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Temperature and precipitation at migratory grounds influence demographic trends of an Arctic-breeding bird

Running title: Weather shifts and Arctic-breeding birds

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Author contributions

SD, DC and BMcM conceived ideas and designed methodology. DC founded the ringing project. DC and AW ringed birds for analysis at Inishkea/Greenland and at Inishkea/Donegal respectively. DC was responsible for collating resightings and collecting all productivity data and made these data available for analysis. SD analysed the data, with assistance from SB, RI and BMcM and led the writing of the manuscript, while all authors contributed critically to drafts and gave final approval for publication.

Data accessibility statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Abstract

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Anthropogenic climate disruption, including temperature and precipitation regime shifts, has been linked to animal population declines since the mid-20th century. However, some species, such as Arctic-breeding geese, have thrived during this period. An increased understanding of how climate disruption might link to demographic rates in thriving species is an important perspective in quantifying the impact of anthropogenic climate disruption on the global state of nature. The Greenland barnacle goose (*Branta leucopsis*) population has increased ten-fold in abundance since the mid-20th century. A concurrent weather regime shift towards warmer, wetter conditions occurred throughout its range in Greenland (breeding), Ireland and Scotland (wintering) and Iceland (spring and autumn staging). The aim of this study was to determine the relationship between weather and demographic rates of Greenland barnacle geese to discern the role of climate shifts in the population trend. We quantified the relationship between temperature and precipitation and Greenland barnacle goose survival and productivity over a 50 year period from 1968 to 2018. We detected significant positive relationships between warmer, wetter conditions on the Icelandic spring staging grounds and survival. We also detected contrasting relationships between warmer, wetter conditions during autumn staging and survival and productivity, with warm, dry conditions being the most favourable for productivity. Survival increased in the latter part of the study period, supporting the possibility that spring weather regime shifts contributed to the increasing population trend. This may be related to improved forage resources, as warming air temperatures have been shown to improve survival rates in several other Arctic and northern terrestrial herbivorous species through indirect bottom-up effects on forage availability.

Keywords: Barnacle Goose, *Branta leucopsis*, Cormack-Jolly-Seber (CJS) model, climate disruption, productivity, survival

Introduction

Some taxa are thriving since the mid-20th century despite the significant biodiversity decline that has occurred throughout the world's major biomes (Ceballos, Ehrlich, & Dirzo, 2017; Inger et al., 2015; Rosenberg et al., 2019). Much of the recent literature concerns the negative impacts of climate shifts on animal population trends across a variety of taxonomic classes (e.g. Albouy et al., 2020; Crewe, Mitchell, & Larrivée,

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2019; Saalfeld et al., 2019; Wismer, Tebbett, Streit, & Bellwood, 2019). Indeed, the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (Díaz et al., 2019; IPBES, 2019) identified anthropogenic climate disruption as one of the main drivers of the global state of nature. However, shifts in the temperature and precipitation regime towards warmer, wetter conditions can benefit species' demographic rates through direct physiological effects or through indirect effects frequently linked to food availability. Among terrestrial mammals, Vetter et al. (2015) and Weiskopf et al. (2019) link increased abundance of wild boar (*Sus scrofa)* in Europe and white-tailed deer (*Odocoileus virginianus*) in North America to improved survival during ambient, warmer winters and to bottom-up effects of warmer temperatures on forage plant availability. Similarly, warmer, wetter weather improves winter survival of waterbirds in northern Europe, likely due to reduced energetic and thermoregulatory costs (Pavón-Jordán, Santangeli, & Lehikoinen, 2017). Warmer early breeding season temperatures are found to improve productivity in pink-footed geese (*Anser brachyrhynchus*) and snow geese (*Anser caerulescens*), likely driven by earlier access to forage and nesting sites because of early snow melt (Jensen, Madsen, Johnson, & Tamstorf, 2014; Morrissette, Bêty, Gauthier, Reed, & Lefebvre, 2010). In marine systems, Henderson and Seaby (2005) found that increased sea temperature during warmer winters in England led to an exponential increase in sole (*Solea solea*) abundance due to faster development. Lynam et al. (2011) also linked *Aurelia* and *Cyanea* jellyfish abundance in the Irish Sea to increased sea temperatures, although the mechanisms behind this trend were unknown. Undoubtedly, it is important to consider species that are thriving alongside those in decline in order to fully comprehend the impact of anthropogenic climate disruption on the global state of nature. It is especially important in vulnerable ecosystems such as the Arctic, where the speed and magnitude of climate disruption is amplified (Praetorius, Rugenstein, Persad, & Caldeira, 2018).

An unprecedented increase in the abundance of Anserinae (true geese) in Europe and North America since the mid-20th century has been observed (e.g. Ross's goose (*Anser rossii*), with numbers increasing by 11.7% per annum between 1975 and 2014) (Fox & Madsen, 2017; Fox & Leafloor, 2018; U.S. Fish and Wildlife Service, 2018). Barnacle geese (*Branta leucopsis*) are among the most successful: census counts show the Greenland barnacle goose population alone has increased ten-fold

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since 1959 (Doyle, Walsh, McMahon, & Tierney, 2018; Mitchell & Hall, 2018). This population breeds in north-east Arctic Greenland and migrates to Ireland and Scotland for winter, staging in Iceland during spring and autumn (Figure 1a). The population growth has been attributed to legislation introduced in the 1980s and agricultural land-use change since the 1950s. The legislation involved protection from winter season hunting and provision of wildlife reserves at key wintering sites (Bainbridge, 2017; Fox, Ogilvie, Easterbee, & Bignal, 1990). Grassland crop intensification using modern agricultural technology also provided an abundant novel forage resource for herbivorous waterfowl in Europe (Fox & Abraham, 2017). However, the role of climate shifts in this exponential population trend is also of great interest, as climate shifts since the mid-20th century have shaped trends in many other animal species.

The most recent Intergovernmental Panel on Climate Change assessment (IPCC, 2013) reports a shift towards a warmer, wetter weather regime throughout Greenland and northern Europe since the mid-20th century that coincides with the increase in Greenland barnacle goose abundance. Existing evidence (e.g. Cabot & West, 1973; Fox & Gitay, 1991; Mason, Keane, Redpath, & Bunnefeld, 2017) suggests climate shifts could strongly influence Greenland barnacle goose survival and productivity and, hence, abundance. The Isle of Islay in Scotland (Figure 1b) is the largest wintering site for Greenland barnacle geese, supporting around half of the wintering population in 2018 (Mitchell & Hall, 2018). Previous research on Islay indicates that goose abundance varies with weather conditions: it is positively associated with warmer, drier conditions in Scotland in winter and in Greenland in August (Mason, Keane, Redpath, & Bunnefeld, 2017). However, the effect of weather conditions on individual demographic rates is only known in part. Fox and Gitay (1991) found that the proportion of juveniles on Islay from 1961 to 1986 was positively associated with warmer, wetter conditions in Scotland in April, but warmer, drier conditions in Iceland in spring and drier conditions in Greenland in May. An earlier study at a second key wintering site on the Inishkea Islands in Ireland (Figure 1b), which supported up to 7% of the total population, also found that mean brood size from 1963 to 1971 was positively associated with warmer conditions in Ireland in winter (Cabot & West, 1973). To our knowledge, there are no similar analyses of survival in the Greenland barnacle goose and the Agreement on the Conservation of African-Eurasian

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Migratory Waterbirds (AEWA) International Single Species Management Plan for the Barnacle Goose (Jensen, Madsen, Nagy, & Lewis, 2018) notes the limited amount of demographic data available outside Islay. Weather conditions often have contrasting effects on survival and productivity rates within a population (e.g. high June North Atlantic Oscillation indices were positively associated with survival and negatively associated with productivity rates of light-bellied Brent goose (*Branta bernicla hrota*) in Canada; Cleasby et al., 2017), therefore testing multiple demographic rates provides a greater understanding of variation in abundance that may not be apparent from a single demographic rate alone.

