Diagnosing the decline of the Greenland White-fronted Goose *Anser albifrons flavirostris* using population and individual level techniques

MITCH D. WEEGMAN[1,2,6]*, ANTHONY DAVID FOX[3], GEOFF M. HILTON[2], DAVID J. HODGSON[1], ALYN J. WALSH[4], LARRY R. GRIFFIN[5] & STUART BEARHOP[1]

[1]Centre for Ecology and Conservation, College of Life and Environmental Sciences, University of Exeter, Cornwall Campus, Penryn TR10 9EZ, UK.
[2]Wildfowl & Wetlands Trust, Slimbridge, Gloucester GL2 7BT, UK.
[3]Department of Bioscience, Aarhus University, Kalø, Grenåvej 14, DK-8410 Rønde, Denmark.
[4]National Parks and Wildlife Service, Wexford Wildfowl Reserve, North Slob, Wexford, Republic of Ireland.
[5]Wildfowl & Wetlands Trust, Caerlaverock Wetland Centre, Eastpark Farm, Caerlaverock, Dumfriesshire DG1 4RS, UK.
[6]Present address: School of Natural Resources, University of Missouri, Columbia, Missouri, 65211 USA.
*Correspondence author. E-mail: weegmanm@missouri.edu

Abstract

Following an increase in numbers from 1982 to 1998, the Greenland White-fronted Goose *Anser albifrons flavirostris* declined over the period 1999–2015, stimulating detailed analyses at the population and individual level to provide a better understanding of the dynamics of this subspecies. Here we synthesise the results of the analyses in order to describe the potential reasons for the decline. Utilising a 27-year capture-mark-recapture dataset from the main wintering site for these birds (Wexford, Ireland), multistate models estimated sex-specific survival and movement probabilities. Our results suggested no evidence of a sex bias in emigration or "remigration" rates. These analyses formed the foundation for an integrated population model (IPM), which included population size and productivity data to assess source-sink dynamics of Wexford birds through estimation of age-, site-, and year-specific survival and movement probabilities. Results from the IPM suggested that Wexford is a large sink, and that a reduction in productivity is an important demographic mechanism underlying population change for birds wintering at the site. Low productivity may be due to environmental conditions in the breeding range, because birds bred successfully at youngest ages when conditions in Greenland were favourable in the year(s) during adulthood prior to and including the year of successful breeding. This effect could be mediated by prolonged parent-offspring

relationships, as birds remained with parents into adulthood, forfeiting immediate reproductive success despite there being no fitness benefits to offspring of family associations after age 3 years. Global Positioning System and acceleration data collected from 15 male individuals suggested that two successful breeding birds were the only tagged individuals whose mate exhibited prolonged incubation. More data is required, however, to determine whether poor productivity is attributable to deferral of nesting or to failure of nesting attempts. Spring foraging did not appear to limit breeding or migration distance because breeding and non-breeding or failed-breeding birds, as well as Irish and Scottish birds, did not differ in their proportion of time spent feeding or on energy expenditure in spring. We recommend that future research should quantify the demography of other Greenland White-fronted Goose wintering flocks, to assess holistically the mechanisms underlying the global population decline.

Arctic-nesting geese are key species of northern hemisphere polar regions, acting as arctic ecosystem bioengineers through their grazing and grubbing of vegetation, and as important prey for other species (Bantle & Alisauskas 1998; Gauthier *et al*. 2004). Their conservation and management therefore is important to maintaining the integrity of arctic ecosystem functions. In recent decades, many goose populations around the world have increased, largely as a result of greater food availability associated with agricultural practices (Fox & Abraham 2017) and more informed management of hunting as a conservation tool (Owen 1990; Abraham & Jeffries 1997; Madsen *et al*. 1999; Gauthier *et al*. 2005). Typically, populations that remain of concern are those with limited ability to adapt to changing habitats or where hunting is uncontrolled. For example, the Red-breasted Goose *Branta ruficollis*, which is classed as Vulnerable by the International Union for Conservation of Nature (IUCN

2016), is believed to be hunted illegally particularly during migration in Kazakhstan and Russia, which has resulted in additive mortality and reduced population size in recent years (Cranswick *et al*. 2012). Likewise, a combination of decreased habitat availability and increased hunting in China of the Lesser White-fronted Goose *Anser erythropus*, also classed as Vulnerable globally by IUCN, is believed to have contributed to population decline (Wang *et al*. 2012). Nonetheless, there remain reasons to be cautious about the conservation and management of all arctic-nesting geese in future years, particularly with habitat changes associated with the warming climate, the resulting temperature increases of which are greatest at polar latitudes (IPCC 2014). These increases in temperature have already changed arctic ecosystems, contributing to greater variation in predator-prey interactions (Nolet *et al*. 2013) and "phenological mismatch" in food abundance as a result of differential changes

in the onset of summer between temperate and polar regions (Durant *et al.* 2007; Tulp & Schekkerman 2008; Gilg *et al.* 2012).

To understand how these changes might influence arctic-nesting goose populations worldwide, it is critical to understand the population biology and ecology of these goose systems. It is therefore timely to examine these processes in the Greenland White-fronted Goose *Anser albifrons flavirostris*. This taxon is protected from hunting throughout almost its entire range, albeit illegal hunting is believed to persist at low levels. Site protection measures have been enacted on breeding, staging and wintering sites. In 1989, five sites on summering areas in west Greenland were designated as Wetlands of International Importance ("Ramsar Sites") under the terms of the Ramsar Convention and subsequently, in 2013, the main Icelandic staging site at Hvanneyri was also listed by Icelandic Government as a Ramsar Site. The entire world population winters in Great Britain and Ireland, where protection and increased food availability due to intensive agriculture have resulted in increases in most goose populations in recent decades. Indeed, there are 14 Ramsar Sites in Great Britain and 11 in Ireland utilised by Greenland White-fronted Geese. Yet the Greenland White-fronted Goose population has declined by 47% over the past two decades (Fig. 1) for reasons that are not clear (Fox *et al.* 2016).

