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Using accelerometry to compare costs of extended migration in an arctic herbivore

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Abstract

Understanding how individuals manage costs during the migration period is challenging because individuals are difficult to follow between sites; the advent of hybrid Global Positioning System–acceleration (ACC) tracking devices enables researchers to link spatial and temporal attributes of avian migration with behavior for the first time ever. We fitted these devices on male Greenland white-fronted geese *Anser albifrons flavirostris* wintering at 2 sites (Loch Ken, Scotland and Wexford, Ireland) to understand whether birds migrating further during spring fed more on wintering and staging areas in advance of migration episodes. Although Irish birds flew significantly further (ca. 300 km) than Scottish birds during spring, their cumulative hours of migratory flight, flight speed during migration, and overall dynamic body ACC (i.e., a proxy for energy expenditure) were not significantly different. Further, Irish birds did not feed significantly more or expend significantly more energy in advance of migration episodes. These results suggest broad individual plasticity in this species, although Scottish birds arriving on breeding areas in Greenland with greater energy stores (because they migrated less) may be better prepared for food scarcity, which might increase their reproductive success.

Key words: avian migration cost, energy expenditure, global positioning system–acceleration tracking devices, Greenland white-fronted geese, individual decision-making, proportion of time feeding.

Migration is one of the most energetically costly periods in the avian annual cycle (Newton 2008) and species manage these costs in multiple ways. Staging sites in between breeding and wintering areas are often used to replenish energy stores (Klaassen 1996; Chevallier et al. 2010), where some individuals "prepare" for the continued cost of migration by increasing foraging rate, duration, and digestion efficiency immediately prior to departure (e.g., 14–21 days pre-departure; Fox et al. 2014) through hyperphagia (Odum 1960; McWilliams and Karasov 2001), while other individuals (and indeed, species) undergo changes in the digestive tract (Piersma et al. 1993; Hume and Biebach 1996). Still yet, other species such as blackcaps *Sylvia atricapilla* exhibit broad morphological characteristics among individuals and between ages, including greater wing length and pointedness in migratory individuals compared with

those sedentary or migrating shorter distances (Perez-Tris and Telleria 2001; Rolshausen et al. 2009). Thus, there exist a variety of adaptations associated with minimizing the cost of migration.

Emergent tracking technologies have provided unprecedented opportunities for researchers to follow individuals through space and time as never before, enabling studies of the consequences of adopting different migration strategies by individuals (Wikelski et al. 2007; Bridge et al. 2011). For example, the advent of miniature accelerometers now enables the calculation of overall dynamic body acceleration (ODBA; Wilson et al. 2006) of a bird as a direct proxy for energy expenditure (Green et al. 2009; Elliott et al. 2013; Spivey and Bishop 2013) throughout its annual cycle to compare the energetic consequences associated with different migration strategies (Bishop et al. 2015). Hence, we are now able to approximately test the assumption that if an individual flies 10% further than another in the course of a single migration episode, it should previously acquire and then expend that much more energy based on cumulative hours of migratory flight alone (all other things being equal).

Greenland white-fronted geese *Anser albifrons flavirostris* wintering in the southernmost part of the winter range at Wexford Slobs, Ireland (52° 22′N, 6° 24′W) tend to stage in western Iceland and breed in the northernmost part of the range in western Greenland, while those wintering in the northern part of the wintering range in Scotland (e.g., at Loch Ken, 55° 0′N, 4° 3′W) tend to stage in southern Iceland and breed further south in Greenland (Fox et al. 1983; Kampp et al. 1988). As a result of this leapfrog migration, a bird wintering in the south of the range may fly up to 300 km further over the course of a ca. 3,000 km spring migration than a bird wintering further north (Kampp et al. 1988).