The role of climate shifts in thriving populations receives less attention compared to declining populations. The aim of this study was to determine the relationship between weather and demographic rates of a species thriving since the mid-20th century, to understand the role of climate shifts in the population trend. Using an extensive 50 year demographic dataset from 1968 to 2018, we quantify the effects of temperature and precipitation on Greenland barnacle goose survival and productivity. This analysis provides new insight into factors affecting survival and expands on previous research by Cabot and West (1973) and Fox and Gitay (1991) using more recent productivity data from Inishkea (proportion juveniles and mean brood size in the overwintering population). The results add to our understanding of the impact of anthropogenic climate disruption on animal populations.

Materials and methods

Study system

In the present study, we define the breeding-year as October to October and categorise five life history stages based on breeding biology: winter (October to March on wintering grounds in Ireland and Scotland), spring (April and May on staging grounds in Iceland), early summer (May to July on breeding grounds in Greenland), late summer (August and September on breeding grounds in Greenland) and autumn (September and October on staging grounds in Iceland) (Figure 1a). The five stages reflect (i) overwintering, (ii) pre-breeding spring migration, (iii) nesting and gosling care, (iv) post-breeding summer and (v) autumn migration. We divided the analysis into life history stages to avoid a large number of

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covariates in one model that may introduce multicollinearity, yet retain detailed resolution and account for spatial movement.

Data collection

Between breeding-year 1968 and 2017, 574 adult male, 585 adult female, 50 juvenile male and 124 juvenile female Greenland barnacle geese were captured in Greenland and Ireland. Captures took place annually, but the timing, locations and numbers captured varied (see Supporting Information S1 for full details). All geese were aged based on plumage (juvenile up to one year or adult), sexed by cloacal examination and tagged with individual three-digit alpha-numeric leg-rings. Subsequent resightings, recaptures or other recoveries of tagged geese, were submitted by a network of volunteers from all parts of the range throughout the year. The initial captures and 22,849 resightings/recaptures/recoveries were used to construct encounter histories at breeding-year intervals for each goose. Annual survival rates based on these encounter histories were generated using Cormack-Jolly-Seber (CJS) models (Seber, 1982) conducted in Programme MARK 8.2 (White & Burnham, 1999) via the R statistical language and environment 3.5.1 (R Core Team, 2018) using the RMark package 2.2.5 (Laake, 2013). The two CJS parameters were apparent survival (ϕ) and encounter probability (p), as defined by Lebreton et al. (1992).

Two measures of productivity were estimated to allow for comparison to previous studies: proportion juveniles and mean brood size in the overwintering population on Inishkea from breeding-year 1968 to 2017. Data were collected annually through ~16 days of observation between October and March. The exact timing and length of collection varied due to restricted site access (e.g. storms).

Mean temperature (°C) and accumulated precipitation (mm) values recorded at weather stations were included as covariates in our analysis. To cover the range of the geese, values from two weather stations in each part of the range were averaged: 54°13'N 10°0'W and 56°30'N 6°52'W (wintering grounds; Met Éireann and Met Office), 65°41'N 18°06'W and 64°16'N 15°13'W (staging grounds; Veðurstofa Íslands) and 76°46'N 18°40'W and 70°29'N 21°57'W (breeding grounds; Danish Meteorological Institute). Values were then averaged for each life history stage.

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Table 1 provides a summary of all environmental covariates and Supporting Information S2 provides full details of data acquisition.

Data on the overall population trend were drawn from the International Census of Greenland barnacle geese. Full censuses were conducted 10 times within the 1968 to 2018 study period at approximately five-year intervals (see Mitchell & Hall (2018) and references within). The censuses provide the total number of geese in breeding-year 1972, 1977, 1982, 1987, 1993, 1998, 2002, 2007, 2012 and 2018, from which the population trend can be gauged.

Trends in environmental covariates and demographic rates

Survival and productivity rates over time were non-linear. Residual plots indicated that models assuming a fixed linear form of the relationship between survival or productivity and breeding-year did not adequately describe the data, yet the specific functional form remained unclear. Because of this, generalised additive models (GAM) in R with a thin plate regression spline for breeding-year were used to investigate and visualise patterns in survival, proportion juveniles and mean brood size over time. A logit link and beta distribution were specified for survival and proportion juveniles (because these assumed values within the interval 0-1) and an identity link and gaussian distribution were specified for mean brood size. All population rates are presented in Figure 2, with values available in Supporting Information S3.

The long-term trend in each environmental covariate was tested using linear regression in R (Table 1 and Supporting Information S2). All temperature covariates showed significant increases since 1968. Precipitation covariates also showed significant increases, although increases during spring and autumn did not become evident until the late 1970s/early 1980s.

Statistical models

The statistical analysis comprised four tests: i) survival ii) proportion juveniles and iii) mean brood size as a function of environmental covariates, and (iv) the proportion of the overall population trend explained by environmental covariates. As the environmental covariates were in time series and on assorted scales, each variable

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was detrended by subtracting the least-squares regression fitted values and then scaled by subtracting the mean and dividing by the standard deviation. The former removes systematic trends from data to reveal annual fluctuations, whilst the latter standardises measurements on different scales to test for meaningful additive effects.

i) Goodness of fit of the survival data to our global CJS model was tested using program RELEASE (Burnham, Anderson, White, Brownie, & Pollock, 1987). The data violated the assumption of equal probability of recapture. This individual heterogeneity in detection among tagged geese could have a number of biological explanations. Because geese are monogamous, tags on pair-bonded couples are likely to be seen together. Also, there may be bias in data collection when birdwatchers are attracted to certain sites with predictable aggregations of geese and because geese are faithful to particular sites. A preliminary analysis was conducted to test if ϕ or p were dependent on age, sex and time and if there were interactive effects of age and sex. This revealed that ϕ was sex-dependent and p was age-dependent, therefore these parameters were included in the main analysis. In the main analysis, a full model was fitted to test if ϕ was dependent on temperature or precipitation or if there were interactive effects of temperature and precipitation:

$$\phi(\sim \text{sex} + \text{Temp} * \text{Prec})\ p(\sim \text{age})$$

ii) The relationship between proportion juveniles and environmental covariates was analysed using beta regression models (betareg package 3.1-1; Cribari-Neto & Zeileis, 2010) in R, with a logit-link for the mean parameter and identity-link for the precision parameter. Beta regression is advantageous to transformations (such as log) as it better accommodates natural heteroscedasticity and asymmetry in 0-1 data (Ferrari & Cribari-Neto, 2004). A full model was fitted to test the relationship between proportion juveniles and the interaction of temperature and precipitation:

$$\text{betareg}(\text{proportion juveniles} \sim \text{Temp} * \text{Prec})$$

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iii) The relationship between mean brood size and environmental covariates was analysed using linear regression models in R. A full model was fitted to test the relationship between mean brood size and the interaction of temperature and precipitation:

lm(mean brood size ~ Temp * Prec)

Model simplification was conducted for each of the full models described above. The significance of the interaction term and the individual covariates were determined using likelihood ratio tests until all uninformative parameters were removed and results were derived from the final model. This process was repeated for each of the five life history stages.

iv) In the final stage of our analysis, we quantified what proportion of the Greenland Barnacle Goose population trend could be explained by significant environmental covariates identified in the preceding models. Census counts were modelled as a function of the selected covariates using generalised linear regression with quasi-poisson errors, as census counts were overdispersed and the sample size was small. Because censuses were conducted at five-year intervals, we averaged covariate values for each interval rather than estimating intra-interval population size by linear interpolation. Despite a much smaller sample size (n = 10 versus n = 50), this method was preferable because interpolated values produced non-random patterns in model residuals and are unlikely to be representative of the true population size. The proportion of the Greenland barnacle goose population trend explained by the selected covariates was taken as the proportion deviance explained (adjusted-D2; Guisan & Zimmermann, 2000) by the model.

