**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 ≥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 resoultion; 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) 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; cite), and extracted values using the R package ‘raster’ (Hijmans 2022). Daily temperature and precipitation did not exhibit a strong correlation (*xxxx*).

**Statistical analyses**

We investigated the proportion of daily cumulative ODBA from feeding, ODBAgraze, as a measure of energy intake relative to expenditure. 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). Continuous variables were standardized to have a mean of 0 and standard deviation of 1. The 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**

**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)

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**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.

Map

Description automatically generated

Fig. 1

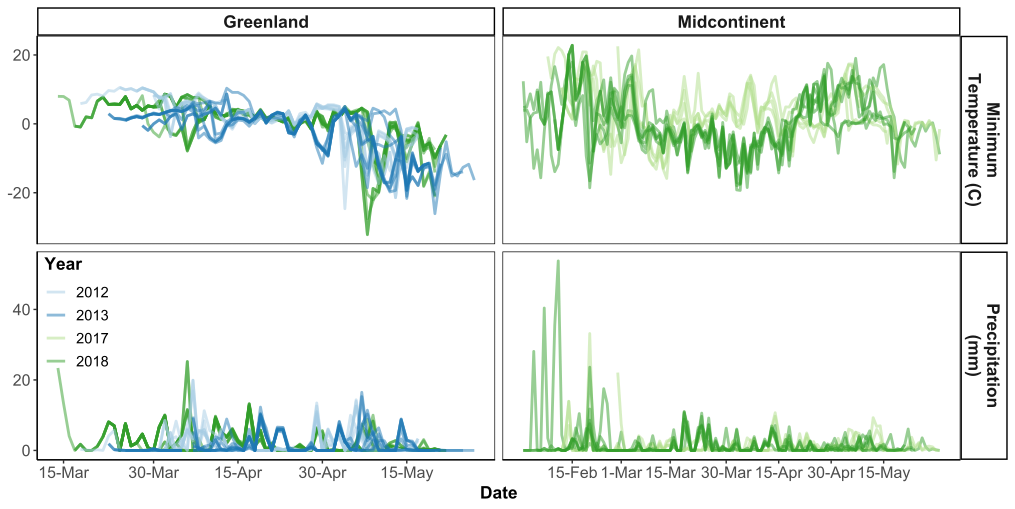


Fig. 2

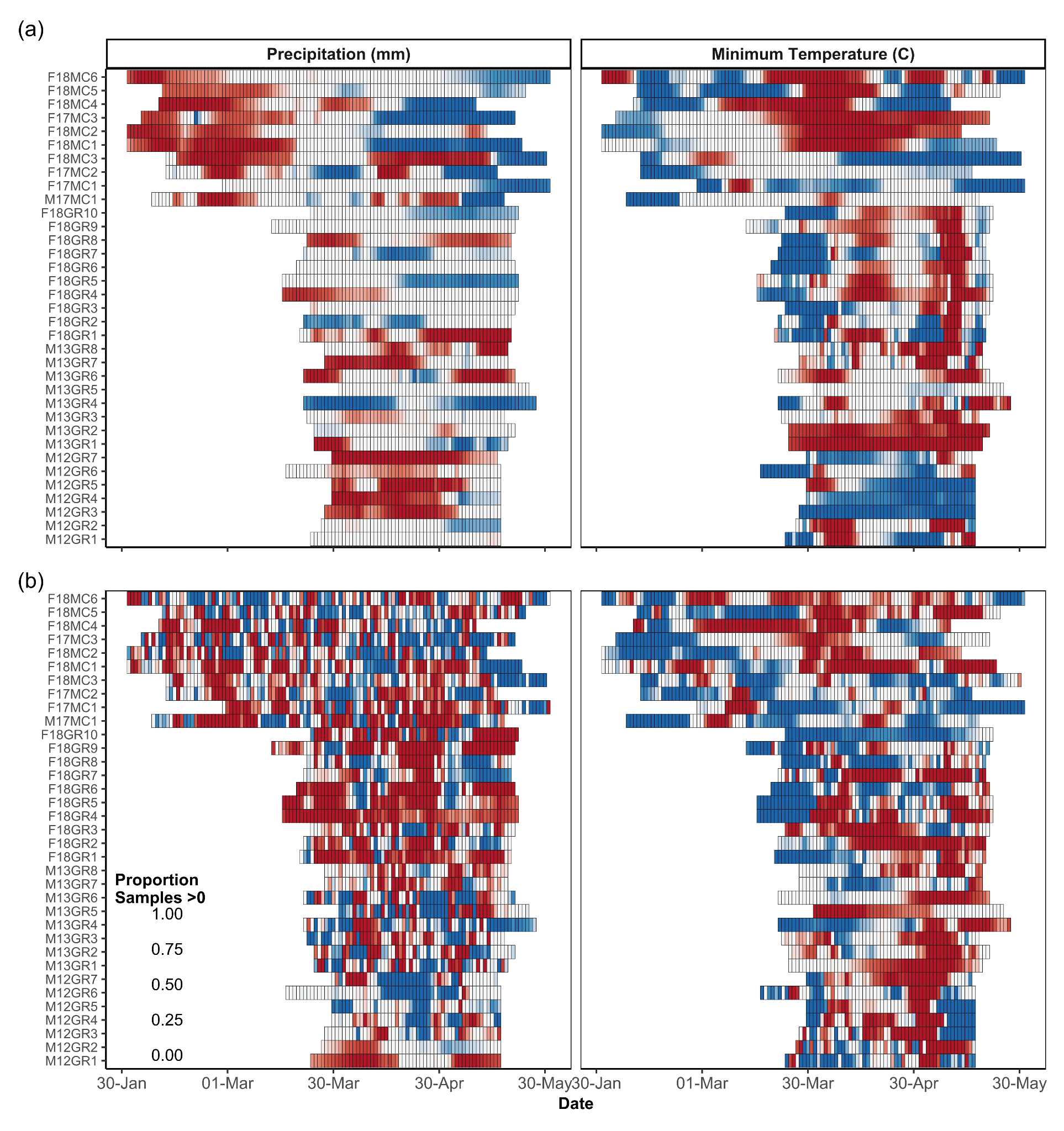


Fig. 3

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)