In this analysis, we use hybrid Global Positioning System (GPS) and acceleration (ACC) tracking devices fitted to Greenland white-fronted geese to compare the migration distance, cumulative hours of migratory flight, and flight speed during migration between Irish and Scottish birds during spring (i.e., from wintering to breeding areas). We test whether birds migrating further expended more energy (i.e., exhibited greater ODBA). We compare the average proportion of daily feeding behavior between Irish and Scottish birds during "important" phases of the migration period (i.e., 14 days prior to departure from wintering areas, 14 days prior to departure from Icelandic staging areas, and overall, from 14 days prior to departure from wintering areas to the first 14 days on breeding areas) when individuals of this subspecies are known to forage extensively to increase nutrient reserves for migration (Fox 2003; Fox et al. 2014). We also compare the total time feeding during migration for Irish and Scottish birds to assess whether birds exhibiting greater ODBA during migration feed proportionally more to "prepare" for longer migration events. Finally, we compare ODBA in Irish and Scottish birds during important phases of the migration period to robustly assess trade-offs in migration preparation (where individuals should theoretically maximize energy acquisition and minimize ODBA).

Materials and Methods

During winter in 2012 and 2013, 157 Greenland white-fronted geese were caught using traditional cannon-netting methods at Loch Ken, Scotland (22 birds) and Wexford Slobs, Ireland (135 birds) under ringing endorsements granted to A.J. Walsh, J. Skilling, and C. Mitchell from the British Trust for Ornithology (BTO). Both sites comprised intensively managed grassland; Wexford is also partially cropland (Fox et al. 1998). Caught birds were marked with a white

plastic leg ring and an orange neck collar (both inscribed with the identical unique alphanumeric code, see Warren et al. 1992) as well as a standard numbered metal leg ring. Collar code combinations were visible from up to 800 m using a 20–60× spotting scope. Individual geese were aged on capture by plumage characteristics (presence/absence of white frons on face and black belly bars) and sexed by cloacal examination (Cramp and Simmons 1977; Warren et al. 1992).

Deployment of and subsequent data download from GPS–ACC tracking devices

Forty-one adult male birds (12 at Loch Ken and 29 at Wexford; 6 and 14 in 2012; and 6 and 15 in 2013; respectively) were fitted, under license from the BTO, with 28 g GPS–ACC tracking devices (with internal GPS and ultra high frequency [UHF] antennae; e-obs GmbH: Grünwald, Germany) as a backpack behind the wing bases using an 83 cm single piece of pre-stretched 3 mm elastic shock cord, which was crossed on the belly and ran in front of the leg joints (i.e., total weight of device and harness 39 g, 1.4% of mean body mass of tagged geese). Tags comprised (i) a GPS device which measured spatial position (i.e., latitude, longitude, and elevation) at each fix and (ii) an accelerometer which measured ACC on 3 axes at a frequency of 10.5 Hz each. Tags were programmed to record one GPS fix per day and one 3-s ACC bout every 6 min (i.e., 240 fixes per day). Tagged individuals were resighted by A.J. Walsh, L.R. Griffin, and M.D. Weegman when the birds returned to the wintering areas the following year (i.e., during late autumn in 2012 and 2013) and the previous ≥8 months of GPS–ACC data (1,163,553 fixes and 4,831 goose-days) were downloaded from 15 individual birds (Loch Ken: 3 birds in 2012, 2 birds in 2013; Wexford: 4 birds in 2012, 6 birds in 2013) to a receiver via UHF radio link at distances up to 800 m. An additional 10 birds (5 in 2012, 5 in 2013) were resighted on staging or wintering areas, from which no data were downloaded because of tag loss or malfunction.

Matching ACC data with animal behavior from film

GPS–ACC tracking devices were deployed on 2 captive Greenland white-fronted Geese at Wildfowl & Wetlands Trust, Slimbridge, UK (51° 44′N, 2° 24′W) during winter 2012 and these individuals filmed for a total of 30 h to "ground truth" ACC traces with known behaviors. Thus, the dataset included 155 observed instances of feeding, stationary, and walking behavior in total. Flight was identified retrospectively based on (i) visual inspection of wild bird ACC data and (ii) z-axis standard deviation >0.50 m s^{-2} which indicated large amplitude and frequency of a burst that was uniquely distinguishable from all other behaviors. We randomly sampled 100 instances of flight and included these in our "known" behavior dataset.