Results

Survival

Apparent female survival (mean 0.88 ± 0.004) was marginally but significantly higher than male survival (mean 0.86 ± 0.005). Adult encounter probability (0.65 ± 0.006) was significantly higher than juvenile encounter probability (0.53 ± 0.017). Annual survival was derived from female values extracted from the ϕ(~ sex + time) p(~ age) model (Figure 2a). The GAM indicated an association between annual survival and

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breeding year ($P < 0.001$). Plotting the smoothed term of the fitted GAM suggests an increase in survival over time is evident in the latter part of the study period (Figure 2b).

The final spring model included additive effects of the covariates temperature (β = 0.16, 95% CI 0.07 - 0.26) and precipitation (β = 0.35, 95% CI 0.24 - 0.47). A 1 s.d. (standard deviation) increase in spring temperature was associated with an 18% relative increase in survival (Figure 3a), while a 1 s.d. increase in spring precipitation was associated with a 42% relative increase (Figure 3b). These units represent large but relevant regime shifts: 1 s.d. in spring temperature and precipitation in Iceland equates to 1.2°C and 46mm, while mean spring temperature and precipitation in Iceland over the study period was 4.2°C and 85mm. The final autumn model also included additive effects of temperature (β = -0.16, 95% CI -0.26 - -0.07) and precipitation (β = 0.22, 95% CI 0.14 - 0.30). In contrast to the effect of spring temperature, a 1 s.d. increase in autumn temperature was associated with an 15% relative decrease in survival (Figure 3c). Similar to the effect of spring precipitation, a 1 s.d. increase in autumn precipitation was associated with a 25% relative increase in survival (Figure 3d). A 1 s.d. in autumn temperature and precipitation in Iceland equates to 1.2°C and 74mm, while mean autumn temperature and precipitation over the study period was 5.5°C and 171mm.

Productivity

The mean proportion of juveniles on Inishkea during the study period was 0.07 (range 0.01 - 0.19) (Figure 2c). The GAM did not indicate an association between annual proportion juveniles and breeding year ($P = 0.36$) and a plot of the smoothed term suggests a stable trend over time (Figure 2d). The final autumn model included additive effects of the covariates temperature (β = 0.16, 95% CI -0.01 - 0.33) and precipitation (β = -0.30, 95% CI -0.47 - -0.13). A 1 s.d. increase in autumn temperature was associated with a 17% relative increase in the proportion juveniles (Figure 3e), while a 1 s.d. increase in autumn precipitation was associated with a 26% relative decrease (Figure 3f). This model explained 17% of variation in the annual proportion juveniles (pseudo-R^2).

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Mean brood size on Inishkea during the study period was 1.81 young (range 1.00 - 2.26) (Figure 2e). Although the GAM did not indicate an association between annual mean brood size and breeding year (P = 0.23), a plot of the smoothed term suggests a slight decrease over time (Figure 2f). Similar to proportion juveniles, the final autumn model included additive effects of the covariates temperature and precipitation. A 1 s.d. increase in autumn temperature was associated with a 0.11 ± 0.04 increase in mean brood size (Figure 3g), while a 1 s.d. increase in autumn precipitation was associated with a -0.10 ± 0.04 decrease (Figure 3h). This model explained 13% of variation in mean brood size (adjusted-R^2).

Total population trend

The environmental covariates of interest identified in the survival and productivity models were: $spring_{Temp}$, $spring_{Prec}$, $autumn_{Temp}$ and $autumn_{Prec}$. The association between these covariates and census counts was analysed in two separate models to avoid variance inflation. A model containing additive effects of spring temperature and spring precipitation had an adjusted-D^2 of 0.73, indicating spring weather explains 73% of the Greenland barnacle goose population trend. A second model containing additive effects of autumn temperature and autumn precipitation had an adjusted-D^2 of 0.47, indicating autumn weather explains 47% of the population trend (note that each model must be interpreted separately and the adjusted-D^2 of the two models cannot be considered additively).

Discussion

This study examined demographic trends in Greenland barnacle geese during a time of intense anthropogenic climate disruption from 1968 to 2018. Census counts demonstrate that the population increased markedly over this period. Based on our capture-mark-recapture data, survival also increased and is positively associated with temperature and precipitation on the spring migration staging grounds, while weather station records confirm that spring temperature and precipitation increased on the staging grounds over the study period. Taken together, we suggest that weather regime shifts towards warmer, wetter spring conditions in Iceland improved survival rates. Barnacle goose population growth rate is most strongly influenced by adult survival (Layton-Matthews et al., 2019), therefore even a modest increase in survival rate may have contributed, in part, to the thriving population trend. This is

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further supported in that spring weather could explain 73% of variation in census counts (bearing in mind that *n* = 10). This result is in contrast to the negative impacts of anthropogenic climate disruption on animal population trends frequently reported in the literature. For example, the increasing Greenland barnacle goose trend contrasts sharply with the declining trend observed in white-fronted geese (*Anser albifrons flavirostris*) that breed in west Greenland. Boyd and Fox (2008) suggest that increased precipitation in west Greenland has had a negative impact on productivity in this species since the 1980s, possibly because snow cover inhibits access to forage plants in the early breeding season. Such contrasts among closely related species highlight the importance of determining links between climate disruption and demographic rates, even among species with subtle life history variations.

In addition, our analysis detected contrasting effects of autumn migration weather conditions on survival and productivity. Based on observations at a key wintering site on Inishkea, productivity remained stable or decreased slightly over the study period. Autumn temperature was positively associated with productivity but negatively associated with survival, while autumn precipitation was negatively associated with productivity but positively associated with survival. Weather station records confirm that autumn temperature and precipitation also increased on the staging grounds over the study period and our model indicates that autumn weather explained 47% of variation in census counts (*n* = 10). Taken together, we suggest that conditions during autumn migration influence the number of juveniles that ultimately survive to be recruited into the overwintering population the following breeding-year. We further suggest that there is trade-off between survival and productivity related to weather conditions during this period of the annual cycle, with warm, dry conditions being most favourable for productivity rate and least favourable for survival rate. Parental investment and survival trade-offs may occur during autumn migration if the presence of offspring delays departure or increases danger en route, as suggested by Cleasby et al. (2017)

Global change and herbivorous species

Greenland barnacle goose survival was positively affected by above average mean temperature and accumulated precipitation during April and May on the staging

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grounds in Iceland. This could be related to the improved natural and agricultural forage growth observed in Iceland following weather regime shifts (Helgadóttir, Eythórsdóttir, & Jóhannesson, 2013). In a recent study of Svalbard barnacle geese, Tombre et al. (2019) suggest that increased temperatures in the Norwegian spring staging grounds improved forage growth at more sites, reducing competition by allowing geese to colonise additional areas and contributing to the dramatic increase in overall population size. Svalbard pink-footed goose survival was similarly positively associated with warmer springs in their Norwegian staging grounds (Kéry, Madsen, & Lebreton, 2006), suggesting that conditions during spring migration are an important factor in annual survival of Arctic-breeding Anserinae. Based on six species of Arctic-breeding migrant waders, Weiser et al. (2018) also concluded that adult survival rates were closely associated with conditions at the staging grounds. However, it must be recognised that tagging and resighting of birds in our analysis encompassed only a subset of a larger population. Because this population is open, permanent emigration among sites and leg-ring loss could be misconstrued as mortality. Therefore, these values represent minimum apparent survival estimates.