Tackling a conservation challenge using population and individual level techniques

In this paper, following suggestions by Green (1995) and Gibbons *et al.* (2011), we synthesise a series of recently published results on Greenland White-fronted Goose demography, to diagnose the demographic mechanisms underlying population change of the geese at their main wintering site (Wexford, Ireland) for improved inference of factors influencing the global population decline. The studies were aided by long-term capture-mark-recapture (CMR), population size and productivity (*i.e.* the proportion of juveniles) datasets of Greenland White-fronted Geese from Wexford, which permitted estimates of the birds' survival and breeding success. Critically, these data encompassed a period of population increase between the early 1980s and the late 1990s (Fig. 1), and a subsequent decrease. Further, the percentage juveniles during winter (a productivity metric) at Wexford steadily declined from the early 1980s to mid-2010s (Fig. 2). Using these data, we were therefore able to examine and compare demographics associated with each period, and not just during the population decline. Very few studies on this population to date have been conducted on breeding grounds in Greenland, because of the remoteness of the area and the dispersed, low density of individuals across the landscape (Fox & Stroud 1988, 2002). Instead, most previous research has been carried out at staging sites (Francis & Fox 1987; Fox *et al.* 1999; Nyegaard *et al.* 2001; Fox *et al.* 2002; Fox *et al.* 2012) or wintering areas (Ruttledge & Ogilvie 1979; Mayes 1991; Wilson *et al.* 1991; Warren *et al.* 1992; Fox 2003). Novel tracking devices therefore were used to quantify behaviours and movements during the breeding season in Greenland. In particular we examined whether reductions
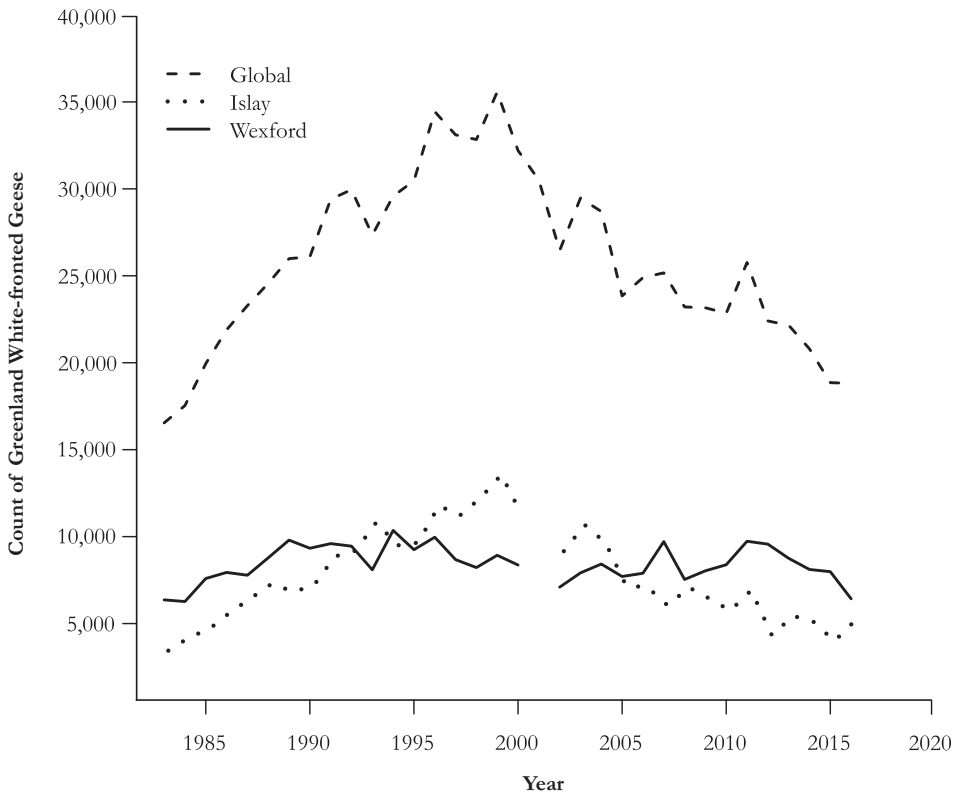
Figure 1. Greenland White-fronted Goose count of global population (dashed line), Islay subpopulation (*i.e.* wintering flock; dotted line) and Wexford subpopulation (solid line), 1983–2016.

in juvenile and adult survival, or in productivity, contributed to the population trajectories. This is a taxon with a complex social system and life history; previous studies have highlighted that these birds are long-lived (*e.g.* maximum age 22 years; A.D. Fox, unpubl. data) and exhibit prolonged family relationships (Warren *et al.* 1993). These factors may be interacting to influence population demography in subtle ways.