Processing GPS and ACC data

Daily movement (km) was calculated using the Haversine formula to determine the great circle distance between 2 successive points (Sinnott 1984). In cases where a GPS fix was missing, we calculated the average daily difference from the previous GPS fix. The ACC data output in millivolts was transformed to ACC m s^{-2} using Program R, version 2.14.2 (R Development Core Team 2012), based on tag-specific calibrations prior to tag deployment. Using a suite of machine learning algorithms (e.g., linear discriminant analysis, classification regression trees, and random forest, see Nathan et al. [2012] for review) in the AcceleRater web tool (Resheff et al. 2014), initial

behavioral classification was carried out based on inputted known behavioral ACC signatures derived from the observational study of 2 tagged captive birds and (in the case of flight) 3 tagged wild birds to train the algorithms to identify unknown behavior. An algorithm was selected to classify known behaviors when 95% accuracy was achieved. However, none of the models were able to distinguish feeding from walking behavior (i.e., we could not reach 95% accuracy using any machine learning algorithm); thus, we combined these behaviors as most walking activity in geese is associated with feeding. Behaviors were classified as feeding/walking (hereafter feeding), flying, and stationary (i.e., encompassing resting, sleeping, and surveillance). The random forest algorithm correctly labeled 95% of the captive bird behavior and was selected to classify behaviors in the wild bird dataset.

Calculations of the proportion of time feeding and ODBA

Irish and Scottish birds forage on food items of similar nutrient contents in Great Britain and Ireland, Iceland, and Greenland (Fox and Madsen 1981; Mayes 1991; Kristiansen et al. 1998; Glahder 1999; Fox 2003). As such, we used the proportion of time feeding as a proxy for energy acquisition across important phases of the migration period and assumed minimal differences in nutrient quality among food types within these places. Energy expenditure is often more difficult to measure because of biases associated with determining the conditions to which individuals are exposed (Furness and Bryant 1996) and potential variation between captive and wild individuals of the same species (Costa 1987; Culik and Wilson 1991). However, ODBA has recently been used as a proxy (Wilson et al. 2006; Shepard et al. 2008; Gleiss et al. 2011) where aggregate ACC of an individual is based on the assumption that most expenditure in animals is due to movement (Tatner and Bryant 1986). ODBA is measured in $m\ s^{-2}$ and calculated by subtraction of static ACC (i.e., force from Earth's gravity) from total values of the 3 ACC axes, followed by summation of the resulting dynamic ACC (i.e., animal movement) values. Importantly, actual energy expenditure cannot be inferred from ODBA values, but greater ODBA values are indicative of greater energy expenditure.

Based on previous records of a leapfrog migration in Greenland white-fronted geese, we hypothesized that birds wintering in Ireland migrated further total distance than Scottish birds, with greater cumulative hours of migratory flight and ODBA, at similar flight speeds during migration for both Irish and Scottish birds. We also hypothesized that Irish birds prepared for the additional cost of further migration by feeding more than Scottish birds prior to and immediately following migration events. Thus, we expected that the overall feeding time during spring migration would be greater for Irish birds than Scottish birds. Finally, we hypothesized that Irish birds that fed more prior to and immediately following migration events would exhibit greater ODBA by flying and walking to feed.

Statistical analyses

Tagged Greenland white-fronted geese were grouped according to whether they were marked in Ireland (Wexford) or Scotland (Loch Ken). Body mass, skull, and tarsus measurements at capture among Irish birds were in the 50th percentile of all tagged birds. We could not estimate mass prior to and just after migration events. However, abdominal profile indices (a field index of mass scaled to capture mass) at departure from wintering areas suggest no difference between Irish and Scottish birds (Walsh AJ, Griffin LR, unpublished

data). We considered movement to be migration when continuous flight (identified by the random forest algorithm) occurred for more than 5 h (i.e., 50 ACC fixes) and consecutive GPS fixes suggested northwesterly progress during spring.