Improved forage growth and protein content as a result of weather regime shifts has been a significant factor in population trends of other thriving herbivorous birds and mammals. Kéry et al. (2006) attributes improved survival in pink-footed geese to improved forage growth during warmer and wetter winters. Albon et al. (2017) found that female reindeer (*Rangifer tarandus platyrhynchus*) in Svalbard gained heavier body weights following warm summers with increased forage biomass. The analysis indicated that June and July temperature accounted for 36% of variation in body mass at summer's end. Longer growing seasons and vegetation shifts due to warmer temperatures have allowed sub-Arctic herbivores such as moose (*Alces* spp.). and snowshoe hare (*Lepus americanus*) to extend their range northward (Ewacha, Roth, & Brook, 2014; Tape, Gustine, Ruess, Adams, & Clark, 2016). In temperate climates, Vetter et al. (2015) demonstrate how warmer winters indirectly contributed to the boom in wild boar across Europe through increased food availability. Beech mast years, which are highly beneficial to the wild boar, have also increased in frequency since the 1980s. Weather shifts are also the primary driver of range expansion in white-tailed deer in North America: longer plant growing seasons as a result of warming temperatures improved survival (Dawe & Boutin, 2016).

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Clearly, terrestrial herbivores are prevalent among thriving taxa, suggesting that the indirect effect of climate disruption on forage resources is a key factor in current animal population trends. Indeed, de Sassi and Tylianakis (2012) showed experimentally that climate warming can disproportionately increase herbivore over plant biomass and that herbivores will be the most likely taxonomic group to thrive under warming conditions – a situation observed in many ecosystems today. Land-use change such as agricultural intensification and specialisation also plays an additive role by improving forage resources. Many herbivorous waterfowl preferentially forage on cultivated grass and cereal crops (Fox & Abraham, 2017) and Greenland barnacle goose abundance on Islay was strongly linked to the area of managed grassland available in winter by Mason et al. (2017). Again, this highlights the contrast between thriving and declining species: land-use change was also identified as one of the main anthropogenic drivers of change in the global state of nature (IPBES, 2019).

Hunting

Direct exploitation, such as hunting for sport, was another main driver of change identified by (IPBES, 2019). Greenland barnacle geese are legally protected from winter season hunting since the 1980s, which likely contributed to the increasing population trend (Fox et al., 1990). Cessation of winter season hunting of the Svalbard barnacle goose, for example, allowed the population recover from just 300 birds in 1948 to 4,000 by the 1960s (Mitchell et al., 2010). Hunting of the Greenland population remains legal in Greenland and Iceland during autumn but official bag statistics are only available from 1995 to 2017 (Statistics Iceland, 2020) and indicate stable trends. The population also experiences lethal management on Islay since 2001 under the Derogation provided by Article 9 of the Birds Directive (2009/147/EC). Official bag statistics (Scottish Natural Heritage, 2020) indicate that the bag trebled between 2001 and 2015. It is possible that hunting mortality could mask weather effects on demographic rates in our analysis by augmenting the "natural" mortality rate of juveniles or tagged birds.

Comparison to previous studies

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Our analysis did not detect the effect of winter, spring and early summer conditions on the proportion juveniles detected on Islay by Fox and Gitay (1991). Furthermore, the positive effect of winter temperature on mean brood size found by Cabot and West (1973) on Inishkea between 1963 and 1971 was no longer apparent for 1968 to 2018. It could be that with continued weather shifts, advantages at one stage in the breeding cycle are now offset by disadvantages at other stages and masked because juveniles are counted in winter (Nolet, Schreven, Boom, & Lameris, 2019). It is also possible that our results are influenced by annual variation in the distribution of juveniles among wintering sites and that effects of weather on productivity are only apparent in some subsets of the population.

The absence of a difference between adult and juvenile survival was expected because most juveniles were tagged on the wintering grounds after completing first migration, which is one of the highest periods of juvenile mortality (Owen & Black, 1989). Survival values based on the preliminary CJS model indicated that female survival (88%) was marginally but significantly higher than males (86%). Overall mean adult survival (87%) was similar to mean adult survival on Islay (84%) based on capture-mark-recapture data between 1983 and 2006 (Trinder, 2014). It should be noted, however, that 'natural' mortality is not distinguished from leg-ring loss or hunting in these estimates. Hunting mortality on Islay may explain the lower survival estimates at this site, although geese within our analysis were regularly recorded on Islay.

Consequences of weather regime shifts

Despite the current population trend, continued climate disruption in northern Europe and Greenland may ultimately have negative consequences for Greenland barnacle geese and other Arctic species. For example, phenological mismatches during warmer springs are being observed among Arctic-breeding migrants (Clausen & Clausen, 2013; Leung et al., 2018). During migration, Arctic geese depend on seasonal forage peaks to fuel energetically costly activities. With continued weather regime shifts, phenological mismatches can develop between forage peaks and energetic requirements, often with negative consequences for productivity (Lameris et al., 2017). Climate disruption may also alter the traditional predator-prey relationships of the tundra by increasing goose predator numbers such as Arctic fox

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(*Vulpes lagopus*) (Layton-Matthews, Hansen, Grøtan, Fuglei, & Loonen, 2019). Among herbivorous mammals, reindeer in the Arctic are being negatively affected by warmer, wetter winters due to "rain-on-snow" events – icing caused by rain falling on snow that restricts access to forage, resulting in starvation – as observed in Svalbard reindeer (Albon et al., 2017; Pedersen et al., 2018). It is interesting to note that the greatest variation in summer precipitation coincides with the greatest variation in barnacle goose productivity in our dataset. Variation in Greenland summer precipitation increased substantially in the 2010s (see Supporting Information S2). The highest proportion juveniles since 1968 was recorded in 2016 (0.19), while the lowest was recorded in 2012 (0.01), Although we cannot draw conclusions from this, future research may reveal significant patterns and potential population fluctuations.

Intensified changes in structure and functioning of the tundra ecosystem may also have negative consequences. In Arctic Alaska, Thompson et al. (2016) investigated the response of 17 passerines, ptarmigan and shorebirds to increased vegetation biomass in their nesting habitat associated with climate warming. They found that initial increases in vegetation height and cover were beneficial to most species but, as the magnitude of change increased, predicted that the height and cover of vegetation would render the habitat unsuitable for a considerable number of species. Sometimes the thriving species themselves are responsible for structural change: hyper-intensive grazing by hyper-abundant snow goose populations has altered tundra structure and functioning in parts of Arctic Canada (Mariash, Smith, & Mallory, 2018). Similar ecosystem impacts have been observed in temperate climates: epidemics of mountain pine beetle (*Dendroctonus ponderosaeon*) *Pinus* trees, for example, are becoming more prevalent in North America (Mitton & Ferrenberg, 2012).

Conclusion

Anthropogenic climate disruption has mixed effects on animal population trends. Our study shows that survival in an Arctic-breeding migrant bird was positively associated with warmer, wetter conditions during spring staging over the past 50 years. Adult survival is known to have a greater influence on population growth rate than productivity in this species. Survival rates increased, while a concurrent regime shift towards warmer, wetter conditions occurred, supporting the view that weather

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regime shifts contributed in part to the increasing population trend observed since the mid-20th century. Our study also detected contrasting effects of warmer, wetter conditions during autumn staging on survival and productivity. Warm, dry conditions were the most favourable for the number of juveniles recruited into the overwintering population on Inishkea, but no long-term trends in productivity were observed aside from increased variability in recent years. Greenland barnacle geese are one of a number of herbivorous birds and terrestrial mammals with thriving population trends, and the indirect effect of climate disruption on forage resources is likely a key factor explaining this pattern. However, continued climate disruption could ultimately have negative consequences for Arctic species, such as phenological mismatches, altered community composition and ecosystem function and population fluctuations.