To examine the demographics of this system, we developed multistate models based on CMR life histories of collared birds, which estimated age- and sex-specific survival and movement probabilities. Our results suggested that there were no differences between sexes in emigration probabilities at ages 1 year (males: mean = 0.18, 95% credible intervals (CRI) = 0.14–0.22, females: mean = 0.17, 95% CRI = 0.13–0.22) and 2+ years (males: mean 0.11, 95% CRI = 0.09–0.14, females: mean = 0.11, 95% CRI = 0.08–0.13) or remigration probabilities (*i.e.* the return of birds to sites where they were originally marked after
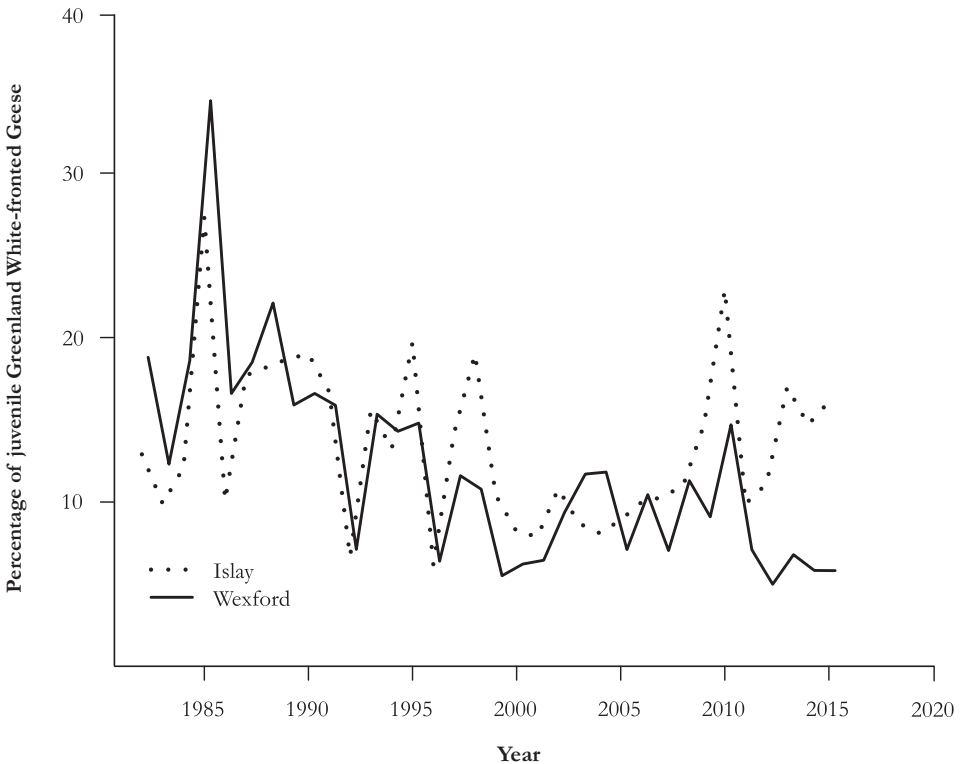
Figure 2. Percentage juvenile Greenland White-fronted Geese counted at Islay (dotted line) and Wexford (solid line), 1982–2015.

a period elsewhere) at ages 2+ year (males: mean = 0.11, 95% CRI = 0.08–0.15, females: mean= 0.13, 95% CRI = 0.09–0.18; Weegman *et al*. 2015). These findings confirmed published estimates of emigration (Marchi *et al*. 2010), and provided previously unknown estimates of remigration for this population.

   This model framework formed the foundation for development of an integrated population model (IPM) which estimated age-, site- and year-specific survival and movement probabilities, and utilised population size and productivity

data to yield population growth rates over the 27-year study period (Weegman *et al*. 2016a). Importantly, observations of the Wexford population size showed that the flock has remained relatively stable during the study, despite large fluctuations (increases in the early period and declines in recent years) in the size of *c*. 70 other wintering flocks in Great Britain and Ireland. This includes a major increase and subsequent decline on Islay, Scotland, which is the second-largest wintering area (collection of flocks) for the subspecies, despite stable productivity for these birds

(Fig. 1, Fig. 2; Fox *et al.* 2016). Over the 27-year study period, the Wexford population constituted 25–42% of all Greenland White-fronted Geese globally and, prior to demographic analyses, appeared to be a classic source-sink system (Pulliam 1988), whereby large wintering aggregations (such as at Wexford) act as "sources" to support the smaller "sink" flocks, which explains persistence of the latter. However, our IPM revealed the exact opposite in that the largest concentration of wintering Greenland White-fronted Geese in the world (Wexford) is in fact a large sink, whose population size is maintained only by substantial annual immigration from other (smaller) sites (Weegman *et al.* 2016a). Indeed, model estimates of population growth rate reached *c.* 1.0 (the level required to match the observed stability at Wexford) only on invoking immigration at a remarkable *c.* 17% *per annum*.

Recruitment rate (*i.e.* a demographic measure of productivity) at Wexford generally declined over the study period, reflecting the observed percentage of juveniles there (Fig. 2). Taking into account juvenile and adult survival at Wexford, and based on previous approaches to identifying the causes of population declines through modelling exercises (Thomson *et al.* 1997; Robinson *et al.* 2004; Freeman *et al.* 2007), we identified that a reduction in productivity is an important demographic mechanism of Greenland White-fronted Goose population change at Wexford, but that this is masked by immigration (Fig. 3). Assuming factors contributing to Wexford's sink status occur during winter (and not where Wexford birds breed in Greenland or stage in Iceland),

these findings indicate that researchers should not necessarily use Wexford as a model of "optimal" environmental conditions (because the site functions as a sink). Researchers do however need to understand more about the constraints and restraints of this system throughout the annual cycle, including as it pertains to Wexford, and specifically whether successful breeding birds are leaving (thus creating the impression of low productivity there), the type of birds that move into Wexford (age, family status, reproductive success, *etc.*), and why they do so.