We calculated the individual (bird) and group (Irish or Scottish) means for the migration distance (km) and cumulative hours of migratory flight from wintering to staging areas and staging to breeding areas. Rarely, individuals landed in the Atlantic Ocean for short periods (<1 day) during migration; these instances were not included in calculation of cumulative hours of migratory flight. For each bird, we divided the migration distance by cumulative hours of migratory flight to calculate flight speed during migration (km/hour). We also summed ODBA of flight of each migration leg (i.e., from wintering to staging areas and staging to breeding areas) for each individual and calculated means by group.

To compare the proportion of time feeding and ODBA between Irish and Scottish birds prior to (in the case of departure from wintering and staging areas) and just after (in the case of arrival to breeding areas) migration events, we calculated means of the daily proportion of time feeding and ODBA for each individual for each important phase. To account for the possibility that not all tags experienced zero movement (i.e., a "bottom line" for comparisons of the proportion of time feeding and ODBA among Irish and Scottish birds), we identified the 4-week period when individuals were flightless during wing molt based on (i) phenological records of molt in other Arctic-nesting geese (Salomonsen 1968; Cramp and Simmons 1977; Owen and Ogilvie 1979) and (ii) average movement of less than 1 km for 5 consecutive 5-day periods and calculated the proportion of time feeding and ODBA for each individual during this period. We divided the proportion of time feeding and ODBA during important phases of the migration period by those during the molt. For tests of group means of migration distance, cumulative hours of migratory flight, flight speed, and ODBA, as well as proportion of time feeding and ODBA during important phases of the migration period, we used 10,000 permutations (i.e., randomized draws) of data from individuals (e.g., individual migration distance from wintering to staging areas or means of the proportion of time feeding prior to departure from wintering areas) for each test in Program R. We fixed permutations by year to account for variation shared among individuals within years. This approach allowed us to test group means from small sample sizes against many randomized samples, with no distributional assumptions (Anderson 2001). We report P values as the percentile position of the difference between group means (i.e., difference = Irish value – Scottish value) in relation to the distribution of randomized values and claim "significance" when values were ≤ 0.05 or ≥ 0.95. Given the potential for false negatives (i.e., Type II errors) with low sample sizes, we conservatively interpret our results.

Results

The average distance flown from wintering areas to staging areas was significantly greater for Irish (mean $1{,}608.44 \pm$ SE 28.53 km) than Scottish ($1{,}354.82 \pm 9.47$ km) birds ($P < 0.001$; Figures 1 and 2A). However, the cumulative hours of migratory flight between wintering and staging areas were only marginally greater for Irish birds than Scottish birds (Irish duration: 27.94 ± 1.69 h, Scottish duration 26.46 ± 3.91 h) and not significantly different ($P = 0.09$; Figure 2B). Thus, the flight speed for individual Irish (59.54 ± 3.72 km/h) birds was also only marginally greater than that of Scottish birds (56.79 ± 9.48 km/h) and not significantly

different ($P = 0.59$; Figure 2C). Further, the summed ODBA during migration from wintering to staging areas was not significantly different among Irish ($290.79 \pm 18.79 \, \text{m s}^{-2}$) and Scottish ($272.49 \pm 42.89 \, \text{m s}^{-2}$) birds ($P = 0.10$; Figure 2D). Although Irish birds flew on average 19% further than Scottish birds from wintering to staging areas, they exhibited on average only 7% more ODBA doing so.

The average distance flown from staging to breeding areas was not significantly different between Irish ($1,591.28 \pm 45.35 \, \text{km}$) and Scottish ($1,503.30 \pm 30.03 \, \text{km}$) birds ($P = 0.12$; Figures 1 and 2E). Similarly, the cumulative hours of migratory flight, flight speed, and ODBA from staging to breeding areas for Irish (duration: $27.52 \pm 2.15 \, \text{h}$, flight speed: $59.98 \pm 3.53 \, \text{km/h}$, ODBA $285.97 \pm 23.67 \, \text{m s}^{-2}$) and Scottish (duration: $26.84 \pm 1.09 \, \text{h}$, flight speed: $56.54 \pm 3.31 \, \text{km/h}$, ODBA $270.76 \pm 12.12 \, \text{m s}^{-2}$) birds were not significantly different (duration $P = 0.25$, flight speed $P = 0.46$, ODBA $P = 0.14$; Figure 2F–H). Whereas all 5 Scottish and 4 of 10 Irish birds completed their migration on arrival to southern breeding areas, 3 Irish birds staged on southern breeding areas and migrated to northern breeding areas, and 3 Irish birds migrated directly to northern breeding areas (Figure 3). Over the entire spring migration period, from wintering to breeding areas, Irish birds flew on average significantly further than Scottish birds (Irish $3,199.72 \pm 59.20 \, \text{km}$, Scottish $2,858.12 \pm 30.58 \, \text{km}$; $P < 0.001$).

