**Examining differences in daily behavior, energy expenditure, and local weather conditions related to breeding deferral in geese with over-land and over-sea migrations**

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**ABSTRACT**

Migratory birds face energetic challenges as they travel between wintering and breeding areas, including ecological barriers and weather conditions, which can impact the likelihood of reproduction. Greater white-fronted geese (*Anser albifrons)* are found through most of the northern hemisphere, so migration routes can be starkly different in length and barriers from one population to another. We used Global Positioning System/acceleration data collected from 35 greater white-fronted geese of the North American midcontinent (10) and Greenland (25) subspecies and novel applications of Bayesian dynamic linear models and stochastic antecedent models to test daily effects of minimum temperature and precipitation on energy expenditure (i.e., overall dynamic body acceleration, ODBA) and proportion of time spent feeding (PTF), and then examined the daily and additive importance of ODBA and PTF on probability of breeding deferral. We expected that birds would show distinct responses within and between flyways to cope with challenges encountered during migration.

Our results suggest that Greenland white-fronted geese may be more sensitive to weather conditions than that of midcontinent geese because of the population-specific barriers encountered during migration.

**KEYWORDS:** accelerometer, ecological barrier, energy expenditure, reproduction, stopover, time-varying covariates

Long-lived species are expected to forego reproduction when

Herein, we employ two novel applications of modeling approaches to investigate the daily and cumulative effects of weather conditions on goose behavior and how behavior relates to subsequent probability of a breeding deferral in two populations of greater white-fronted geese (*Anser albifrons*). … The second, described by Ogle et al. (2015), builds on the concept of ecological memory, which is the contribution of previous experiences or states to current or future responses, and is modeled using an antecedent variable (Padisák 1992).

**MATERIALS and METHODS**

**Study populations**

The midcontinent white-fronted goose population is estimated at >1.3 million birds (U.S. Fish and Wildlife Service 2020) while the Greenland white-fronted goose population consists of approximately 21,500 birds (Fox et al. 2020). Habitat in Arctic regions of Alaska, Canada and Greenland consists mainly of tundra, characterized by moss- and lichen-covered uplands with flood-prone grassy lowlands and sedge meadows (Ely and Raveling 1984; Fox and Stroud 1988). The distribution of these birds across the respective wintering areas also differs between flyways. The largest wintering flocks of Greenland birds congregate on agricultural fields near Wexford, Ireland and Islay, southwest Scotland, while ~70 other flocks are relatively small in number and have shown high fidelity to grass swards (Wilson et al. 1991; Warren et al. 1992). During the winter, midcontinent geese are much more itinerate and spread across agricultural landscapes of the southern United States and Mexico (Anderson and Haukos 2003; Ely et al. 2013), and individuals often use multiple areas within a single winter (VonBank et al. 2021).

**Goose captures and tracking devices**

Greenland geese were captured on wintering areas in Ireland (52° 22′N, 6° 23′W) in 2012, 2013, 2017, and 2018, autumn staging areas in Iceland (64° 33′N, 21° 45′W) in 2016 and 2017, and in Scotland (52° 0′N, 4° 2′ W) in 2012 and 2013. Midcontinent geese were captured on wintering areas across Texas (32° 54′N, 99° 53′W; 38° 53′N, 98° 52′W; 27° 20′N, 97° 46′W) in 2016, 2017 and 2018. Geese were captured by cannon or rocket netting on both continents, as well as modified leg-hold traps in Texas (King et al. 1998), and were fitted with collars or backpack devices bearing GPS and accelerometer (ACC) technologies. The latter measured movement in three directions as a change in velocity (Shepard et al. 2008, Gómez Laich et al. 2011).

Thirty-one Greenland geese and 50 midcontinent geese were fitted with Cellular Tracking Technologies (CTT) neck collars (CTT LLC, Rio Grande, NJ, USA; model BT 3.0 [54 g] and BT 3.5 [45 g]), and 41 Greenland geese were fitted with backpack devices attached with elastic shock cord (e-obs GmbH, Grünwald, Germany, 39 g). Greenland geese fitted with backpacks also received an orange neck collar (17 g) with an alpha-numeric code and matching white leg ring, and the CTT devices on Greenland birds were mounted to the uniquely identifiable orange neck collars. Fourteen Greenland geese and 7 midcontinent geese were fitted with Ornitela neck collars (Vilnius, Lithuania, model OrniTrack-N38; 38 g). Geese were sexed via cloacal examination. In 2012 and 2013, only males received tracking devices, otherwise adult females were chosen. Ideally, our analysis would have included only female geese, but we considered males as proxies for assessing incubation indirectly because long-term pair bonds are common in geese (Black 1996) and males are known to guard incubating females (i.e., we anticipate males are relatively stationary when guarding an incubating female compared to males not associated with an incubating female; Dittami et al. 1977; Madsen et al. 1989; Samelius and Alisauskas 2006). We attempted to fit only one individual of a pair or family group with a tracking device to maximize independence of data, given that white-front families migrate together (Weegman et al. 2016c). GPS fixes were recorded at 1 point per day (e-obs devices), every 2 hours (Greenland CTT devices), every 30 minutes (all midcontinent), or every 15 minutes (Greenland Ornitela).

Twenty-five Greenland (from 2012, 2013 and 2018; 15 backpacks, all male; 10 neck collars, all female) and 10 midcontinent individuals (from 2017 and 2018, 1 male and 9 females) had sufficient data to be included in the analysis (i.e., >75% of expected daily accelerometer bursts through June, and not more than day without a location out of every 3 days through May). Twenty of 31 Greenland geese fitted with neck collar transmitters with uniquely identifiable codes in 2017 and 2018 were resighted alive by ADF, LG, GMH, AJW, or colleagues during regular surveys of Greenland white-fronted geese (i.e., Fox et al. 2020) ≥1 year after initial capture, and an additional 6 were seen >6 months but <1 year after capture, though the tags were not transmitting data at these times. Based on estimated resight rates of Greenland white-fronted geese of approximately 0.86 at Wexford and 0.60 elsewhere throughout their range (Weegman et al. 2016a), we assumed low samples sizes were due to transmitter failure rather than collar-induced mortality. We were unsuccessful in relocating midcontinent geese due to an extensive wintering range, large flock sizes, and cryptic collar color.

**Processing and classification of ACC data**

ACC data were recorded at 10 (CTT and Ornitela units) or 10.5 Hz (e-obs units) for a duration of 3 seconds, yielding ~30 points per axis, every 6 minutes. Prior to classification, we calibrated all devices according to manufacturer specifications. We used two CTT (BT 3.0 and BT 3.5), and six Ornitela units to calibrate devices according to manufacturer-specific specifications, to ensure a consistent baseline across units for converting ACC data from millivolts to gravitational acceleration (*g*).