Worsening environmental conditions in Greenland explain cohort effects

In a population characterised by learned behaviour and complex social interactions (Fox 2003), declining productivity may be a product of subtle changes. For example, if adverse environmental conditions mitigate in favour of prolonged parent-offspring relationships, age at first successful reproduction would increase, causing a decline in *per capita* productivity. The environmental drivers of demographic change can be studied through cohort effects (Lindström 1999), because prevailing environmental conditions experienced by members of a hatch-year cohort affect their individual (and collective cohort) fitness, with subsequent impacts on population dynamics. On considering breeding success among cohorts (with successful reproduction measured as marked individuals returning to the wintering areas with young), environmental conditions (using North Atlantic Oscillation (NAO) values as a proxy) were found to
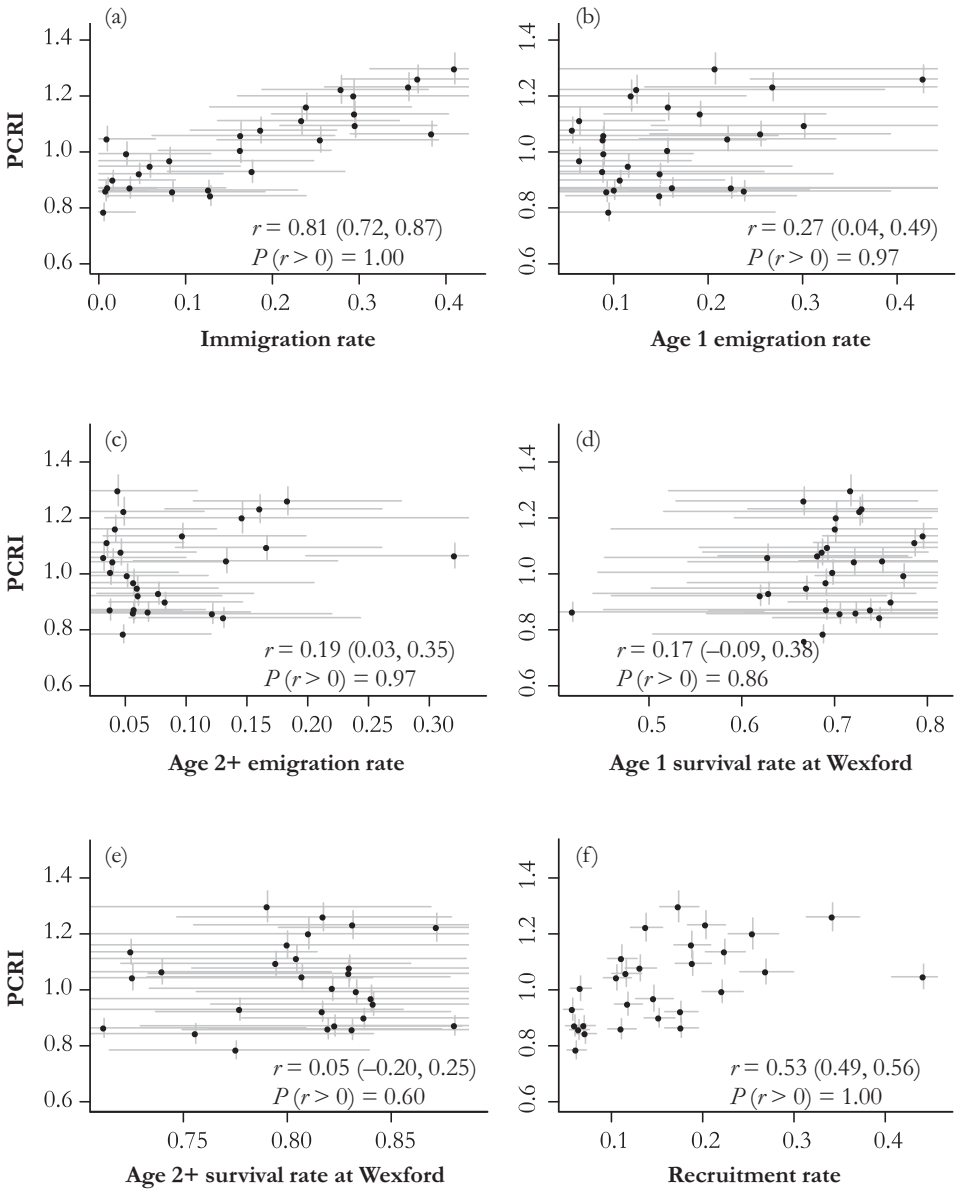
Figure 3. Immigration (a), emigration of geese aged 1 (b) and 2+ years (c), survival of geese aged 1 (d) and 2+ years (e) and recruitment rate (f) against *per capita* rate of increase per annum in population size (PCRI) of Greenland White-fronted Geese at Wexford, 1983–2010. Black dots show posterior means (with 95% CRI, grey lines). The posterior mode of the correlation coefficients (*r* with 95% CRI) and probability of a positive correlation ($P (r > 0)$) are inset (from Weegman *et al.* 2016a).

explain variation in age at first successful reproduction, but not the first successful brood size, for Greenland White-fronted Geese (Weegman *et al.* 2016b). Positive NAO values tended to result in relatively cold, dry conditions in west Greenland and were associated with earlier ages at first successful reproduction (the so-called "silver spoon" effect from Grafen 1988) and *vice versa*. However, the silver spoon effect was relatively minor and environmental conditions experienced in adulthood prior to successful reproduction and in the year of first successful reproduction had a much stronger influence on age at first successful reproduction. Cohorts bred successfully at younger ages when they experienced favourable environmental conditions, but this effect was far stronger when the preceding years were also favourable. These results confirm an association between environmental conditions on the breeding grounds and population productivity, and imply that such effects may be carried over multiple years.

The fitness implications of extended parent-offspring relationships

We also studied whether there was an association between the social system and productivity in Greenland White-fronted Geese. Previous work on this population suggested that some birds exhibit uniquely prolonged parent-offspring relationships (up to 6 years; Warren *et al.* 1993). However, the fitness implications of these extended relationships had never been studied. Our more recent analyses suggested that parent-offspring and sibling-sibling associations varied from 1–13 years but were only

beneficial through to age 3 years in Greenland White-fronted Geese, whereby fitness (*i.e.* survival and eventual breeding probability) of birds that maintained such associations was significantly greater than those that did not (Weegman *et al.* 2016c). Conversely, birds that maintained extended family associations (> 3 years) gained no significant fitness benefit over individuals that left parents or siblings at the same age. We combined these results to form a cost-benefit model, which suggested that fitness was lower among birds that remained with their parents or siblings than simulated birds who were forced into independence at ages 6 and 7 years. Although subsequent breeding probability was greatest for "older" individuals (*i.e.* those aged 5 years) associating with siblings, these gains were offset by non-significant survival differences between birds with siblings and those that were independent, yielding lower overall fitness for birds aged 5 years than those aged 3 (Weegman *et al.* 2016c). Independence after just 2 or 3 years may be especially important for species characterised by very few breeders or poor productivity such as Greenland White-fronted Geese because younger individuals have more potential breeding opportunities.

Other factors, such as density dependence, might limit productivity in this population. We studied whether these regulatory processes, which are known to occur in other systems (Newton 1998; Rodenhouse *et al.* 2003; Norris *et al.* 2004), influenced Greenland White-fronted Geese at the population and individual levels. Using IPM, we found for the Wexford population a strong positive correlation

between emigration and immigration rates, and between emigration and recruitment rates, providing evidence of density-dependent regulation during winter. Hence, more birds immigrated to Wexford in years when more birds emigrated from Wexford; likewise more birds emigrated from Wexford in years when the recruitment rate at Wexford was larger. In our study of cohort effects, population sizes in the winter prior to hatch year or breeding year did not explain variation in age at first successful reproduction or the proportion of successful breeders by cohort (Weegman et al. 2016b). Thus, we found no evidence of density-dependent regulation of productivity. Overall, although the IPM suggested density-dependent processes may be occurring in this population, further studies are needed to: (i) examine the effect of Wexford regulation on the dynamics of the overall system, and (ii) determine whether similar density-dependent effects occur among other Greenland White-fronted Goose flocks.