Irish birds did not forage significantly more than Scottish birds as a proportion of their daily behavior (calibrated for each individual according to no movement during molt; see Materials and Methods) in the 14 days prior to departure from wintering areas ($P = 0.32$; Figure 4A), 14 days prior to departure from staging areas ($P = 0.43$; Figure 4B), or first 14 days after arrival on breeding areas ($P = 0.41$; Figure 4C). Further, there were no significant differences between Irish and Scottish birds in their overall feeding time during the entire spring migration period (i.e., 14 days prior to migration from wintering areas to the first 14 days after arrival on breeding areas; Irish $777.76 \pm 36.89 \, \text{h}$, Scottish $770.20 \pm 46.87 \, \text{h}$; $P = 0.45$), suggesting Irish birds are physiologically capable of flying the extra distance without additional feeding prior to and during the migration period.

Irish birds did not exhibit significantly greater ODBA than Scottish birds (also calibrated for each individual according to no movement during molt) in the 14 days prior to departure from wintering areas ($P = 0.09$; Figure 4D) or 14 days prior to departure from staging areas ($P = 0.66$; Figure 4E). However, Irish birds exhibited significantly lower ODBA during the first 14 days after arrival on breeding areas ($P = 0.01$; Figure 4F). Despite their greater ODBA during the first 14 days on breeding areas, Scottish bird movements were generally local and limited to southern breeding areas (Figure 3).
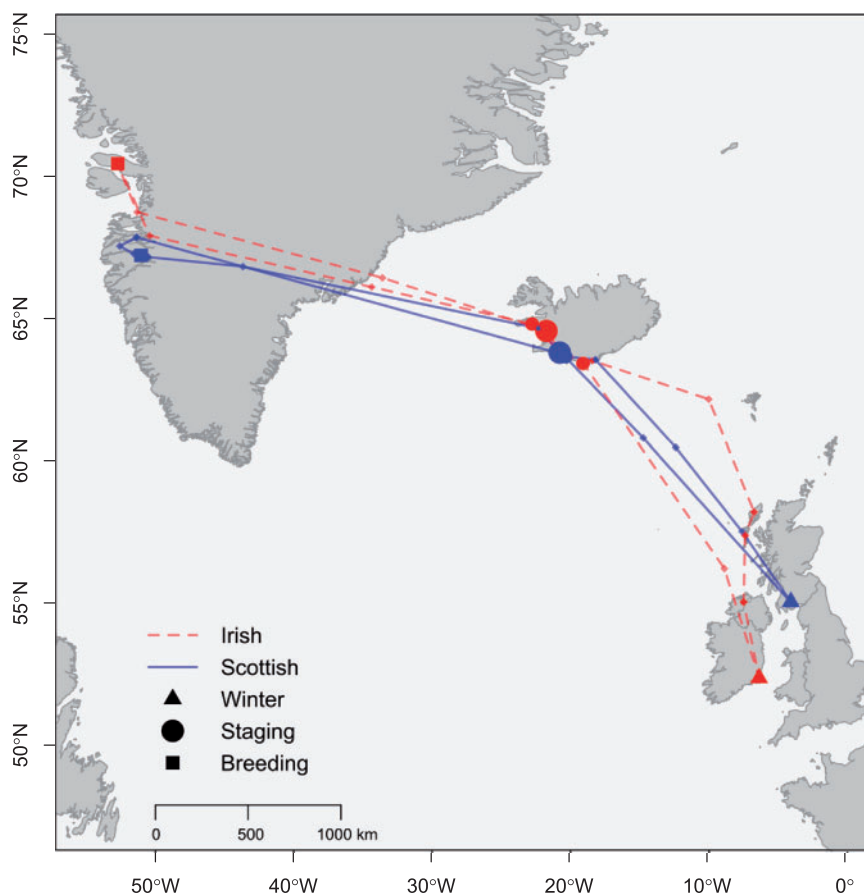