Classification of data from e-obs devices is described in Weegman et al. (2017a). For collared geese, we filmed birds for behavioral classification between 1 day and 6 months post-tagging, collecting 54 hours of video footage of wild Greenland white-fronted geese in Iceland and Ireland, encompassing nine CTT and nine Ornitela units. We obtained 65.5 hours of footage from two captive birds at Texas A&M-Kingsville, Texas, USA, who we rotated through three collars: Ornitela unit N38, CTT BT 3.0, and CTT BT 3.5. To increase the likelihood of capturing acceleration bursts on film, we increased the rate of ACC collection in two CTT devices deployed in Iceland from every 6 minutes to every 2 minutes for five days and collected approximately 6 hours of footage from these birds, and ACC duty cycles for devices on captive birds were increased to every minute.

We documented goose behavior using the ‘JWatcher’ program (Blumstein et al. 2006), classifying behaviors as feeding, stationary, and walking, though we later combined feeding and walking, as geese do not regularly walk long distances unless feeding (Weegman et al. 2017a), and to maintain consistency with e-obs units. Flight bursts were obtained from observed migration periods, based on GPS tracks for all device types, and stationary bursts were taken from video observations but supplemented with periods of overnight roosting for Ornitela and CTT units (Weegman et al. 2017a). All flight and stationary bursts based on GPS behavior were visually checked to ensure conformity with known ACC traces for each behavior (i.e., either extreme oscillation or stable line). Undoubtedly, geese exhibit more than three behaviors, but we assumed that maintenance behaviors such as preening would not be captured frequently enough by accelerometers to be classified, as Fox & Ridgill (1985) observed preening comprising <5% of daily activity in geese.

We compared 37 minutes of video classifications between observers (SAC and JAV) to determine inter-observer reliability (Kaufman and Rosenthal 2009) and accepted that observers were classifying behaviors equally if >95% of the video was assigned the same behavior. ACC bursts were extracted and assigned a behavior according to video time. Each burst was plotted and visually checked to ensure only 1 behavior was present during the 3-second burst, and the signature appeared reasonable for the behavior (e.g., bursts that were labeled ‘feeding’ but appeared as a straight line were removed, *n* = 21 +?CTT bursts removed), as there may have been error introduced by reaction time while videos were being scored. We identified 797 flight bursts, 106 feeding bursts, 892 stationary bursts and 75 walking bursts from Ornitela units and 569 flight bursts, 90 feeding bursts, 1381 stationary bursts and 199 walking bursts from CTT units. Due to variation in number of bursts per behavior, 150 bursts of each behavior were randomly selected to be included in the tag-specific training sets so as not to artificially inflate overall accuracy. Because they were housed in a planted wheat field (i.e., with considerable bare dirt between rows of wheat), captive birds did not display feeding behavior representative of wild grazing, so all feeding bursts came from wild Greenland white-fronted geese.

We calculated a total of 37 summary measures to describe the acceleration behavior in each burst, based on metrics used in the AcceleRater web tool (Resheff et al. 2014). We tested five machine learning algorithms for behavior classification: K-nearest neighbors, classification and regression trees, random forest, linear discriminant analysis and support vector machines. We split training data into 70% training and 30% test sets to test each of the 5 methods (e.g., Glass et al. 2020). We calculated the mean overall accuracy for each model from ten-fold cross validation in order to select the best model (Nishizawa et al., 2013; Olden et al. 2008). Random forest and support vector machine algorithms both exceeded 95% overall accuracy. We selected the random forest algorithm to classify data from all tags, as this algorithm has been used to successfully classify behaviors from a variety of taxa (e.g., Fehlmann et al. 2017; Lush et al. 2016; Pagano et al. 2017; Tatler et al. 2018). Tag- and behavior-specific accuracy and performance metrics are shown in Table S1.

We used overall dynamic body acceleration (ODBA) as a proxy for energy expenditure from ACC data (Wilson et al. 2019). To increase consistency between devices, we used quantile mapping, a technique common in climate modeling for correcting bias (Piani et al., 2010; Reiter et al. 2018) using the package ‘qmap’ version 1.0-4 (Gudmundsson et al. 2012). Due to manufacturer settings, Ornitela ACC data were bounded, meaning that recorded values were forced between a minimum and maximum (i.e., -4000 and 4000 mV). Therefore, we opted to stretch Ornitela and e-obs values to match CTT. We visually assessed the plots of the empirical cumulative density function of the CTT, Ornitela, and transformed Ornitela data and selected the empirical quantiles over smoothing splines as the most appropriate mapping function.

**Defining migration period and reproductive outcome**

We considered the migration period to start no earlier than 14 days prior to geese leaving wintering areas to incorporate preparations for departure; however, some geese were tagged <14 days prior to departure from wintering areas. We defined the end of the spring migration period as the end of the 14-day period after departing the last major staging area defined in the literature (Prairie Pothole Region spanning Alberta to Manitoba and South Dakota for midcontinent geese, and west Iceland for Greenland geese; Fig. 1; Ely et al. 2013; Fox et al. 2014; Weegman et al. 2017b), because geese often stage in the Arctic prior to nest site selection (Fox and Bergersen 2005). Geese use these staging areas consistently and in large numbers to rebuild nutrient stores, generally for >1 week just before moving to breeding areas (Fox et al. 2002; Anderson and Haukos 2003; Hübner 2006).

We classified geese as having attempted or deferred reproduction based on retrospective analysis of patterns in GPS and ACC data, following the methods described in Schreven et al. (2021). Two midcontinent geese failed to transmit ACC data after the first week of June, so we followed the procedures for identifying incubation from only the GPS signals, which persisted through July. The method described by Schreven et al. (2021) can identify incubation events as short as 3 days; therefore, while we could not differentiate between deferral and early failure,

Reproductive success of 15 male Greenland geese with backpack devices (2012–2013) was confirmed by resighting marked individuals associating (or not) with young on wintering areas (i.e., 5–8 months post-hatch; Weegman 2014).

**Weather covariates**

GPS points from neck collars were thinned to one per day in the late afternoon, at approximately 1600 h local time (i.e., mean deviation from 1600 h was 39 minutes), to match frequency of backpack devices, using the package ‘adehabitatLT’ version 0.3.23 (Calenge, 2006; Calenge et al., 2009). We interpolated missing GPS coordinates during spring migration (*n* = 35 across 13 individuals with e-obs backpack devices; Figure S1 in Supporting Information) using the ‘move’ package version 3.2.0 (Kranstauber et al. 2019). The maximum number of consecutive missing locations was ≤3 days, so we expected that these missing locations would not negatively impact results, as the analyses were predominately based on fine-scale ACC data, and weather patterns are likely large enough to account for small imprecision in interpolated locations

Minimum temperature (°C) data were extracted for each once-daily GPS goose location from the National Centers for Environmental Prediction (NCEP)/Department of Energy Reanalysis II data set (2.5 x 2.5 degree spatial resolution; Kanamitsu et al. 2002) using the package ‘RNCEP’ version 1.0.1 (Kemp et al. 2012) in Program R version 4.0.2 (R Core Team 2020). The ‘RNCEP’ package provided four interpolated values (corresponding to approximately 0400, 1000, 1600 and 2200 h local time) at each location, which were averaged to obtain a daily value. We downloaded daily precipitation data from the Global Precipitation Climatology Project (CPCP) Version 1.3 (1-degree spatial resolution; Adler et al. 2017, Huffman et al. 2001) and extracted values using the R package ‘raster’ (Hijmans 2022). Daily temperature and precipitation were not strongly correlated (r = 0.15; p < 0.001; 95%CI: 0.12, 0.18).