Quantifying drivers of poor productivity at the individual level

Whilst we assessed the influence of environmental factors on fitness by linking age at first successful reproduction with NAO data, there are specific facets of breeding biology that we were not able to examine using these methods, but which also might explain the recent decline in productivity in Greenland. These might include decreased breeding propensity (the probability that an adult female attempts to breed in a given year), decreased clutch size, decreased incubation success, decreased

fledging success, or even lower survival during the post-fledging phase prior to winter (before juveniles are counted). These questions are difficult to answer because of the remoteness of the breeding range and low nesting densities of Greenland White-fronted Geese in west Greenland (Salomonsen 1967; Fox & Stroud 1988; Malecki et al. 2000). A novel method to answer these questions uses hybrid Global Positioning System (GPS) and acceleration (ACC) tracking devices to determine time- and energy-budgets throughout the year. We deployed these units on male geese during winter and downloaded data when the birds returned the following winter. Two of 15 tagged geese were categorised as having bred successfully during the study year because they were resighted repeatedly (> 5 times) with juveniles during winter. Thus, we used these individuals to understand the behavioural "traces" associated with the breeding event and compared these to birds resighted without juveniles during winter to determine whether individuals in the latter group deferred breeding or failed during incubation or chick-rearing. There were indications that the behaviour and energetics of birds that were either unsuccessful or deferred reproductive attempts diverged from those of the successful breeders early in the breeding season (Weegman 2014). However, with only two successful breeding birds tracked, larger sample sizes are needed for a robust assessment of whether low breeding propensity or high failure rates during early incubation are the most likely cause of low productivity in Greenland White-fronted Geese.

Constraints on breeding may occur in the pre-breeding migration and immediate post-migration periods, when it is assumed that individuals "prepare" for the anticipated cost of breeding by accumulating greater energy stores (Fox & Madsen 1981). To assess this, we compared: (a) the proportion of time feeding, and (b) energy expenditure, for tagged birds that bred successfully *versus* non-breeding (or failed-breeding) birds during spring migration and the pre-breeding period in Greenland (*i.e.* the first 14 days after arrival there), and found no substantive differences between these birds (Weegman 2014). That time- and energy-budgets through spring and early summer were indistinguishable between successful breeding birds and those without young in winter (*i.e.* which either failed in their nesting attempt or deferred breeding) suggests that all geese were "prepared" for a breeding attempt, and that any decision to defer was made immediately prior to incubation in Greenland, presumably in relation to the conditions encountered on breeding areas (Weegman *et al.* 2016b). It is possible, but we believe unlikely, that birds which decided not to attempt to breed made this decision before arrival in Greenland, and then simply showed no difference in time- and energy-budgets during spring and early summer.

These preliminary findings also suggest that Greenland White-fronted Geese not successful in reproduction are not limited by the amount of time spent feeding during spring migration from wintering to breeding areas (when birds must replenish energy stores). We infer this based on the observation that there was no difference in the proportion of time spent feeding between successful breeders and non-breeders or failed breeders. Hence, these limited data do not provide support for carry-over effects in which condition during winter or spring influences productivity on breeding areas (Harrison *et al.* 2013), but are consistent with previous findings from field scores of abdominal profiles on wintering and staging areas during spring, which indicated that birds attained departure body condition on wintering and staging areas earlier in recent years than in any other period of the 27-year study (Fox *et al.* 2014), due to improved food availability (Francis & Fox 1987; Fox *et al.* 2012) and warmer springs (Fox *et al.* 2014). These shifts in phenology have increased the spring Icelandic staging period to one much longer than the birds require to replenish energy stores (Fox *et al.* 2014). Despite the low sample size, our findings build on previous Greenland White-fronted Goose work to suggest that the decision to lay a clutch is made on arrival in the breeding range. For instance, irrespective of whether the birds defer or fail in their breeding attempt, the lack of evidence to date for a carry-over effects supports the hypothesis of Boyd & Fox (2008) that increased spring snowfall in west Greenland in recent years (likely driven by changes in the NAO due to a warming climate; Hoerling *et al.* 2001; Johannessen *et al.* 2004) has created a phenological mismatch between weather conditions in Greenland and the timing of the breeding season. Hence, birds continue to arrive in west Greenland within a few days of historical arrival dates (Salomonsen 1950, 1967; Fox *et al.* 2014), but increased snow cover in some years may have reduced

foraging opportunities. As a result, birds may be constrained to wait for snowmelt in order to reacquire necessary fat stores for reproduction. Phenological mismatches in chick-rearing and peak food abundance have been documented in a variety of other arctic-nesting birds, including Greater Snow Geese *Anser caerulescens atlantica* (Dickey *et al.* 2008) and Thick-billed Murres *Uria lomvia* (Gaston *et al.* 2009). However, further research on the ecosystem consequences of a warming arctic climate is necessary to understand how these processes potentially interact to affect the breeding biology of Greenland White-fronted Geese.