Figure 1. Migration routes of 4 Greenland white-fronted geese fitted with GPS–ACC tracking devices deployed on wintering areas (triangles) during 2012 in Ireland (2 red tracks) and Scotland (2 blue tracks). Individuals staged in Iceland for 2–4 weeks before migrating to breeding areas in Greenland (squares). GPS–ACC devices measured one GPS location per day. The size of the circle represents the duration of the staging period (where larger circles indicate a greater duration).
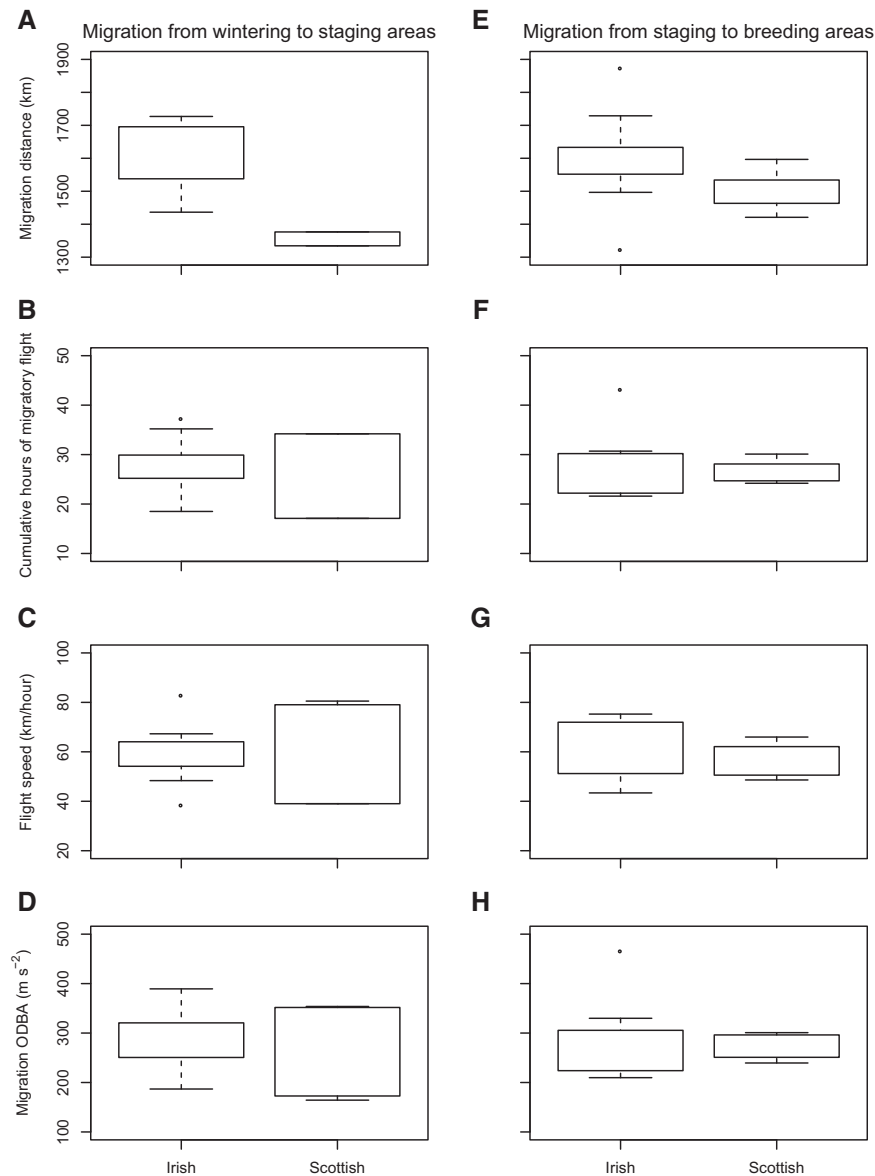
Figure 2. The migration distance (km), cumulative hours of migratory flight, flight speed during migration (km/hour), and overall dynamic body acceleration (ODBA, measured in $m\,s^{-2}$ and a proxy for energy expenditure) from wintering to staging areas (A–D) and staging to breeding areas (E–H) for Greenland white-fronted geese marked in Ireland ($n = 10$) and Scotland ($n = 5$) in 2012 and 2013.