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Author contributions

SD, DC and BMcM conceived ideas and designed methodology. DC founded the ringing project. DC and AW ringed birds for analysis at Inishkea/Greenland and at Inishkea/Donegal respectively. DC was responsible for collating resightings and collecting all productivity data and made these data available for analysis. SD analysed the data, with assistance from SB, RI and BMcM and led the writing of the manuscript, while all authors contributed critically to drafts and gave final approval for publication.

Data accessibility statement

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The data that support the findings of this study are available from the corresponding author upon reasonable request.

References

Albon, S. D., Irvine, R. J., Halvorsen, O., Langvatn, R., Loe, L. E., Ropstad, E., … Stien, A. (2017). Contrasting effects of summer and winter warming on body mass explain population dynamics in a food-limited Arctic herbivore. *Global Change Biology*, *23*(4), 1374–1389. https://doi.org/10.1111/gcb.13435

Albouy, C., Delattre, V., Donati, G., Frölicher, T. L., Albouy-Boyer, S., Rufino, M., … Leprieur, F. (2020). Global vulnerability of marine mammals to global warming. *Scientific Reports*, *10*, 548. https://doi.org/10.1038/s41598-019-57280-3

Bainbridge, I. (2017). Goose management in Scotland: An overview. *Ambio*, *46*(Suppl 2), 224–230. https://doi.org/10.1007/s13280-016-0883-5

Boyd, H., & Fox, A. D. (2008). Effects of climate change on the breeding success of White-fronted Geese Anser albifrons flavirostris in west Greenland. *Wildfowl*, *58*, 55–70.

Burnham, K. P., Anderson, D. R., White, G. C., Brownie, C., & Pollock, K. H. (1987). *Design and analysis methods for fish survival experiments based on release-recapture. American Fisheries Society Monograph No. 5*. Maryland, USA: Amer Fisheries Society.

Cabot, D., & West, B. (1973). Population dynamics of Barnacle Geese, Branta leucopsis, in Ireland. *Proceedings of the Royal Irish Academy. Section B: Biological, Geological, and Chemical Science*, *73*, 415–443.

Ceballos, G., Ehrlich, P. R., & Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences*, *114*(30), E6089–E6096. https://doi.org/10.1073/pnas.1704949114

Clausen, K. K., & Clausen, P. (2013). Earlier Arctic springs cause phenological mismatch in long-distance migrants. *Oecologia*, *173*(3), 1101–1112. https://doi.org/10.1007/s00442-013-2681-0

Cleasby, I. R., Bodey, T. W., Vigfusdottir, F., McDonald, J. L., McElwaine, G., Mackie, K., … Bearhop, S. (2017). Climatic conditions produce contrasting influences on demographic traits in a long-distance Arctic migrant. *Journal of Animal Ecology*, *86*(2), 285–295. https://doi.org/10.1111/1365-2656.12623

This article is protected by copyright. All rights reserved

Accepted Article

Crewe, T. L., Mitchell, G. W., & Larrivée, M. (2019). Size of the canadian breeding population of monarch butterflies is driven by factors acting during spring migration and recolonization. *Frontiers in Ecology and Evolution*, *7*, 308. https://doi.org/10.3389/fevo.2019.00308

Cribari-Neto, F., & Zeileis, A. (2010). Beta regression in R. *Journal of Statistical Software*, *34*(2), 1–24. https://doi.org/10.18637/jss.v034.i02

Dawe, K. L., & Boutin, S. (2016). Climate change is the primary driver of white-tailed deer (Odocoileus virginianus) range expansion at the northern extent of its range; land use is secondary. *Ecology and Evolution*, *6*(18), 6435–6451. https://doi.org/10.1002/ece3.2316

de Sassi, C., & Tylianakis, J. M. (2012). Climate change disproportionately increases herbivore over plant or parasitoid biomass. *PLoS ONE*, *7*(7), e40557. https://doi.org/10.1371/journal.pone.0040557

Díaz, S., Settele, J., Brondízio, E. S., Ngo, H. T., Agard, J., Arneth, A., … Zayas, C. N. (2019). Pervasive human-driven decline of life on Earth points to the need for transformative change. Science, 366(6471), eaax3100. https://doi.org/10.1126/science.aax3100

Directive 2009/147/EC of the European Parliament and of the Council of 30 November 2009 on the conservation of wild birds

Doyle, S., Walsh, A., McMahon, B. J., & Tierney, T. D. (2018). Barnacle Geese Branta leucopsis in Ireland: results of the 2018 census. *Irish Birds*, *11*, 23–28.

Ewacha, M. V., Roth, J. D., & Brook, R. K. (2014). Vegetation structure and composition determine snowshoe hare (Lepus americanus) activity at arctic tree line. *Canadian Journal of Zoology*, *92*(9), 789–794. https://doi.org/10.1139/cjz-2014-0058

Ferrari, S. L. P., & Cribari-Neto, F. (2004). Beta Regression for Modelling Rates and Proportions. *Journal of Applied Sciences*, *31*(7), 799–815. https://doi.org/10.1080/0266476042000214501

Fox, A. D., & Madsen, J. (2017). Threatened species to super-abundance: the unexpected international implications of successful goose conservation. Ambio, 46(Suppl. 2), 179–187. https://doi.org/10.1007/s13280-016-0878-2

Fox, A. D., & Abraham, K. F. (2017). Why geese benefit from the transition from natural vegetation to agriculture. *Ambio*, *46*(Suppl. 2), 188–197. https://doi.org/10.1007/s13280-016-0879-1

This article is protected by copyright. All rights reserved

Accepted Article

Fox, A. D., & Gitay, H. (1991). Breeding success in Greenland barnacle geese Branta leucopsis wintering on Islay, Scotland. *Ardea*, *79*(2), 359–364.

Fox, A. D., & Leafloor, J. O. (2018). *A global audit of the status and trends of Arctic and Northern Hemisphere goose population*. Akureyri, Iceland. Retrieved from http://hdl.handle.net/11374/2162

Fox, A. D., Ogilvie, M. A., Easterbee, N., & Bignal, E. M. (1990). East Greenland barnacle geese in Scotland, spring 1988. *Scottish Birds*, *16*(1), 1–9.

Guisan, A., & Zimmermann, N. E. (2000). Predictive habitat distribution models in ecology. Ecological Modelling, 135(2–3), 147–186. https://doi.org/10.1016/S0304-3800(00)00354-9

Helgadóttir, Á., Eythórsdóttir, E., & Jóhannesson, T. (2013). Agriculture in Iceland - a grassland based production. In *Proceedings of the 17th Symposium of the European Grassland Federation* (pp. 30–43). Akureyri, Iceland. Retrieved from https://www-cabdirect-org.ucd.idm.oclc.org/cabdirect/FullTextPDF/2013/20133335535.pdf

Henderson, P. A., & Seaby, R. M. (2005). The role of climate in determining the temporal variation in abundance, recruitment and growth of sole Solea solea in the Bristol Channel. *Journal of the Marine Biological Association of the United Kingdom*, *85*, 197–204. https://doi.org/10.1017/S0025315405011069h

Inger, R., Gregory, R., Duffy, J. P., Stott, I., Voříšek, P., & Gaston, K. J. (2015). Common European birds are declining rapidly while less abundant species' numbers are rising. Ecology Letters, 18, 28–36. https://doi.org/10.1111/ele.12387

IPBES. (2019). *Global assessment on biodiversity and ecosystem services*. Bonn, Germany. Retrieved from https://www.ipbes.net/global-assessment-report-biodiversity-ecosystem-services

IPCC. (2013). *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. (T. F. Stocker, D. Qin, G.-K. Plattner, M. M. B. Tignor, S. K. Allen, J. Boschung, … P. M. Midgley, Eds.) (1st ed.). Cambridge, United Kingdom and New York, USA: Cambridge University Press. Retrieved from https://www.ipcc.ch/site/assets/uploads/2018/02/WG1AR5_all_final.pdf

James, G., Witten, D., Hastie, T., & Tibshirani, R. (2013). *An Introduction to Statistical Learning with Applications in R*. New York: Springer-Verlag.