It is also possible that birds wintering in different parts of the range in Great Britain and Ireland have different time- and energy-budgets (especially energy expenditure) because of shorter or longer spring migration journeys. Greenland White-fronted Geese exhibit a "leap-frog" migration, whereby birds wintering in Scotland stage in the southern lowlands of Iceland and breed in the southernmost part of the breeding range in Greenland and those wintering in Ireland stage in western Iceland and breed in the northernmost part of the breeding range in Greenland (Salomonsen 1950; Kampp *et al.* 1988). These differences may lower productivity if birds migrating further do not feed more in advance of each stage of migration, because the greater energy expenditure associated with migrating longer distances would result in greater depletion of fat stores for these individuals than for those making shorter flights (assuming that northern breeding birds do not replenish nutrient stores in southern breeding areas before continuing

to their northern nest sites). We compared time- and energy-budgets using GPS-ACC data from birds wintering at Wexford, Ireland and Loch Ken, Scotland (Weegman *et al.* 2017). Although Irish birds flew significantly further than Scottish birds (but did not expend significantly more energy doing so), there were no significant differences in their proportion of time spent feeding during spring migration (*i.e.* from wintering to staging sites, staging to breeding sites and overall). These findings suggest plasticity in this species, whereby similar energy stores accrued by Irish and Scottish birds allow greater migration distances (of up to *c.* 300 km), if necessary. Nonetheless, that Scottish birds migrated significantly shorter distances suggests that they arrived in west Greenland with greater energy stores than Irish birds (assuming that Scottish birds were heavier than Irish birds on arrival in Greenland), which may facilitate greater reproductive success, as in other species (Ankney & MacInnes 1978; Newton 2008). Additional GPS-ACC data are needed to understand fully the extent to which migration distance influences reproductive success in Greenland White-fronted Geese, both directly on arrival at the breeding areas and as carry-over effects from wintering or staging areas.

One limitation of this study is that the majority of the long-term data we used was derived from one wintering site (Wexford). Although population survey data exist for *c.* 70 other wintering flocks, no consistent marking efforts have been conducted at these sites. It is now clear that there is a need to understand the dynamics of other flocks, particularly in the context of Wexford's

function as a sink. The dynamics at the second-largest wintering area (Islay) are of greatest importance to understand in the short-term. Over our 27-year study period, the Islay population increased and subsequently decreased, mirroring global population fluctuations (Fig. 1). It would be particularly useful to understand what makes Wexford "more appealing" for immigrants than Islay and why apparently more families occur amongst birds wintering on Islay. One hypothesis might be that Islay does not function as a reserve like Wexford, where croplands and grasslands are managed for Greenland White-fronted Geese. In fact, an increasing Barnacle Goose *Branta leucopsis* population on Islay in recent years has led to shooting of those birds under license to decrease crop damage. It is possible that Greenland White-fronted Geese are experiencing increased disturbance resulting from shooting activities, perhaps discouraging immigration and encouraging emigration there. Results exploring disturbance on Islay are forthcoming (E. Burrell, unpubl. data). Furthermore, unlike Wexford, the population on Islay does not function as a single unit (*i.e.* one that roosts at one site) because population surveys and telemetry suggest there are over 50 separate roosts associated with different feeding areas on the island. Recent telemetry data suggests these flocks remain separated throughout winter. Thus, it might be more informative to study the dynamics of these flocks in the context of a geographical area with a particularly high density of small peripheral populations. To better understand the network of flocks at Islay and their

relationship to the Wexford flock, consistent CMR efforts are necessary to model site demography in the IPM framework.

Diagnosis of population decline and future work

Using novel Bayesian IPMs, our diagnosis is that declining productivity measured at Wexford is the demographic mechanism for Greenland White-fronted Goose population change there, but immigration has masked these effects (Fig. 3; Weegman *et al.* 2016a). Declining productivity is possibly due to a reduced frequency of successful breeding, which could be the result of low breeding propensity or high failure rates in early incubation. Our work supports the suggestion that the drivers of low breeding success are likely to occur on breeding areas in west Greenland, perhaps related to weather conditions rather than carry-over effects from the preceding winter or spring. A priority for future work is to understand the processes occurring during the first 14 days after birds arrive in west Greenland, when foraging is required for replenishing energy stores prior to nesting (Fox & Madsen 1981). It is critical to understand whether increased snow cover is limiting forage availability and hence, given habitat requirements, the number of potential breeding territories (Fox & Stroud 1988). Additional conservation and management of breeding areas to increase productivity will be difficult because of the remoteness of such sites and the extent to which uncontrollable factors such as weather explain variation in productivity. Nonetheless, modelling exercises that estimate the survival rates required to match current low

productivity rates would provide insight into whether additional spring and winter conservation efforts could mitigate poor productivity, assuming that survival can be increased further during these periods. Environmental variability in Greenland could also be included in such models in the IPM framework to predict population responses in future years. Indeed, if a warming climate is causing increased snowfall, further increases in temperatures will lead to rainfall (not snowfall), which might allow geese to arrive earlier, extend the breeding period and potentially improve habitat availability (Boyd & Fox 2008), as is currently the case for arctic-nesting geese in Svalbard (Jensen *et al.* 2008). Finally, these data could be incorporated into integrated metapopulation models to understand how processes at Wexford contribute to demography of the global population, to explain the consistent overall decline in recent years.

Acknowledgements

References

Abraham, K.F. & Jefferies, R.L. 1997. High goose populations: causes, impacts and implications. *In* B.D.J. Batt (ed.), *Arctic ecosystems in peril: report of the arctic goose habitat working group*, pp. 7–22. Arctic Goose Joint Venture Special Publication, U.S. Fish and Wildlife Service, Washington D.C., USA and Canadian Wildlife Service, Ottawa, Canada.

Ankney, C.D. & MacInnes, C.D. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. *The Auk* 95: 459–471.

Bantle, J.L. & Alisauskas, R.T. 1998. Spatial and temporal patterns in Arctic Fox diets at a large goose colony. *Arctic* 51: 231–236.

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.

Cranswick, P.A., Raducescu, L., Hilton, G.M. & Petkov, N. 2012. *International Single Species Action Plan for the conservation of the Red-breasted Goose (*Branta ruficollis*)*. AEWA Technical Series No. 46, The Wildfowl & Wetlands Trust, Slimbridge, UK.

Dickey, M.-H., Gauthier, G. & Cadieux, M.-C. 2008. Climatic effects on the breeding phenology and reproductive success of an arctic-nesting goose species. *Global Change Biology* 14: 1973–1985.

Durant, J.M., Hjermann, D.Ø., Ottersen, G. & Stenseth, N.C. 2007. Climate and the match or mismatch between predator requirements and resource availability. *Climate Research* 33: 271–283.

Fox, A.D. 2003. *The Greenland White-fronted Goose* Anser albifrons flavirostris. Doctor's

dissertation (D.Sc.), National Environmental Research Institute, Denmark.