**Statistical analyses**

We developed Bayesian hierarchical models and implemented them in JAGS using the package ‘jagsUI’ version 1.5.0 (Plummer 2003; Kellner 2018) in Program R version 4.0.2 (R Core Team 2020). Convergence was assessed via the Gelman-Rubin statistic (Brooks and Gelman, 1998) and visual inspection of traceplots. Continuous variables were standardized to have a mean of 0 and standard deviation of 1.

***Impact of daily conditions on ODBA and PTF***

We modeled the relationship between ODBAand weather conditions (minimum temperature and precipitation) using a dynamic linear model (e.g., Holmes et al. 2019, Laine 2020). The daily effects of each weather covariate on ODBA were estimated for each individual (i.e., one model per goose yielded estimates for each day of that bird’s migration). A linear regression model with dynamic coefficients was used to model daily effects of weather covariates on median daily ODBA. For each individual, the model was specified as:

where PRCP*t* and MTEMP*t* were precipitation and minimum temperature, respectively, for day *t*. *β0* represented the intercept and had a relatively vague normal prior with mean = 0 and standard deviation = 10. *β1,t* and *β2,t* were the slope parameters for the effects of covariates on day *t*. The priors for the effect on the first day, *β1,1* and *β2,1* were normal with mean = 0 and standard deviation = 10. *φ* represented the precision parameter and had a gamma prior with shape and rate = 0.1, and *μt* represented the expected value. The dynamic evolution of the regression coefficients *β1,t and β2,t* was modeled independently as:

where we assumed a random walk—and therefore imposing strong autocorrelation between the estimates—by fixing *ψk*to 1 for all *k*, and *υk,it*~ *N*(*0, ηk,i*) where *ηk,i* was process precision for covariate *k*, which had a gamma prior distribution with shape = 0.1 and rate = 1. We sampled three Markov Chain Monte Carlo (MCMC) chains, each with 120,000 iterations and a burn-in of 80,000, yielding 120,000 posterior samples.

We used the same approach for the effects of weather on proportion of time feeding, but replaced the linear model with a binomial generalized linear model, with the response consisting of the number of bursts classified as feeding and the total number of bursts such that:

The priors for the effect on the first day, *β1,1* and *β2,1* were normal with mean = 0 and standard deviation = 1.5. All other aspects of the model were the same as for ODBA.

***Influence of ODBA and PTF on probability of reproductive deferral***

We used a stochastic antecedent model (Ogle et al. 2015) to quantify the extent to which daily and cumulative ODBA and PTF during spring migration explained variation in the probability of an individual deferring reproduction. The antecedent variable is a cumulative measure of daily ODBA or PTF values weighted by the importance of each day (Ogle et al. 2015). If the antecedent variable explained substantial variation in the probability of incubation success, then a larger weight for one day than other days would indicate that specific day significantly affected the difference between individuals that successfully completed incubation and those that did not more than other days during spring migration. This may reveal time-lags in effects (e.g., if ODBA or PTF during staging was more important than ODBA or PTF on breeding areas in the days leading up to incubation; Ogle et al. 2015). We used a logistic regression for the likelihood of incubation success given the antecedent effects over a span of 54 days, which was the shortest-duration migration period due to limitations of different-length time series. This time period was unique to each individual and represented the last 54 days of migration as defined in the Methods section, and did not necessarily match calendar dates. The approach can be mathematically described as:

where *Yi(j)* was the binary response variable (1 for defer; 0 for attempt) for individual *i* in associated year *j,* *αj* was the random intercept for year *j*, *βk* represented slope parameters for *k*=1,2,3, which were the realized effects of the antecedent variable, Greenland or midcontinent population, and the interaction between these, on probability of deferral. The antecedent variable for individual *i* is noted as *antXi* and population of each individual is represented by *popi* (midcontinent = 0, Greenland = 1). A relatively vague uniform prior was used for between 0 and 100 and relatively vague normal prior was used for *βk* with mean = 0 and standard deviation = 10. Following Ogle et al. (2015), antecedent variables were calculated as:

where *D* indicated the duration of migration period, *Xi(j)* was the daily value for individual *i*, and *wX(j)* was the daily weight. A Dirichlet prior was used for weights (specified via the gamma distribution in JAGS with rate and shape = 1). MCMC chains each had 5,000 iterations and burn-in 2,500 samples, yielding 7,500 total posterior samples over three chains. The daily and cumulative weights estimated from the stochastic antecedent models were examined to determine temporal variation in importance of ODBA and PTF.

**RESULTS**

Based on movement and ODBA characteristics of collared birds, 3 out of 10 Greenland birds deferred nesting, and 4 of 10 midcontinent birds deferred (Table S1 in Supporting Information).

**DISCUSSION**

We applied an ecological modeling framework that, to our knowledge, has not been used in behavioral studies of animals. Our study is an initial example of blending temporally frequent ACC data with GPS data for birds of contrasting migration routes to uniquely quantify how individuals respond to their environment and the implications of individual behavioral patterns on reproduction. While the number of tracking devices included in our study is relatively low and we interpret our results cautiously, each unit collected thousands of data points which provides unique richness in behavioral data. Inferences from tracking studies are commonly limited because of the relatively low number of individuals tagged, but advances in miniaturized tracking technologies such as accelerometers allows for a substantial amount of information to be collected from each individual. This will increase our capacity to link animal behavior and individual reproductive output with environmental conditions (Valletta et al. 2017). Understanding linkages among behavior, environmental conditions, and reproductive success will allow practitioners to pinpoint critical periods of the annual cycle to ascribe priority areas for improved conservation efforts.

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**Competing interests:** The authors have no conflicts of interest to declare.

**Ethics approval:** Captures and handling of wild geese were permitted through the US Geological Survey (USGS Banding Permit #21314), Icelandic Institute of Natural History, and British Trust for Ornithology. The Texas A&M University-Kingsville Institutional Animal Care and Use Committee approved the capture and handling of wild geese (Approval #2015-09-01B) and use of captive-bred geese (Approval #2018-01-11).

**Consent to participate:** Not applicable.

**Consent for publication:** Not applicable.

**Availability of data and material:** The data analyzed in the current study are available from the corresponding author upon reasonable request.

**Code availability:** Code for analyses is available on GitHub (github.com/s-cunningham/GeeseBehavior-Weather)

**REFERENCES**

Adler R, Wang J-J, Sapiano M, Huffman G, Bolvin D, Nelkin E, NOAA CDR Program (2017). Global Precipitation Climatology Project (GPCP) Climate Data Record (CDR), Version 1.3 (Daily). NOAA National Centers for Environmental Information. Doi: 10.7289/V5RX998Z. Accessed 3 August 2022.

