**INTRODUCTION**

Arctic-nesting geese obtain resources for reproduction before and during migration, as well as after arrival to breeding areas (Gauthier et al. 2003; Drent et al. 2007), and of particular importance are the stopover areas birds use to refuel and build fat and protein stores before continuing migration (Weber et al. 1998). These resources are important in explaining variation in clutch size of Arctic-nesting geese (Alisauskas 2002; Inger et al. 2010), as well as ensuring survival of the female through incubation (Ankney and MacInnes, 1978). Many migrants move north in early spring to arrive at staging or breeding areas before food sources are readily available (Si et al. 2015; Li et al. 2020) because it is generally advantageous for offspring survival that adults arrive and initiate nests early (Bêty et al. 2004). However, recent climate change and Arctic amplification of warming effects have resulted in earlier springs, leading geese to experience mismatches in the timing of their optimal food sources as they migrate to and arrive on breeding areas (Lameris et al. 2018).

Conditions driven by large-scale climate patterns have been linked to life-history tradeoffs, with lower reproduction in years when environmental conditions are less favorable (Cubaynes et al. 2011; Cleasby et al. 2017) because individuals of long-lived species are expected to forego reproduction if conditions are such that expending energy in a reproductive attempt would compromise future survival and/or reproductive success (Erikstad et al. 1998). Conditions at staging areas can influence food availability in addition to affecting individual energy expenditure via increased thermoregulation (Wiersma and Piersma 1994; Bauer et al. 2008), with subsequent influence on reproductive performance (Inger et al. 2010; Harrison et al. 2011; van Oudenhove et al. 2014). Yet Arctic-nesting geese are resilient; for example, they can often compensate for poor winter conditions as they migrate north (Clausen et al. 2015).

In addition to weather conditions, physical characteristics of migration routes can present challenges that limit where birds can stop to refuel. Different strategies are likely required to overcome the various barriers encountered en route in order to arrive at breeding areas with sufficient body condition for reproduction. While birds undertaking an overall longer migration may be challenged by increased energy requirements, they generally have more flexibility to adjust their migration to conditions they encounter (La Sorte and Fink 2017). Similarly, large water crossings such as across oceans can diminish the predictability of conditions from one stopover location to the next and therefore reduce a bird’s ability to respond to changes in timing of the onset of spring, which is related to forage quality (Tombre et al. 2008). A potential earlier onset of spring is particularly problematic for populations that are limited in their ability to use environmental cues to adjust their migration route and timing.

In this paper, we examined how weather conditions and behavioral responses to weather conditions encountered during migration explained variation in reproductive success of greater white-fronted geese *Anser albifrons* across two flyways: the Greenland subspecies *A. a. flavirostris* and the North American mid-continent population *A. a. frontalis* (hereafter ‘Greenland geese’ and ‘mid-continent geese’). Greenland geese cross the North Atlantic from wintering areas in Britain and Ireland to Icelandic staging areas, and to breeding areas in western Greenland, with relatively few sustained stops (Fox et al. 2003). In contrast, mid-continent geese migrate entirely over land from southern US wintering areas to breeding areas in the Canadian and Alaskan Arctic, with much more frequent shorter, stops to refuel (Ely et al. 2013; VonBank 2020; Fig. 1). Thus, individuals in each flyway experience potentially different weather conditions as they travel to the Arctic, which we anticipate yields differences in migration strategy between mid-continent and Greenland birds.

The population size of mid-continent geese has been stable or increasing in recent years (U.S. Fish and Wildlife Service 2020, R. Alisauskas, unpublished data) while the Greenland population has declined 39% since 1999 (Fox et al. 2020). Recent demographic modelling has suggested that reduced recruitment is the most likely demographic mechanism for the Greenland white-fronted goose population decline (Fox et al. 2003; Boyd and Fox 2008; Weegman 2014; Weegman et al. 2022) and very few individuals successfully reproduce more than once during their lifetime (Weegman et al. 2016b). Researchers have not yet quantified whether low productivity in Greenland white-fronted geese is explained by breeding deferral or failed attempts, and whether such rates are similar or different to those in mid-continent white-fronted geese.

We had two objectives for this study: 1) assess the influence of fine-scale (i.e., daily) temperature and precipitation patterns on daily energy expenditure (ODBA) and proportion of time spent feeding (PTF) during spring migration, and 2) determine the extent to which ODBA and PTF explain variation in probability of deferred reproductiction of birds in each flyway, based on daily and summarized values. While average daily ODBAgraze is expected to increase to a certain extent with time spent feeding due to body motion while feeding (Wilson et al. 2019), we also expected that it would be reflective of individual patterns of space use. Therefore, we expected that geese with higher ODBAgraze (i.e., greater proportion of daily ODBA from feeding) would be more likely to succeed in reproduction, and days later in spring migration (e.g., within 2 weeks prior to average initiation of incubation) would have larger weights, as individuals migrating and preparing to incubate/nest guard require more energy than those migrating and not preparing to incubate/nest guard. We hypothesized that feeding behavior and energy expenditure would be positively associated with minimum temperature because low temperatures were expected to increase energetic costs due to thermoregulation (Krams et al. 2010) and negatively associated with precipitation (Reed et al. 2004).

**RESULTS**

**Incubation outcome**

Using characteristics of movement and ODBA, successful (full term) incubation was identified in 4 (50%) mid-continent and 6 (23%) Greenland geese.