Fox, A.D. & Abraham, K.F. 2017. Why geese benefit from the transition from natural vegetation to agriculture. *Ambio* 46: 188–197.

Fox, A.D. & Madsen, J. 1981. The pre-nesting behaviour of the Greenland White-fronted Goose. *Wildfowl* 32: 48–53.

Fox, A.D. & Stroud, D.A. 1988. The breeding biology of the Greenland White-fronted Goose (*Anser albifrons flavirostris*). *Meddelelser Om Grønland, Bioscience* 27: 1–14.

Fox, A.D. & Stroud, D.A. 2002. Greenland White-fronted Goose *Anser albifrons flavirostris*. *Birds of the Western Palearctic Update* 4: 65–88.

Fox, A.D., Hilmarsson, J.Ó., Einarsson, Ó., Boyd, H., Kristiansen, J.N., Stroud, D.A., Walsh, A.J., Warren, S.M., Mitchell, C., Francis, I.S. & Nygaard, T. 1999. Phenology and distribution of Greenland White-fronted Geese *Anser albifrons flavirostris* staging in Iceland. *Wildfowl* 50: 29–43.

Fox, A.D., Hilmarsson, J.Ó., Einarsson, Ó., Walsh, A.J., Boyd, H. & Kristiansen, J.N. 2002. Staging site fidelity of Greenland White-fronted Geese in Iceland. *Bird Study* 49: 42–49.

Fox, A.D., Boyd, H., Walsh, A.J., Stroud, D.A., Nyeland, J. & Cromie, R.L. 2012. Earlier spring staging in Iceland amongst Greenland White-fronted Geese *Anser albifrons flavirostris* achieved without cost to refuelling rates. *Hydrobiologia* 697: 103–110.

Fox, A.D., Weegman, M.D., Bearhop, S., Hilton, G.M., Griffin, L., Stroud, D.A. & Walsh, A.J. 2014. Climate change and contrasting plasticity in timing of a two-step migration episode of an arctic-nesting avian herbivore. *Current Zoology* 60: 233–242.

Fox, A.D., Francis, I., Norriss, D. & Walsh, A. 2016. *Report of the 2015/16 International Census of Greenland White-fronted Geese*. Greenland White-fronted Goose Study, Rønde, Denmark.

Francis, I.S. & Fox, A.D. 1987. Spring migration of Greenland White-fronted Geese through Iceland. *Wildfowl* 38: 7–12.

Freeman, S.N., Robinson, R.A., Clark, J.A., Griffin, B.M. & Adams, S.Y. 2007. Changing demography and population decline in the Common Starling *Sturnus vulgaris*: a multisite approach to Integrated Population Monitoring. *Ibis* 149: 587–596.

Gaston, A.J., Gilchrist, H.G., Mallory, M.L. & Smith, P.A. 2009. Changes in seasonal events, peak food availability, and consequent breeding adjustment in a marine bird: a case of progressive mismatching. *The Condor* 111: 111–119.

Gauthier, G., Bêty, J., Giroux, J.-F. & Rochefort, L. 2004. Trophic interactions in a high arctic Snow Goose colony. *Integrative and Comparative Biology*, 44: 119–129.

Gauthier, G., Giroux, J.-F., Reed, A., Béchet, A. & Bélanger, L. 2005. Interactions between land use, habitat use, and population increase in Greater Snow Geese: what are the consequences for natural wetlands? *Global Change Biology* 11: 856–868.

Gibbons, D.W., Wilson, J.D. & Green, R.E. 2011. Using conservation science to solve conservation problems. *Journal of Applied Ecology* 48: 505–508.

Gilg, O., Kovacs, K.M., Aars, J., Fort, J., Gauthier, G., Grémillet, D., Ims, R.A., Meltofte, H., Moreau, J., Post, E., Schmidt, N.M., Yannic, G. & Bollache, L. 2012. Climate change and the ecology and evolution of arctic vertebrates. *Annals of the New York Academy of Sciences* 1249: 166–190.

Grafen, A. 1988. On the uses of data on lifetime reproductive success. *In* T.H. Clutton-Brock (ed.), *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems*,

pp. 454–471. University of Chicago Press, Chicago, USA.

Green, R.E. 1995. Diagnosing causes of bird population declines. *Ibis* 137 (Suppl.): 47–55.

Harrison, X.A., Hodgson, D.J., Inger, R., Colhoun, K., Gudmundsson, G.A., McElwaine, G., Tregenza, T. & Bearhop, S. 2013. Environmental conditions during breeding modify the strength of mass-dependent carry-over effects in a migratory bird. *PLOS ONE* 8: e77783.

Hoerling, M.P., Hurrell, J.W. & Xu, T. 2001. Tropical origins for recent North Atlantic climate change. *Science* 292: 90–92.

Intergovernmental Panel on Climate Change (IPCC). 2014. *Working Group II contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. IPCC, Geneva, Switzerland.

International Union for Conservation of Nature (IUCN) 2016. Red List of Threatened Species, version 2016.1. IUCN, Cambridge, UK. Available from www.iucnredlist.org (last accessed 5 October 2017).

Jensen, R.A., Madsen, J., O'Connell, M., Wisz, M.S., Tømmervik, H. & Mehlum, F. 2008. Prediction of the distribution of arctic-nesting Pink-footed Geese under a warmer climate scenario. *Global Change Biology* 14: 1–10.

Johannessen, O.M., Bengtsson, L., Miles, M.W., Kuzmina, S.I., Semenov, V.A., Alekseev, G.V., Nagurnyi, A.P., Zakharox, V.F., Bobylev, L.P., Pettersson, L.H., Hasselmann, K. & Cattle, H.P. 2004. Arctic climate change: observed and modeled temperature and sea-ice variability. *Tellus* 56A: 328–341.

Kampp, K., Fox, A.D. & Stroud, D.A. 1988. Mortality and movements of the Greenland White-fronted Goose *Anser albifrons flavirostris*. *Dansk Ornitologisk For Tidsskrift* 82: 25–36.