Discussion

Using retrospective analyses of behavioral data collected from GPS–ACC tracking devices fitted to male Greenland white-fronted geese, we found Irish-marked birds migrated significantly greater distances than Scottish-marked birds during spring, but that the 2 groups showed no significant differences in cumulative hours of migratory flight, flight speed, and ODBA (energy expenditure). Further, we found no significant differences between Irish and Scottish birds in their proportion of daily feeding activity and ODBA during critical fuelling periods on wintering, staging, and breeding areas, as well as total time feeding throughout the entire spring migration.

That Irish birds migrated significantly further than Scottish birds, but did not feed significantly more, suggests broad individual plasticity in this species, which may allow individuals to adapt to a wide range of conditions. For instance, Scottish birds may be better prepared for food scarcity (which negatively affects survival; Martin

1987; Sherry et al. 2005; Newton 2008) in Greenland because they have greater energy stores than those required for migration alone. Studies of migratory bird life histories suggest that individuals with greatest fat stores have greater reproductive success (Ankney and MacInnes 1978; Drent and Daan 1980; Monaghan et al. 1989; Newton 2008). Thus, individuals may attempt to decrease their mortality probability and increase their breeding probability by arriving on breeding areas with additional body reserves. Some Irish birds may have been able to increase their breeding probability and compensate for the additional distance flown simply by refuelling at arrival sites in west Greenland before completing their spring migration (i.e., balancing energy expenditure of an additional flight of ca. 200–300 km), but such rates could resemble those of Scottish birds also refuelling and/or preparing for the breeding season. It remains possible that any differences in the energy costs of migration between Irish and Scottish birds were non-detectable because of nutrient differences in food types
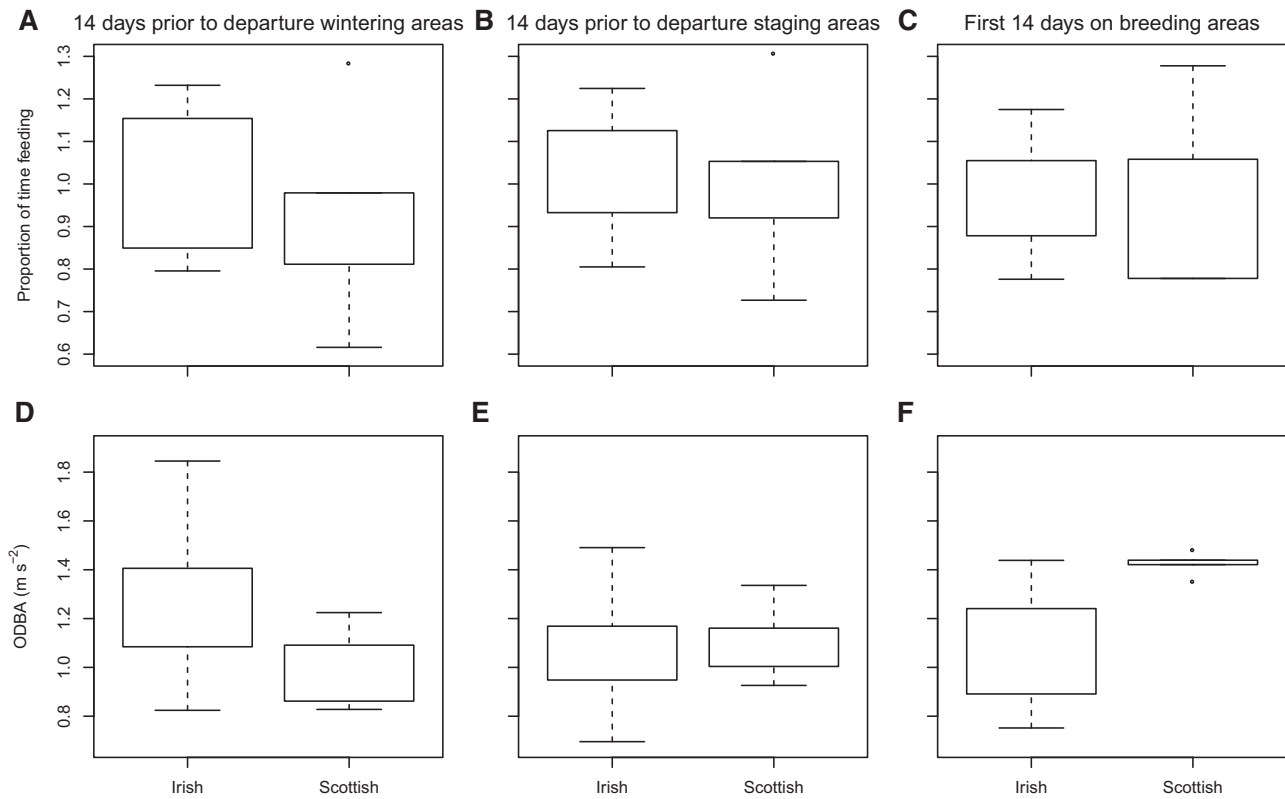
Figure 3. The proportion of time feeding among Greenland white-fronted geese marked in Ireland ($n = 10$) and Scotland ($n = 5$) during (**A**) 14 days prior to departure from wintering areas, (**B**) 14 days prior to departure from staging areas, and (**C**) the first 14 days on breeding areas, and ODBA during (**D**) 14 days prior to departure from wintering areas, (**E**) 14 days prior to departure from staging areas, and (**F**) the first 14 days on breeding areas.