Afton AD, Paulus SL (1992) Incubation and brood care. In B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, & G. L. Krapu (Eds.), *Ecology and Management of Breeding Waterfowl*. University of Minnesota Press. pp. 62-108.

Alisauskas RT (2002) Arctic climate, spring nutrition, and recruitment in mid-continent lesser snow geese. Journal of Wildlife Management, 66:181–192.

Anderson JT, Haukos DA (2003) Breeding ground affiliation and movements of greater white-fronted geese staging in northwestern Texas. The Southwestern Naturalist 48:365–372 doi: 10.1894/0038-4909(2003)048<0365:BGAAMO>2.0.CO;2

Ankney CD, MacInnes CD (1978) Nutrient reserves and reproductive performance of female lesser snow geese. Auk 95:459–471.

Anthony RM, Flint PL, Sedinger JS (1991) Arctic fox removal improves nest success of black brant. Wildlife Society Bulletin 19:176–184.

Bauer S, Van Dinther M, Høgda, K-A, Klaassen M, Madsen J (2008) The consequences of climate-driven stop-over site changes on migration schedules and fitness of Arctic geese. Journal of Animal Ecology 77:654–660.

Bêty J, Giroux JF, and Gauthier G (2004) Individual variation in timing of migration: Causes and reproductive consequences in greater snow geese (*Anser caerulescens atlanticus*). Behavioral Ecology and Sociobiology 57:1–8 doi: 10.1007/s00265-004-0840-3

Black JM (1996) Introduction: pair bonds and partnerships. In Black, J. M. (Ed.), *Partnerships in birds: The study of monogamy.* Oxford University Press, pp. 3-20.

Black JM, Carbone C, Wells RL, Owen M (1992) Foraging dynamics in goose flocks: the cost of living on the edge. Animal Behavior 44:41–50.

Blumstein D, Evans C, Daniel J.(2006) *JWatcher*. Animal Behavior Laboratory at Macquarie University. https://www.jwatcher.ucla.edu/

Bowman TD, Stehn RA, Scribner KT (2004) Glaucous gull predation of goslings on the Yukon-Kuskokwim Delta, Alaska. Condor 106:288–298.

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

Boyd H, Fox AD, Kristiansen JN, Stroud DA, Walsh AJ, Warren SM (1998) Changes in abdominal profiles of Greenland White-fronted Geese during spring staging in Iceland. Wildfowl 49:57–71.

Brooks SP, Gelman A (1998) General methods for monitoring convergence of iterative simulations. Journal of Computational and Graphical Statistics 7:434–455.

Calenge C (2006) The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516-519 doi: 10.1016/j.ecolmodel.2006.03.017

Calenge C, Dray S, Royer-Carenzi M (2009) The concept of animals’ trajectories from a data analysis perspective. Ecological Informatics 4:43-41 doi: 10.1016/j.ecoinf.2008.10.002

Clausen KK, Madsen J, Tombre IM (2015) Carry-over or compensation? The impact of winter harshness and post-winter body condition on spring-fattening in a migratory goose species. PLoS ONE, 10, e0132312 doi: 10.1371/journal.pone.0132312

Cleasby IR., Bodey TW, Vigfusdottir F, McDonald JL, McElwaine G, Mackie K, Colhoun K, Bearhop S (2017) Climatic conditions produce contrasting influences on demographic traits in a long-distance Arctic migrant. Journal of Animal Ecology 86:285–295 doi: 10.1111/1365-2656.12623

Cubaynes S, Doherty PF, Schreiber EA, Gimenez O (2011) To breed or not to breed: a seabird’s response to extreme climatic events. Biology Letters 7:303–306 doi: 10.1098/rsbl.2010.0778

Dittami J, Thomforde C, Kennedy S (1977) Preliminary observations on the nesting of Barnacle Geese in Spitsbergen. Wildfowl, 28, 94–100.

Drent RH, Eichhorn G, Flagstad A, van der Graaf AJ, Litvin KE, Stahl J (2007) Migratory connectivity in Arctic geese: Spring stopovers are the weak links in meeting targets for breeding. Journal of Ornithology 148:501–S514 doi: 10.1007/s10336-007-0223-4

Ebbinge BS (1989) A multifactorial explanation for variation in breeding performance of Brent Geese *Branta bernicla*. Ibis 131:196-204 doi: 10.1111/j.1474-919X.1989.tb02762.x

Ely CR, Nieman DJ, Alisauskas RT, Schmutz JA, Hines JE (2013) Geographic variation in migration chronology and winter distribution of mid-continent greater white-fronted geese. Journal of Wildlife Management 77:1182–1191 doi: 10.1002/jwmg.573

Ely CR, Raveling DG (1984) Breeding biology of Pacific white-fronted geese. Journal of Wildlife Management 48:823–837.

Ely CR, Raveling DG (2011) Seasonal variation in nutritional characteristics of the diet of greater white-fronted geese. Journal of Wildlife Management 75:78–91 doi: 10.1002/jwmg.13

Erikstad KE, Fauchald P, Tveraa T, Steen H. (1998) On the cost of reproduction in long-lived birds: The influence of environmental variability. Ecology 79:1781–1788 doi: 10.1890/0012-9658(1998)079[1781:OTCORI]2.0.CO;2

Fehlmann G, O’Riain MJ, Hopkins PW, O’Sullivan J, Holton MD, Shepard ELC, King AJ (2017) Identification of behaviours from accelerometer data in a wild social primate. Animal Biotelemetry 5:1-6 doi: 10.11.86/s40317-017-0121-3.

Fondell TF, Miller DA, Grand JB, Anthony RM (2008) Survival of dusky Canada goose goslings in relation to weather and annual nest success. Journal of Wildlife Management 72:1614–1621 doi: 10.2193/2007-480

Fox AD, Bergersen E (2005) Lack of competition between barnacle geese *Branta leucopsis* and pink-footed geese *Anser brachyrhynchus* during the pre-breeding period in Svalbard. Journal of Avian Biology 36:173-178 doi: 10.1111/j.0908-8857.2005.03540.x

Fox AD, Francis I, Norriss D, Walsh A (2020) *Report of the 2019/2020 International Census of Greenland White-fronted Geese*. Accessed 15 April 2021. Retreived from: https://monitoring.wwt.org.uk/wp-content/uploads/2019/12/Greenland-White-fronted-Goose-Study-report-2019-20.pdf

Fox AD, Glahder CM, Walsh AJ (2003) Spring migration routes and timing of Greenland white-fronted geese - results from satellite telemetry. Oikos 103:415–425. doi: 10.1034/j.1600-0706.2003.12114.x

Fox AD, Hilmarsson JÓ, Einarsson Ó, Walsh AJ, Boyd H, Kristiansen JN (2002) Staging site fidelity of Greenland White-fronted Geese in Iceland. Bird Study 49:42-49.