Lindström, J. 1999. Early development and fitness in birds and mammals. *Trends in Ecology and Evolution* 14: 343–348.

Madsen, J., Cracknell, G. & Fox, A.D., eds 1999. *Goose Populations of the Western Palearctic. A Review of Status and Distribution. Wetlands International Publication 48*. Wetlands International, Wageningen, the Netherlands and National Environmental Research Institute, Rønde, Denmark.

Malecki, R.A., Fox, A.D. & Batt, B.D.J. 2000. An aerial survey of nesting Greenland White-fronted and Canada Geese in west Greenland. *Wildfowl* 51: 49–58.

Marchi, C., Sanz, I.F., Blot, E., Hansen, J., Walsh, A.J., Frederiksen, M. & Fox, A.D. 2010. Between-winter emigration rates are linked to reproductive output in Greenland White-fronted Geese *Anser albifrons flavirostris*. *Ibis* 152: 410–413.

Mayes, E. 1991. The winter ecology of Greenland White-fronted Geese *Anser albifrons flavirostris* on semi-natural grassland and intensive farmland. *Ardea* 79: 295–304.

Newton, I. 1998. *Population Limitation in Birds*. Academic Press, London, UK.

Newton, I. 2008. *The Migration Ecology of Birds*. Academic Press, London, UK.

Nolet, B.A., Bauer, S., Feige, N., Kokorev, Y.I., Popov, I.Y. & Ebbinge, B.S. 2013. Faltering lemming cycles reduce productivity and population size of a migratory arctic goose species. *Journal of Animal Ecology* 82: 804–813.

Norris, D.R., Marra, P.P., Kyser, T.K., Sherry, T.W. & Ratcliffe, L.M. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings of the Royal Society B: Biological Sciences* 271: 59–64.

Nyegaard, T., Kristiansen, J.N. & Fox, A.D. 2001. Activity budgets of Greenland White-fronted Geese *Anser albifrons flavirostris* spring staging on Icelandic hayfields. *Wildfowl* 52: 41–53.

Owen, M. 1990. The damage-conservation interface illustrated by geese. *Ibis* 132: 238–252.

Pulliam, H.R. 1988. Sources, sinks, and population regulation. *The American Naturalist* 132: 652–661.

Robinson, R.A., Green, R.E., Baillie, S.R., Peach, W.J. & Thomson, D.L. 2004. Demographic mechanisms of the population decline of the Song Thrush *Turdus philomelos* in Britain. *Journal of Animal Ecology* 73: 670–682.

Rodenhouse, N.L., Sillett, T.S., Doran, P.J. & Holmes, R.T. 2003. Multiple density-dependence mechanisms regulate a migratory bird population during the breeding season. *Proceedings of the Royal Society B: Biological Sciences* 270: 2105–2110.

Ruttledge, R.F. & Ogilvie, M.A. 1979. The past and current status of the Greenland White-fronted Goose in Ireland and Britain. *Irish Birds* 1: 293–363.

Salomonsen, F. 1950. *Grønland Fugle. The Birds of Greenland*. Munkgaard, Copenhagen, Denmark.

Salomonsen, F. 1967. *Fuglene på Grønland*. Rhodos, Copenhagen, Denmark.

Thomson, D.L., Baillie, S.R. & Peach, W.J. 1997. The demography and age-specific annual survival of Song Thrushes during periods of population stability and decline. *Journal of Animal Ecology* 66: 414–424.

Tulp, I. & Schekkerman, H. 2008. Has prey availability for arctic birds advanced with climate change? Hindcasting the abundance of tundra arthropods using weather and seasonal variation. *Arctic* 61: 48–60.

Wang, X., Fox, A.D., Cong, P., Barter, M. & Cao, L. 2012. Changes in the distribution and abundance of wintering Lesser White-fronted Geese *Anser erythropus* in eastern China. *Bird Conservation International* 22: 128–134.

Warren, S.M., Fox, A.D., Walsh, A. & O'Sullivan, P. 1992. Age at first pairing and breeding among Greenland White-fronted Geese. *Condor* 94: 791–793.

Warren, S.M., Fox, A.D., Walsh, A. & O'Sullivan, P. 1993. Extended parent-offspring relationships in Greenland White-fronted Geese (*Anser albifrons flavirostris*). *The Auk* 110: 145–148.

Weegman, M.D. 2014. The demography of the Greenland White-fronted Goose. Ph.D. thesis, University of Exeter, Cornwall Campus, Penryn, UK.

Weegman, M.D., Fox, A.D., Bearhop, S., Hilton, G.M., Walsh, A.J., Cleasby, I.R. & Hodgson, D.J. 2015. No evidence for sex bias in winter inter-site movements in an arctic-nesting goose population. *Ibis* 157: 401–405.

Weegman, M.D., Bearhop, S., Fox, A.D., Hilton, G.M., McDonald, J.L. & Hodgson, D.J. 2016a. Integrated population modelling reveals a perceived source to be a cryptic sink. *Journal of Animal Ecology* 85: 467–475.

Weegman, M.D., Bearhop, S., Hilton, G.M., Walsh, A. & Fox, A.D. 2016b. Conditions during adulthood affect cohort-specific reproductive success in an arctic-nesting goose population. *PeerJ* 4: e2044.

Weegman, M.D., Bearhop, S., Hilton, G.M., Walsh, A.J., Weegman, K.M., Hodgson, D.J. & Fox, A.D. 2016c. Should I stay or should I go? Fitness costs and benefits of prolonged parent-offspring and sibling-sibling associations in an arctic-nesting goose population. *Oecologia* 181: 809–817.

Weegman, M.D., Bearhop, S., Hilton, G.M., Walsh, A., Griffin, L., Resheff, Y.S., Nathan, R. & Fox, A.D. 2017. Using accelerometry to compare costs of extended migration in an arctic herbivore. *Current Zoology*, https://doi.org/10.1093/cz/zox056.

Wilson, H.J., Norriss, D.W., Walsh, A., Fox, A.D. & Stroud, D.A. 1991. Winter site fidelity in Greenland White-fronted Geese *Anser albifrons flavirostris*, implications for conservation and management. *Ardea* 79: 287–294.