This article is protected by copyright. All rights reserved

Accepted Article

https://doi.org/10.1007/978-1-4614-7138-7

Jensen, G. H., Madsen, J., Nagy, S., & Lewis, M. (2018). *AEWA International Single Species Management Plan for the Barnacle Goose (Branta leucopsis) - Russia/Germany & Netherlands population, East Greenland/Scotland & Ireland population, Svalbard/South-west Scotland population. AEWA Technical Series No. 63*. Bonn, Germany. Retrieved from https://research.tilburguniversity.edu/en/publications/aewa-international-single-species-management-plan-for-the-barnacl

Jensen, G. H., Madsen, J., Johnson, F. A., & Tamstorf, M. P. (2014). Snow conditions as an estimator of the breeding output in high-Arctic pink-footed geese Anser brachyrhynchus. *Polar Biology*, *37*(1), 1–14. https://doi.org/10.1007/s00300-013-1404-7

Kéry, M., Madsen, J., & Lebreton, J. (2006). Survival of Svalbard pink-footed geese Anser brachyrhynchus in relation to winter climate, density and land-use. *Journal of Animal Ecology*, *75*(5), 1172–1181. https://doi.org/10.1111/j.1365-2656.2006.01140.x

Laake, J. L. (2013). *RMark: An R interface for analysis of capture-recapture data with MARK*. *Alaska Fisheries Science Centre Processed Rep. 2013-01*. Alaska Fisheries Science Centre, Seattle. Retrieved from https://www.afsc.noaa.gov/publications/procrpt/pr2013-01.pdf

Lameris, T. K., Jochems, F., van der Graaf, A. J., Andersson, M., Limpens, J., & Nolet, B. A. (2017). Forage plants of an Arctic-nesting herbivore show larger warming response in breeding than wintering grounds, potentially disrupting migration phenology. *Ecology and Evolution*, *7*(8), 2652–2660. https://doi.org/10.1002/ece3.2859

Layton-Matthews, K., Loonen, M. J. J. E., Hansen, B. B., Coste, C. F. D., Sæther, B.-E., & Grøtan, V. (2019). Density-dependent population dynamics of a high Arctic capital breeder, the barnacle goose. *Journal of Animal Ecology*, *88*(8), 1191–1201. https://doi.org/10.1111/1365-2656.13001

Layton- Matthews, K., Hansen, B. B., Grøtan, V., Fuglei, E., & Loonen, M. J. J. E. (2019). Contrasting consequences of climate change for migratory geese: predation, density dependence and carryover effects offset benefits of high- arctic warming. *Global Change Biology*, *00*, 1–16. https://doi.org/10.1111/gcb.14773

This article is protected by copyright. All rights reserved

Accepted Article

Lebreton, J., Burnham, K. P., Clobert, J., & Anderson, D. R. (1992). Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. *Ecological Monographs*, *62*(1), 67–118. https://doi.org/10.2307/2937171

Leung, M. C.-Y., Bolduc, E., Doyle, F. I., Reid, D. G., Gilbert, B. S., Kenney, A. J., … Bêty, J. (2018). Phenology of hatching and food in low Arctic passerines and shorebirds: is there a mismatch? *Arctic Science*, *4*, 538–556. https://doi.org/10.1139/as-2017-0054

Lynam, C. P., Lilley, M. K. S., Bastian, T., Doyle, T. K., Beggs, S. E., & Hays, G. C. (2011). Have jellyfish in the Irish Sea benefited from climate change and overfishing? *Global Change Biology*, *17*(2), 767–782. https://doi.org/10.1111/j.1365-2486.2010.02352.x

Mariash, H. L., Smith, P. A., & Mallory, M. L. (2018). Decadal response of Arctic freshwaters to burgeoning goose populations. *Ecosystems*, *21*(6), 1230–1243. https://doi.org/10.1007/s10021-017-0215-z

Mason, T. H. E., Keane, A., Redpath, S. M., & Bunnefeld, N. (2017). The changing environment of conservation conflict: geese and farming in Scotland. *Journal of Applied Ecology*, *55*(2), 651–662. https://doi.org/10.1111/1365-2664.12969

Mitchell, C., Colhoun, K., Fox, A. D., Griffin, L., Hall, C., Hearn, R. D., … Walsh, A. J. (2010). Trends in goose numbers wintering in Britain and Ireland, 1995 to 2008. *Ornis Svecica*, *20*, 128–143.

Mitchell, C., & Hall, C. (2018). *Greenland barnacle geese Branta leucopsis in Britain and Ireland: results of the international census, spring 2018*. Slimbridge, UK.

Mitton, J. B., & Ferrenberg, S. M. (2012). Mountain Pine Beetle develops an unprecedented summer generation in response to climate warming. *The American Naturalist*, *179*(5), E163–E171. https://doi.org/10.1086/665007

Morrissette, M., Bêty, J., Gauthier, G., Reed, A., & Lefebvre, J. (2010). Climate, trophic interactions, density dependence and carry-over effects on the population productivity of a migratory Arctic herbivorous bird. *Oikos*, *119*(7), 1181–1191. https://doi.org/10.1111/j.1600-0706.2009.18079.x

Nolet, B. A., Schreven, K. H. T., Boom, M. P., & Lameris, T. K. (2019). Contrasting effects of the onset of spring on reproductive success of Arctic-nesting geese. *The Auk*, *137*(1), ukz063. https://doi.org/10.1093/auk/ukz063

Owen, M., & Black, J. M. (1989). Factors affecting the survival of Barnacle Geese on

This article is protected by copyright. All rights reserved

Accepted Article

migration from the breeding grounds. *Journal of Animal Ecology*, *58*(2), 603–617.

Pavón-Jordán, D., Santangeli, A., & Lehikoinen, A. (2017). Effects of flyway-wide weather conditions and breeding habitat on the breeding abundance of migratory boreal waterbirds. *Journal of Avian Biology*, *48*(7), 988–996. https://doi.org/10.1111/jav.01125

Pedersen, Å. Ø., Hansen, B. B., Loe, L. E., Ropstad, E., Irvine, J., Stien, A., … Ravolainen, V. (2018). *When ground-ice replaces fjord-ice - results from a study of GPS-collared Svalbard reindeer females. Brief Report 049*. Tromsø, Norway. Retrieved from https://brage.npolar.no/npolar-xmlui/bitstream/handle/11250/2564043/Kortrapport49.pdf?sequence=1&isAllowed=y

Praetorius, S., Rugenstein, M., Persad, G., & Caldeira, K. (2018). Global and Arctic climate sensitivity enhanced by changes in North Pacific heat flux. *Nature Communication*, *9*, 3124. https://doi.org/10.1038/s41467-018-05337-8

R Core Team. (2018). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. Retrieved from https://www.r-project.org/

Rosenberg, K. V, Dokter, A. M., Blancher, P. J., Sauer, J. R., Smith, A. C., Smith, P. A., … Marra, P. P. (2019). Decline of the North American avifauna. *Science*, *366*(6461), 120–124. https://doi.org/10.1126/science.aaw1313

Saalfeld, S. T., Mcewen, D. C., Kesler, D. C., Butler, M. G., Cunningham, J. A., Doll, A. C., … Lanctot, R. B. (2019). Phenological mismatch in Arctic-breeding shorebirds: Impact of snowmelt and unpredictable weather conditions on food availability and chick growth. *Ecology and Evolution*, *00*, 1–15. https://doi.org/10.1002/ece3.5248

Scottish Natural Heritage. (2020). Islay sustainable goose management strategy. Retrieved May 6, 2020, from https://www.nature.scot/sites/default/files/2017-07/A1760175 - Islay Sustainable Goose Management Strategy - Baseline Report - summary %28A1724076%29.pdf

Seber, G. A. F. (1982). *The estimation of animal abundance and related parameters* (2nd ed.). New York: Macmillan.