Fox AD, Madsen J, Stroud DA (1983) A review of the summer ecology of the Greenland White-fronted Goose *Anser albifrons flavirostris*. Dansk Ornitologisk Forenings Tidsskrift 77:43–55.

Fox AD, Ridgill, SC (1985) Spring activity patterns of migrating Greenland White-fronted Geese in West Greenland. Wildfowl 36:21–28.

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

Fox AD, Walsh A (2012) Warming winter effects, fat store accumulation and timing of spring departure of Greenland White-fronted Geese *Anser albifrons flavirostris* from their winter quarters. Hydrobiologia 697:95–102 doi: 10.1007/s10750-012-1173-2

Fox AD, Weegman M, Bearhop S, Hilton G, Griffin L, Stroud D, Walsh A (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.

Francis IS, Fox AD (1987) Spring migration of Greenland white-fronted geese through Iceland. Wildfowl 38:7–12.

Gauthier G, Bêty J, Hobson KA (2003) Are greater snow geese capital breeders? New evidence from a stable-isotope model. Ecology 84:3250–3264 doi: 10.1890/02-0613

Glass TW, Breed GA, Robards MD, Williams CT, Kielland K (2020) Accounting for unknown behaviors of free-living animals in accelerometer-based classification models: Demonstration on a wide-ranging mesopredator. Ecological Informatics 60:101152 doi: 10.1016/j.ecoinf.2020.101152

Gómez Laich A, Wilson RP, Gleiss AC, Shepard ELC, Quintana F (2011) Use of overall dynamic body acceleration for estimating energy expenditure in cormorants. Does locomotion in different media affect relationships? Journal of Experimental Marine Biology and Ecology 399:151–155 doi: 10.1016/j.jembe.2011.01.008

Gudmundsson L, Bremnes JB, Haugen JE, Engen-Skaugen T (2012) Technical Note: Downscaling RCM precipitation to the station scale using statistical transformations - a comparison of methods. Hydrology and Earth System Sciences 16:3383–3390 doi: 10.5194/hess-16-3383-2012

Harrison XA, Blount JD, Inger R, Norris DR, Bearhop S (2011) Carry-over effects as drivers of fitness differences in animals. Journal of Animal Ecology 80:4–18 doi: 10.1111/j.1365-2656.2010.01740.x

Harrison XA, Hodgson DJ, Inger R, Colhoun K, Gudmundsson GA, 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 doi: 10.1371/journal.pone.0077783

Hijmans RJ (2022) raster: Geographic Data Analysis and Modeling. R package version 3.5-21. https://CRAN.R-project.org/package=raster

Holmes EE, Schuerell MD, Ward EJ (2019) *Applied time series analysis for fisheries and environmental data*. NOAA Fisheries, Northwest Fisheries Science Center.

Hübner CE (2006) The importance of pre-breeding areas for the arctic Barnacle Goose *Branta leucopsis*. Ardea 94:701–713.

Huffman GJ, Adler, RF, Morrissey MM, Bolvin DT, Curtis S, Joyce R, McGavock B, Susskind J. (2001) Global precipitation at one-degree daily resolution from multisatellite observations. Journal of Hydrometeorology 2: 36-50. doi: 10.1175/1525-7541(2001)002<0036:GPAODD>2.0.CO;2

Inger R, Harrison XA, Ruxton GD, Newton J, Colhoun K, Gudmundsson GA, McElwaine G, Pickford M, Hodgson D, Bearhop S (2010) Carry-over effects reveal reproductive costs in a long distance migrant. Journal of Animal Ecology 79:974–982 doi: 10.1111/j.1365-2656.2010.01712.x

Kanamitsu M, Ebisuzaki W, Woollen J, Yang S-K, Hnilo JJ, Fiorino M, Potter GL (2002) NCEP–DOE AMIP-II Reanalysis (R-2). Bulletin of the American Meteorological Society 83:1631–1644 doi: 10.1175/BAMS-83-11-1631

Kaufman, AB, Rosenthal R (2009) Can you believe my eyes? The importance of interobserver reliability statistics in observations of animal behavior. Animal Behavior 78:1487-1491.

Kellner K (2018) *jagsUI: A wrapper around ‘rjags’ to streamline ‘JAGS’ analyses*. R package version 1.5.0. Retrieved from https://cran.r-project.org/package=jagsUI

Kemp MU, van Loon EE, Shamoun-Baranes J, Bouten W (2012) RNCEP: Global weather and climate data at your fingertips. Methods in Ecology and Evolution 3:65–70 doi: 10.1111/j.2041-210X.2011.00138.x

King DT, Paulson JD, Leblanc DJ, Bruce K (1998) Two capture techniques for American white pelicans and great blue herons. Colonial Waterbirds 21:258–260.

Krams I, Cirule D, Suraka V, Krama T, Rantala MJ, Ramey G (2010) Fattening strategies of wintering great tits support the optimal body mass hypothesis under conditions of extremely low ambient temperature. Functional Ecology 24:172–177 doi: 10.1111/j.1365-2435.2009.01628.x

Kranstauber, B., Smolla, M., & Scharf, A. K. (2019). *Move: visualizing and analyzing animal track data. R package version 3.2.0*.

Krapu GL, Reinecke KJ, Jorde DG, Simpson SG (1995) Spring-staging ecology of mid-continent greater white-fronted geese. Journal of Wildlife Management 59:736–746.

Laine, M (2020) Introduction to Dynamic Linear Models for Time Series Analysis. In: Montillet, J-P, Bos, MS (eds) Geodetic Time Series Analysis in Earth Sciences. Springer, Switzerland, pp 139-156.

Lameris TK, van der Jeugd HP, Eichhorn G, Dokter AM, Bouten W, Boom MP, Litvin KE, Ens BJ, Nolet BA (2018) Arctic geese tune migration to a warming climate but still suffer from a phenological mismatch. Current Biology 28:2467–2473 doi: 10.1016/j.cub.2018.05.077

La Sorte FA, Fink D (2017) Migration distance, ecological barriers and en-route variation in the migratory behavior of terrestrial bird populations. Global Ecology and Biogeography 26:216–277 doi: 10.1111/geb.12534

Li H, Fang L, Wang X, Yi K, Cao L, Fox AD (2020) Does snowmelt constrain spring migration progression in sympatric wintering Arctic-nesting geese? Results from a Far East Asia telemetry study. Ibis 162:548–555 doi: 10.1111/ibi.12767

Lush L, Ellwood S, Markham A, Ward AI, Wheeler P (2016) Use of tri-axial accelerometers to assess terrestrial mammal behavior in the wild. Journal of Zoology 298:257-265 doi: 10.1111/jzo.12308

Madsen J, Bregnballe T, Mehlum F (1989) Study of the breeding ecology and behavior of the Svalbard population of Light-bellied Brent Goose *Branta bernicla hrota*. Polar Research 7:1–21 doi: 10.3402/polar.v7i1.6826

