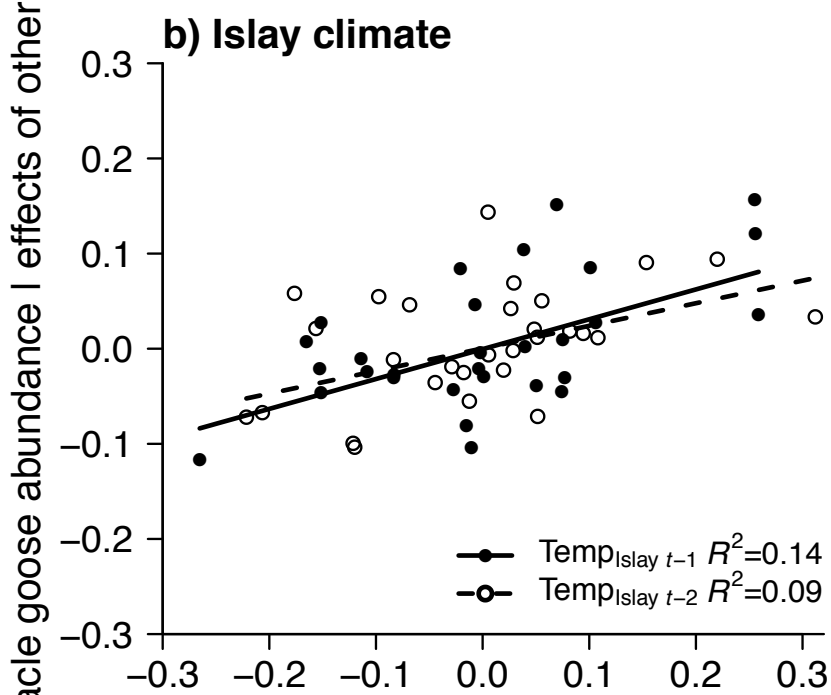
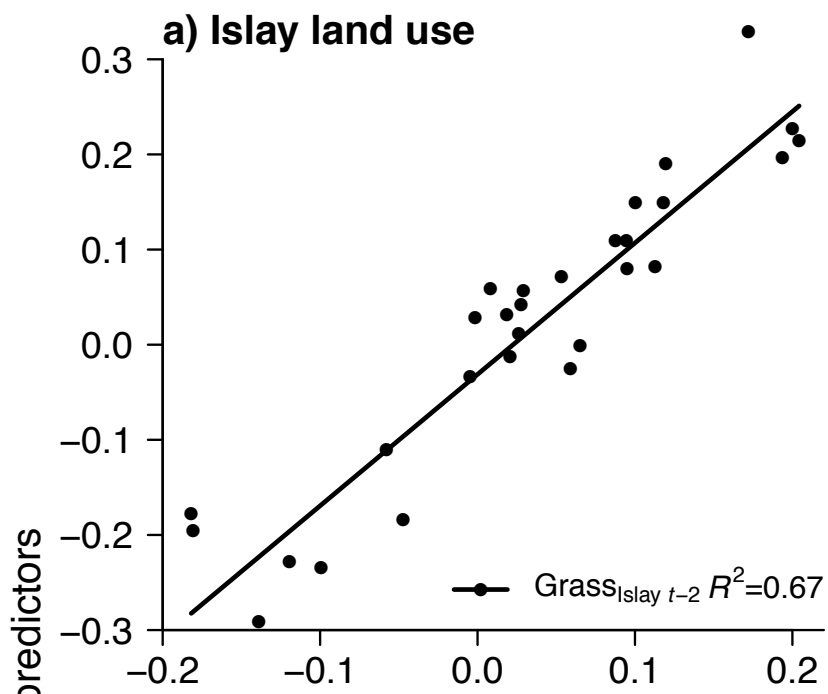
606 **Table S1.** Population-scale model selection table.

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

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

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

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



a)