Statistics Iceland. (2020). Hunting 1995 - 2016. Retrieved May 6, 2020, from https://px.hagstofa.is/pxen/pxweb/en/Atvinnuvegir/Atvinnuvegir__landbunadur__

This article is protected by copyright. All rights reserved

Accepted Article

landveidi/SJA10303.px

Tape, K. D., Gustine, D. D., Ruess, R. W., Adams, L. G., & Clark, J. A. (2016). Range expansion of moose in arctic Alaska linked to warming and increased shrub habitat. *PLoS ONE*, *11*(4), e0152636. https://doi.org/10.1371/journal.pone.0152636

Thompson, S. J., Handel, C. M., Richardson, R. M., & McNew, L. B. (2016). When winners become losers: predicted nonlinear responses of Arctic birds to increasing woody vegetation. *PLoS ONE*, *11*(11), e0164755. https://doi.org/10.1371/journal. pone.0164755

Tombre, I. M., Oudman, T., Shimmings, P., Griffin, L., & Prop, J. (2019). Northward range expansion in spring-staging barnacle geese is a response to climate change and population growth, mediated by individual experience. *Global Change Biology*, *25*(11), 3680–3693. https://doi.org/10.1111/gcb.14793

Trinder, M. (2014). *Status and population viability of Greenland barnacle geese on Islay*. Scottish Natural Heritage, Battleby, Scotland. Retrieved from http://www.snh.org.uk/pdfs/publications/commissioned_reports/568.pdf

U.S. Fish and Wildlife Service. (2018). *Waterfowl Population Status, 2018*. Washington, D.C. USA. Retrieved from https://www.fws.gov/migratorybirds/pdf/surveys-and-data/Population-status/Waterfowl/WaterfowlPopulationStatusReport18.pdf

Vetter, S. G., Ruf, T., Bieber, C., & Arnold, W. (2015). What is a mild winter? Regional differences in within-species responses to climate change. *PLoS ONE*, *10*(7), e0132178. https://doi.org/10.1371/journal.pone.0132178

Weiser, E. L., Lanctot, R. B., Brown, S. C., Gates, H. R., Bentzen, R. L., Bêty, J., … Sandercock, B. K. (2018). Environmental and ecological conditions at Arctic breeding sites have limited effects on true survival rates of adult shorebirds. *The Auk*, *135*(1), 29–43. https://doi.org/10.1642/AUK-17-107.1

Weiskopf, S. H., Ledee, O. E., & Thompson, L. M. (2019). Climate change effects on deer and moose in the Midwest. *The Journal of Wildlife Management*, *83*(4), 769–781. https://doi.org/10.1002/jwmg.21649

White, G. C., & Burnham, K. P. (1999). Program MARK: survival estimation from populations of marked animals. *Bird Study*, *46*(Suppl 1), 120–139. https://doi.org/10.1080/00063659909477239

Wismer, S., Tebbett, S. B., Streit, R. P., & Bellwood, D. R. (2019). Spatial mismatch

This article is protected by copyright. All rights reserved

in fish and coral loss following 2016 mass coral bleaching. *Science of the Total Environment*, *650*, 1487–1498. https://doi.org/10.1016/j.scitotenv.2018.09.114

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TABLE 1 Summary of environmental covariates. The weather measurement, life history stage, months of the breeding-year and area of the Greenland barnacle goose range are outlined. Temporal trends (β) and significance (*P*) based on a linear regression are also provided.

Covariate	Measurement	Life history stage	Months	Area of range	Temporal trend
$winter_{Temp}$	mean temperature	winter	Oct - Mar	wintering grounds (Ireland & Scotland)	1968 - 2018: β = 0.02, *P* = 0.001
$spring_{Temp}$	(°C)	spring	Apr & May	staging grounds (Iceland)	1968 - 2018: β = 0.03, *P* = 0.025
early $summer_{Temp}$		early summer	May - Jul	breeding grounds (Greenland)	1968 - 2018: β = 0.04, *P* < 0.001
late $summer_{Temp}$		late summer	Aug & Sep	breeding grounds (Greenland)	1968 - 2018: β = 0.08, *P* < 0.001
$autumn_{Temp}$		autumn	Sep & Oct	staging grounds (Iceland)	1968 - 2018: β = 0.04, *P* < 0.001
$winter_{Prec}$	accumulated precipitation	winter	Oct - Mar	wintering grounds (Ireland & Scotland)	1968 - 2018: β = 2.48, *P* = 0.008
$spring_{Prec}$	(mm)	spring	Apr & May	staging grounds (Iceland)	1981 - 2018: β = 1.51, *P* = 0.023
early $summer_{Prec}$		early summer	May - Jul	breeding grounds (Greenland)	1968 - 2018: β = 1.86, *P* = 0.049
late $summer_{Prec}$		late summer	Aug & Sep	breeding grounds (Greenland)	1968 - 2018: β = 4.90, *P* = 0.015
$autumn_{Prec}$		autumn	Sep & Oct	staging grounds (Iceland)	1978 - 2018: β = 2.19, *P* = 0.037

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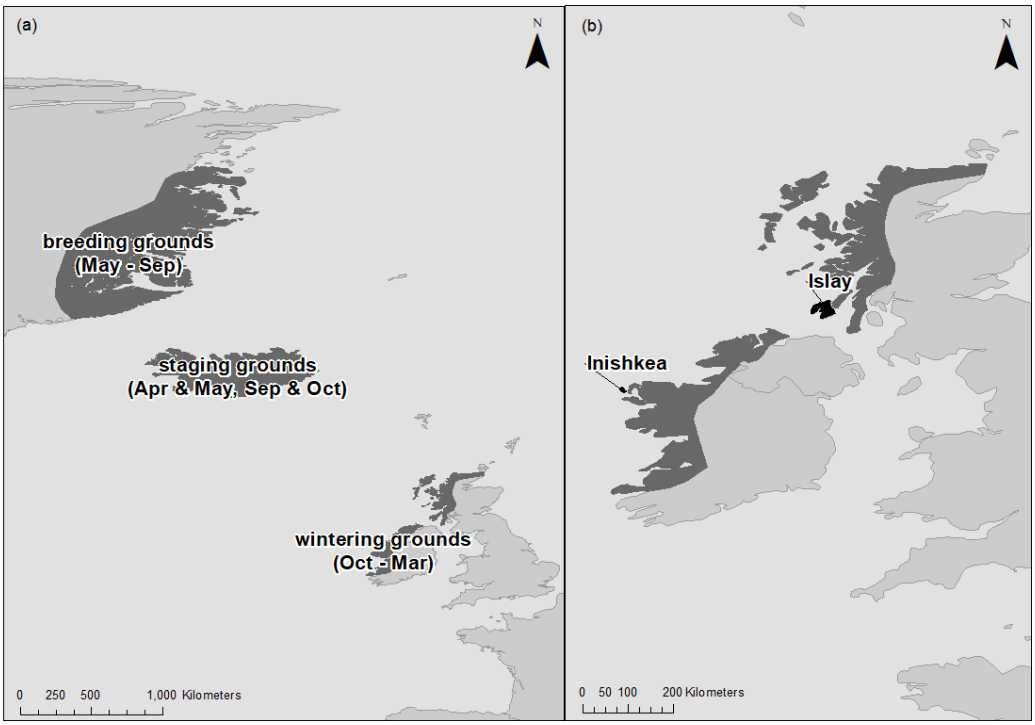
FIGURE 1 (a) Greenland barnacle goose wintering, staging and breeding grounds and (b) two key wintering sites, the Isle of Islay in Scotland and the Inishkea Islands in Ireland. The months of the year spent in each part of the range are in parentheses.