Nathan R, Spiegel O, Fortmann-Roe S, Harel R, Wikelski M, Getz WM (2012) Using tri-axial acceleration data to identify behavioral modes of free-ranging animals: general concepts and tools illustrated for griffon vultures. The Journal of Experimental Biology 215:986–996 doi: 10.1242/jeb.058602

Nishizawa H, Noda T, Yasuda T, Okuyama J, Arai N, Kobayashi M (2013) Decision tree classification of behaviors in the nesting process of green turtles (Chelonia mydas) from tri-axial acceleration data. Journal of Ethology 31:315-322 doi: 10.1007/210164-013-0381-1

Nolet, BA, Schreven, KHT, Boom, MP, Lameris, TK (2020) Contrasting effects of the onset of spring on reproductive success of Arctic-nesting geese. Ornithological Advances 137:1-9. doi: 10.1093/auk/ukz63

Ogle K, Barber JJ, Barron-Gafford GA, Bentley LP, Young JM, Huxman TE, Loik ME, Tissue, DT (2015) Quantifying ecological memory in plant and ecosystem processes. Ecology Letters 18:221–235 doi:10.1111/ele.12399

Olden JD, Lawler JJ, Poff NL (2008) Machine learning method without tears: A primer for ecologists. Quarterly Review of Biology 83:171-193.

Owen M (1972) Some factors affecting food intake and selection in White-fronted Geese. The Journal of Animal Ecology 41:79–92.

Owen, M. (1976). The selection of feeding site by white-fronted geese in winter. Journal of Applied Ecology, 13, 715–729.

Padisák J (1992) Seasonal succession of phytoplankton in a large shallow Lake (Balaton, Hungary) - A dynamic approach to ecological memory, its possible role and mechanisms. Journal of Ecology 80:217–230.

Piani C, Weedon GP, Best M, Gomes SM, Viterbo P, Hagemann S, Haerter JO (2010) Statistical bias correction of global simulated daily precipitation and temperature for the application of hydrological models. Journal of Hydrology 395:199–215 doi: 10.1016/J.JHYDROL.2010.10.024

Plummer M (2003) JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. Proceedings of the 3rd International Workshop on Distributed Statistical Computing 1–10.

R Core Team (2020) *R: a language and environment for statistical computing*. Version 4.0.2. Retrieved from https://www.r-project.org/

Reed ET, Gauthier G, Giroux, JF (2004) Effects of spring conditions on breeding propensity of greater snow goose females. Animal Biodiversity and Conservation 27:35–46.

Reiter P, Gutjahr O, Schefczyk L, Heinemann G, Casper M (2018) Does applying quantile mapping to subsamples improve the bias correction of daily precipitation? International Journal of Climatology 38:1623–1633 doi: 10.1002/joc.5283

Resheff YS, Rotics S, Harel R, Spiegel O, Nathan R (2014) AcceleRater: a web application for supervised learning of behavioral modes from acceleration measurements. Movement Ecology 2:27 doi: 10.1186/s40462-104-0027-0

Samelius G, Alisauskas RT (2006) Sex-biased costs in nest defence behaviors by lesser snow geese (*Chen Caerulescens*): consequences of parental roles? Behavioral Ecology and Sociobiology 59:805–810.

Shamoun-Baranes, J, Liechti, F, Vansteelant, WMG (2017) Atmospheric conditions create freeways, detours and tailbacks for migrating birds. Journal of Comparative Physiology   
A 203:509-529 doi: 10.1007/s00359-017-1181-9

Shepard ELC, Wilson RP, Quintana F, Gómez Laich A, Liebsch N, Albareda DA, Halsey LG, Gleiss A, Morgan DT, Myers AE, Newman C, Macdonand DW (2008) Identification of animal movement patterns using tri-axial accelerometry. Endangered Species Research 10:47–60 doi:10.3354/esr00084

Schreven KHT, Stolz C, Madsen J, Nolet BA (2021) Nesting attempts and success of Arctic- breeding geese can be derived with high precision from accelerometry and GPS-tracking. Animal Biotelemetry 9:25 doi: 10.1186/s40317-021-00249-9

Si Y, Xin Q, de Boer WF, Gong P, Ydenberg RC, Prins HHT (2015) Do Arctic breeding geese track or overtake a green wave during spring migration? Scientific Reports 5:8749 doi: 10.1038/srep08749

Stroud DA (1982) Observations on the incubation and post-hatching behaviuor of the Greenland White-fronted Goose. Wildfowl 33:63–72.

Tombre IM, Høgda KA, Madsen J, Griffin LR, Kuijken E, Shimmings P, Rees E, Vershceure C (2008) The onset of spring and timing of migration in two arctic nesting goose populations: the pink-footed goose *Anser brachyrhynchus* and the barnacle goose *Branta leucopsis*. Journal of Avian Biology 39:691–703.

Trinder MN, Hassell D, Votier S (2009) Reproductive performance in arctic-nesting geese is influenced by environmental conditions during the wintering, breeding and migration seasons. Oikos, 118:1093–1101 doi: 10.1111/j.1600-0706.2009.17429.x

U.S. Fish and Wildlife Service. (2020) *Waterfowl Population Status, 2020*. U.S. Department of the Interior, Washington, D.C. USA.

Valletta JJ, Torney C, Kings M, Thornton A, Madden J (2017) Applications of machine learning in animal behavior studies. Animal Behavior 124:203–220 doi: 10.1016/j.anbehav.2016.12.005

van Oudenhove L, Gauthier G, Lebreton JD (2014) Year-round effects of climate on demographic parameters of an arctic-nesting goose species. Journal of Animal Ecology 83:1322–1333 doi: 10.1111/1365-2656.12230

van Wijk RE, Kölzsch A, Kruckenberg H, Ebbinge BS, Müskens GJDM, Nolet BA (2012) Individually tracked geese follow peaks of temperature acceleration during spring migration. Oikos 121:655–664 doi: 10.1111/j.1600-0706.2011.20083.x

VonBank JA (2020) *Migration, movement, and winter ecology of midcontinent greater white-fronted geese*. PhD Dissertation. Texas A&M University-Kingsville.

VonBank JA, Weegman MD, Link PT, Cunningham SA, Kraai KJ, Collins DP, Ballard BM (2021) Winter fidelity, movements, and energy expenditure of Mid-continent Greater White-fronted Geese. Movement Ecology 9:2 doi: 10.1186/s40462-020-00236-4

Warren SM, Walsh AJ, Merne OJ, Wilson HJ, Fox AD (1992) Wintering site interchange amongst Greenland White-fronted Geese (*Anser albifrons flavirostris*) captured at Wexford Slobs, Ireland. Bird Study 39:186–194 doi: 10.1080/00063659209477117

Weber TP, Ens BJ, Houston AI (1998) Optimal avian migration: A dynamic model of fuel stores and site use. Evolutionary Ecology 12:377–401 doi: 10.1023/A:1006560420310

Weegman MD (2014) *The demography of the Greenland White-fronted Goose*. PhD Thesis. University of Exeter.