**Quantifying weather effects on proportion of energy expenditure from feeding**

Time-varying coefficient effects of minimum temperature were stronger overall than precipitation rate. There was a prominent association between minimum temperature and ODBAgraze in Greenland geese, with all but four birds showing a positive relationship for at least one day for 10-14 days prior to the end of the migration period (Fig. 3). This pattern occurred in Greenland geese that deferred or failed as well as those that completed incubation, but it was only present in two of eight mid-continent geese (one successful). There were also indications of a negative relationship between minimum temperature and ODBAgraze in some Greenland geese early in migration. Precipitation rate was important for only one successful mid-continent bird, with a negative relationship at the end of migration, while the relationship was positive earlier during the migration period and short-lived in Greenland geese (Fig. 3).

**Antecedent effect of proportion of energy expenditure from feeding on probability of reproductive success**

The interaction of flyway and antecedent ODBA (the sum of daily ODBA multiplied by daily weight) weakly explained variation in probability of successful incubation. Further, antecedent ODBAgraze and flyway as separate effects did not explain variation in flyway reproductive success (Table 1). The model did not detect any differentially important time points for antecedent ODBAgraze, and all daily weights were close to 0.02, which is equal to 1 divided by 51, the total number of days in the model (Supporting Information Fig. S1).

**DISCUSSION**

Here we used a combination of GPS and ACC data to assess many temporal relationships (i.e., daily) and the cumulative effect of animal decision-making on productivity, measured as full-term incubation. We found consistent and strong effects of daily minimum temperature but not precipitation on nearly all Greenland white-fronted geese as individuals neared breeding areas. There was not a strong relationship between minimum temperature or precipitation rate on mid-continent white-fronted geese during migration from wintering to breeding areas. The interaction of flyway and the cumulative effect of proportion of energy expenditure from feeding explained limited variation in probability of reproductive success, measured as full-term incubation. Further, we did not identify specific time periods that were differentially important for proportion of time feeding or energy expenditure in explaining reproductive success or failure/deferral. Our approach aimed to examine acute effects, and while the stochastic antecedent framework permitted testing of a summarized variable, we did not examine the cumulative effects of weather on ODBAgraze. Therefore, we suggest that despite physical differences experienced by geese in each flyway, incubation outcome and reproductive success is likely due to events and conditions occurring after geese have arrived on breeding areas.

Relatively few (23%) Greenland geese were successful in completing incubation. Based on movement and ODBA patterns, there were ≥6 geese that failed partway through incubation (i.e., after 3–12 days; IDs 2, 4, 5, 11, 12, 17). Thus, low productivity at least in our tagged Greenland birds comprised high rates of both deferrals and failed attempts. Half of the mid-continent geese were successful in completing incubation. After a successful incubation period, there are still many factors between hatching and arriving at wintering areas that can influence the number of young that recruit into a population. An early onset of spring can lead to increased mortality of offspring due to a mismatch between gosling growth and peak food quality, regardless of parent abilities to refuel after arriving in the Arctic (Lameris et al. 2018). Goslings are vulnerable to a variety of predators (Anthony et al. 1991; Bowman et al. 2004) and harsh weather (Fondell et al. 2008), which makes it difficult to confirm our classifications of reproductive success, deferral, or failure by resighting geese in autumn or winter.

Previous analyses of accelerometer-derived behavior data in geese suggested that they spend nearly 50% of their time feeding during migration, and up to 60% of their daily time budget in the period immediately preceding breeding (Lameris et al. 2018). In our tagged birds, an average of 74% of daily energy expenditure occurred from feeding, which is consistent with observations by Fox and Ridgill (1985). Habitats used by individuals in the two flyways during spring stopovers can be quite different, and we expected that this would be reflected in differences in ODBAgraze between the two flyways. Greenland geese feed primarily on grass in hay meadows and limited waste grain in Iceland (Boyd et al. 1998; Fox and Walsh 2012), while mid-continent geese feed extensively on waste grain (Krapu et al. 1995; Ely et al. 2013). Geese must feed longer on grasses than agricultural grains to acquire energy, and while most grasses are higher in protein, they are lower in lipid content compared to agricultural grains (Ely and Raveling 2011). We suggest that the lack of difference in ODBAgraze between flyways may be due at least in part to geese adjusting feeding rate without increasing total time spent foraging (Owen 1972, 1976). Further, fine-scale behavior related to dominance of individual and feeding position within a flock could impact forage intake (Black et al. 1992) but may not have been evident in accelerometer data. Additionally, our inferences could have been affected by relatively small sample sizes or limited weather variables being tested.

We demonstrated that populations with different migration strategies are impacted differently by precipitation and temperature, and that while some adverse conditions may be overcome by individuals in each population, the effect may be stronger for Greenland geese, which are limited in areas for refueling compared to mid-continent birds (because Greenland birds cross the North Atlantic). Positive effects of minimum temperature on ODBA in Greenland birds were mainly concentrated in the last week before birds departed Iceland. We expected temperature to be linked to forage quality (van Wijk et al. 2012), so this positive association could be a result of increased plant growth providing greater opportunities for geese to feed prior to migration to Greenland. We attribute the lack of weather effects on ODBA in mid-continent geese to their ability to move north in smaller increments, thereby adjusting to ambient temperature at large spatial scales to optimize intake, which is potentially less possible for Greenland white-fronted geese due to crossing the North Atlantic and Greenland Ice Sheet. However, light-bellied brent geese (*Branta bernicla hrota*) follow an almost identical migratory route to Greenland white-fronted geese, with documented effects of weather conditions on demographic rates (Harrison et al. 2013; Cleasby et al. 2017). Thus, further investigation into a broader suite of weather conditions may reveal different patterns in daily and cumulative effects on energy expenditure and reproductive success.