FIGURE 2: Left panels: Greenland barnacle goose demographic rates over time. The dashed line represents a locally weighted smoother added to visualise long-term trends. Right panels: plots of the smoothed term of the fitted generalised additive models (GAM). Breeding-year is plotted against smoothed (s) breeding-year to demonstrate changes in the function of breeding-year. The dashed lines represent standard error around the smooth and the estimated degrees of freedom (edf) for the smooth is indicated. (a - b) Annual apparent survival (adult female values). The function of breeding-year changes from level and horizontal to increasing and upward as breeding-year increases. (c - d) Annual proportion juveniles observed in the overwintering population on Inishkea. The function of breeding-year remains level and horizontal. (e - f) Annual mean brood size observed in the overwintering population on Inishkea. The function of breeding-year is slightly decreasing and downward but remains consistent as breeding-year increases.

FIGURE 3 Relationship between Greenland barnacle goose demographic rates and mean temperature (°C) or accumulated precipitation (mm) during spring (April and May) or autumn (September and October) on the staging grounds in Iceland, based on the final models. (a – d) annual apparent survival (adult female values), (e - f) annual proportion juveniles (birds up to one year old) observed in the overwintering population on Inishkea, (g - h) annual mean brood size observed in the overwintering population on Inishkea. In all plots, the line represents the best fit least squares regression with shaded 95% confidence intervals

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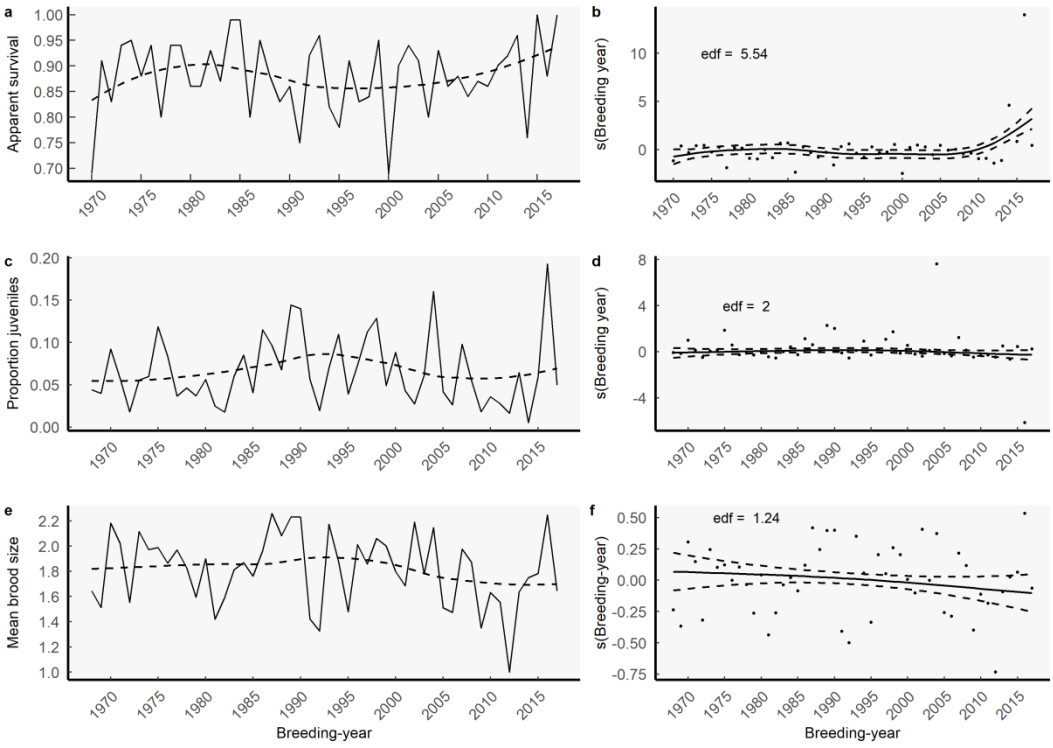
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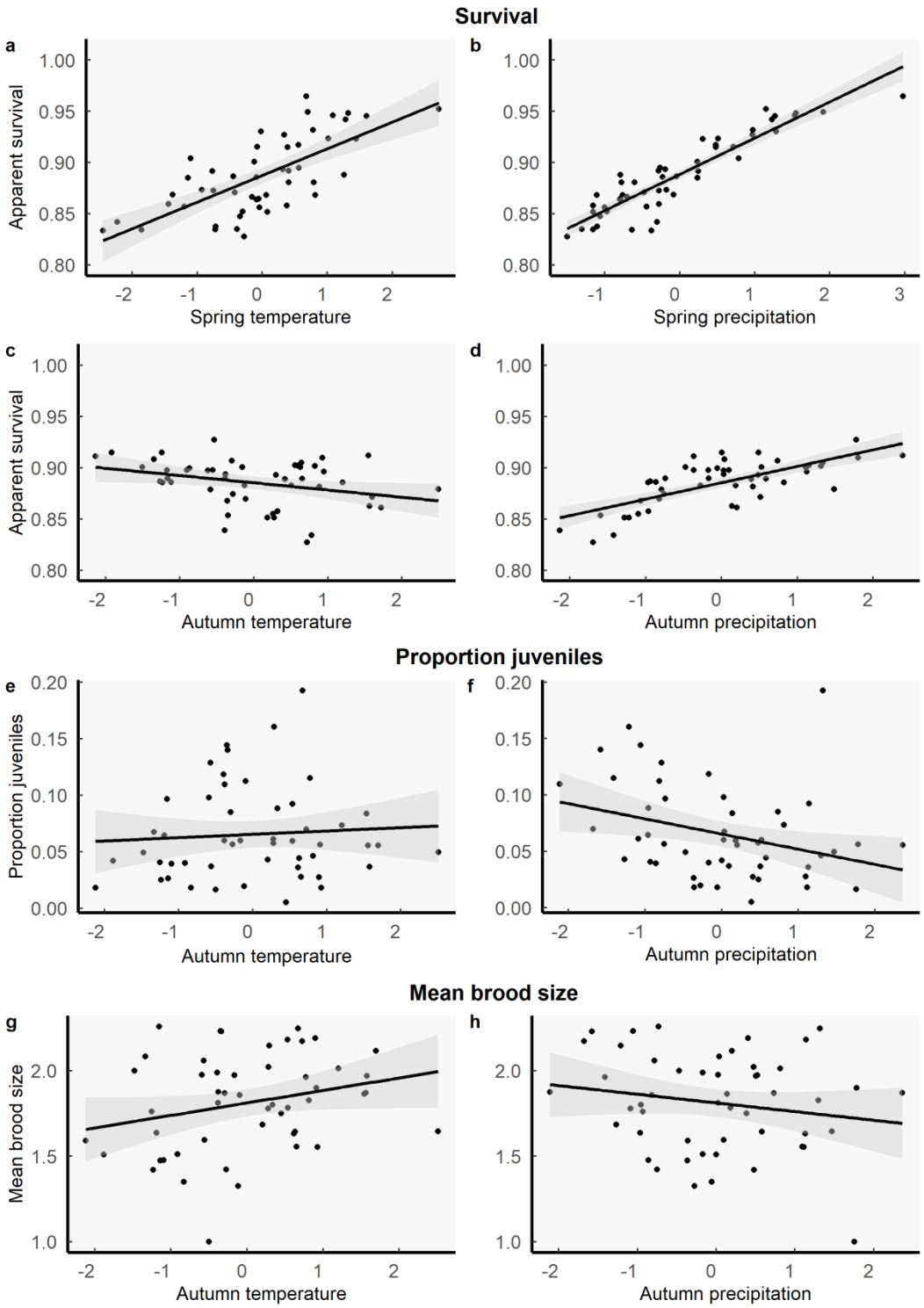
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