Weegman MD, Bearhop S, Fox AD, Hilton GM, Walsh AJ, McDonald JL, Hodgson DJ (2016a) Integrated population modelling reveals a perceived source to be a cryptic sink. Journal of Animal Ecology 85:467–475 doi: 10.1111/1365-2656.12481

Weegman MD, Bearhop S, Hilton GM, Walsh A, Fox AD (2016b) Conditions during adulthood affect cohort-specific reproductive success in an Arctic-nesting goose population. PeerJ 4:e2044 doi: 10.7717/peerj.2044

Weegman MD, Bearhop S, Hilton GM, Walsh A, Weegman KM, Hodgson DJ, Fox AD (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 MD, Bearhop S, Hilton GM, Walsh AJ, Griffin L, Resheff YS, Nathan R, Fox AD (2017a) Using accelerometry to compare costs of extended migration in an arctic herbivore. Current Zoology 63:667-674 doi: 10.1093/cz/zox056

Weegman MD, Fox AD, Hilton GM, Hodgson DJ, Walsh A, Griffin LR, Bearhop S (2017b) Diagnosing the decline of the Greenland White-fronted Goose *Anser albifrons flavirostris* using population and individual level techniques. Wildfowl 67:3–18.

Weegman MD, Walsh AJ, Ogilvie MA, Bearhop S, Hilton GM, Hodgson DJ, Fox AD (2022) Annual survival and per capita production of young explain dynamics of a long-lived goose population. Ibis 162:574–580 doi: 10.1111/ibi.13013

Wiersma P, Piersma T (1994) Effects of microhabitat, flocking, climate and migratory goal on energy expenditure in the annual cycle of red knots. Condor 96:257–279.

Wilson HJ, Norriss DW, Walsh A, Fox AD, Stroud DA (1991) Winter site fidelity in Greenland White-fronted Geese *Anser albifrons flavirostris*: implications for conservation and management. Ardea 79:287–294.

Wilson RP, Börger L, Holton MD, Scantlebury DM, Gómez-Laich A, Quintana F, Rosell F, Graf PM, Williams H, Gunner R, Hopkins L, Marks N, Geraldi NR, Duarte CM, Scott R, Strano MS, Robotka H, Eizaguirre C, Fahlman A, Shepard ELC (2019) Estimates for energy expenditure in free-living animals using acceleration proxies: A reappraisal. Journal of Animal Ecology 89:161–172 doi: 10.1111/1365-2656.13040

**REFERENCES**

Fox AD, Boyd H, Walsh AJ, Stroud DA, Nyeland J, Cromie RL (2012) Earlier spring staging in Iceland amongst Greenland White-fronted Geese *Anser albifrons flavirostris* achieved without cost to refuelling rates. Hydrobiologia 697:103–110 doi: 10.1007/s10750-012- 1174-1

Fox AD, Ridgill SC (1985). Spring activity patterns of migrating Greenland White-fronted Geese in West Greenland. Wildfowl 36:21–28.

Gudmundsson, L., Bremnes, J. B., Haugen, J. E., & Engen-Skaugen, T. (2012). Technical Note: Downscaling RCM precipitation to the station scale using statistical transformations - a comparison of methods. *Hydrology and Earth System Sciences*, *16*, 3383–3390. <https://doi.org/10.5194/hess-16-3383-2012>

Lewis TL, Flint PL, Schmutz JA, Derksen DV (2010) Pre-moult patterns of habitat use and moult site selection by Brent Geese *Branta bernicla nigricans*: individuals prospect for moult sites. Ibis 152:556–568 doi: 10.1111/j.1474-919X.2010.01023.x

Pagano AM, Rode KD, Cutting A, Owen MA, Jensen S, Ware JV, Robbins CT, Durner GM,

Atwood TC, Obbard ME, Middel KR, Thiemann GW, Williams, TM (2017) Using tri-axial accelerometers to identify wild polar bear behaviors. Endangered Species Research 32:19–33.

Piani C, Weedon GP, Best M, Gomes SM, Viterbo P, Hagemann S, Haerter JO (2010) Statistical bias correction of global simulated daily precipitation and temperature for the application of hydrological models. Journal of Hydrology 395:199–215 doi: 10.1016/J.JHYDROL.2010.10.024

Reiter P, Gutjahr O, Schefczyk L, Heinemann G, Casper M (2018) Does applying quantile mapping to subsamples improve the bias correction of daily precipitation? International Journal of Climatology 38:623–1633 doi:10.1002/joc.5283

Tatler J, Cassey P, and Prowse TAA (2018) High accuracy at low frequency: detailed behavioural classification from accelerometer data. Journal of Experimental Biology 221:jeb1814085 doi: 10.1242/jeb.184085.

Weegman MD (2014). *The demography of the Greenland White-fronted Goose*. University of Exeter.

**Figure legends**

**Fig. 1.** Migration locations of 10 midcontinent and 25 Greenland white-fronted geese tracked via GPS across North America and northwest Europe in 2012–2013 and 2017–2018. Shaded areas (Prairie Pothole Region in North America and Iceland) indicate staging areas from which the last day in these regions was used to determine the end of the migration period. Inset shows latitudinal movements of migrating geese by date.

**Fig. 2.** Weather covariates.

**Fig. 3.** Proportion of posterior samples >0 for time-varying regression coefficients of minimum temperature (°C) and precipitation (mm on ODBA. Date is shown on the x-axis (note difference between Greenland and midcontinent populations). Darker red indicates a greater proportion of posterior samples above zero, while darker blue indicates a smaller proportion of posterior samples above zero.

**Fig. 4.** Predicted probability of deferring reproduction according to population and antecedent variable.

Map

Description automatically generated

Fig. 1

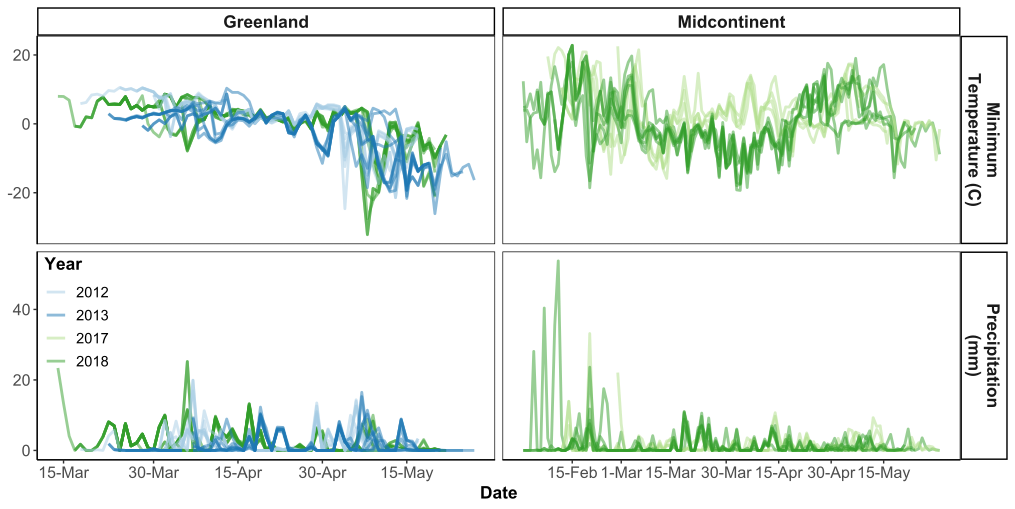


Fig. 2

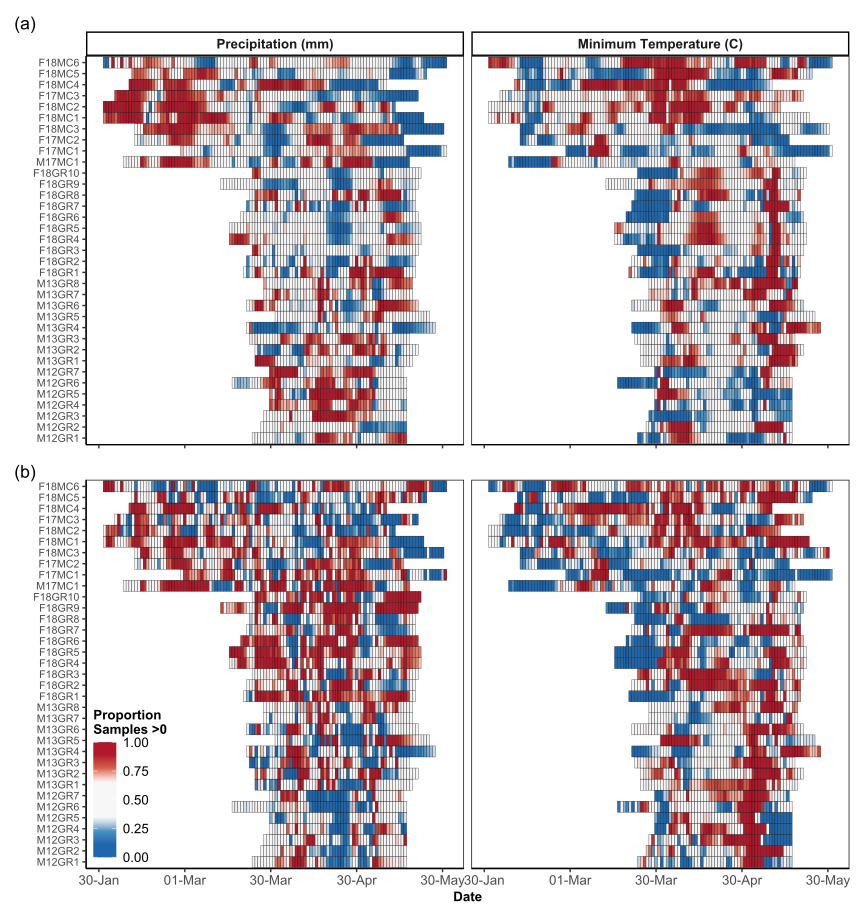


Fig. 3

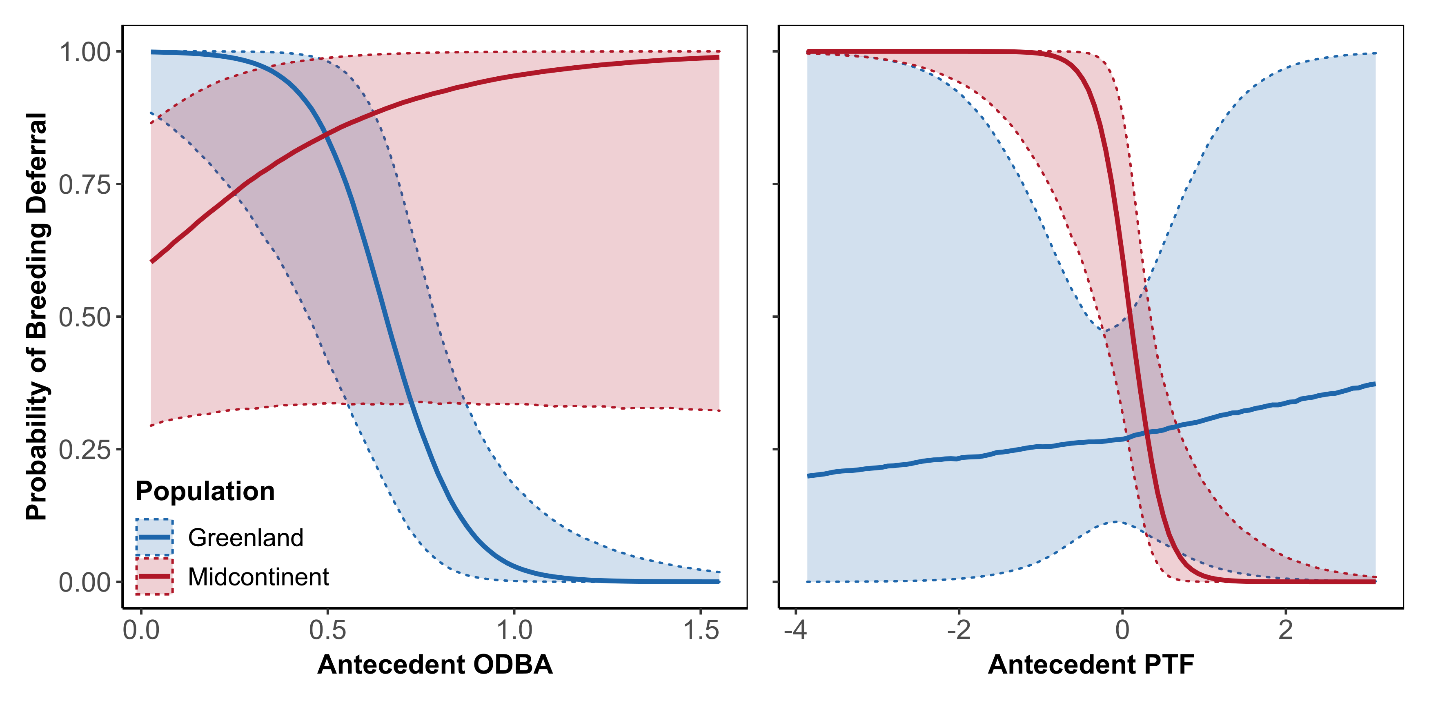


Fig. 4

1. ⱡ**Author contributions:** SAC, BMB, SB, ADF, GMH, LRG, and MDW conceived the ideas; JAV, AJW, LRG and MDW led the fieldwork and data collection with contributions from SAC, ADF, BMB, and TLJS and support from LC; SAC, JAV, and MDW scored the recordings of collared geese; SAC, TLJS, CKW and MDW devised the analytical methodology; SAC and TLJS performed statistical analyses with input from CKW, and MDW. SAC and MDW led the writing of the manuscript. All authors contributed critically to versions of the manuscript and gave final approval for publication. [↑](#footnote-ref-1)