within and among important phases of the migration period (where the frequency and duration of feeding necessary to balance energy costs were non-uniform among food types). Improvements to tracking technologies (e.g., more frequent GPS duty cycles and smaller batteries) are needed for researchers to more closely follow tagged individuals and explicitly test this assumption.

Arctic-nesting geese adopt a mixed strategy of "capital" and "income" energy accumulation for reproduction (Gauthier et al. 2003), acquiring stores en route and on arrival to breeding areas. In Greenland white-fronted geese, males may be expected to incur costs of breeding because geese form long-term pair bonds (Black 1996) and thus share parental duties (e.g., chick-rearing). Thus, it is advantageous for male and female long-distance migrant birds during the spring pre-breeding period to "hedge their bets" and depart areas in the best condition possible because birds are not able to predict environmental conditions at the next stage (Bauer et al. 2008; Fox et al. 2014). In this study, Irish birds migrated further overall (a potential cost to capital energy accumulation), but Scottish birds exhibited greater ODBA on arrival to breeding areas (a potential cost to income energy accumulation); thus, any fitness benefits for males arriving on breeding areas with additional body mass seem due to individual (and not group) strategy.

Traditionally, time- and energy-budgets of migratory individuals have been difficult to measure because individuals must be followed from one area to the next. The advent of hybrid GPS–ACC tracking devices now enables such comparisons, without observer bias. We used such tracking devices to compile movement and behavioral data to understand the relationships between migration distance, cumulative hours of migratory flight, flight speed, and ODBA, as well as the

proportion of time feeding and ODBA prior to and immediately after migration events among individuals of differing winter provenance. Researchers may also link these consequences with fitness, as breeding events may be identified by incubation behavior through analyses of GPS and ACC data and observations of tagged individuals with and without young. In this study, 2 tagged individuals were observed with juveniles the following winter (i.e., were confirmed successful breeders; one in Ireland and one in Scotland). However, a greater sample size from both Irish and Scottish flocks is required to fully understand the energetic consequences and fitness implications of migration distance in this population. Continued advances to tracking devices (where lightweight devices have even been fitted to much smaller organisms such as bumblebees *Bombus* spp.; Hagen et al. 2011) increasingly make such studies possible.
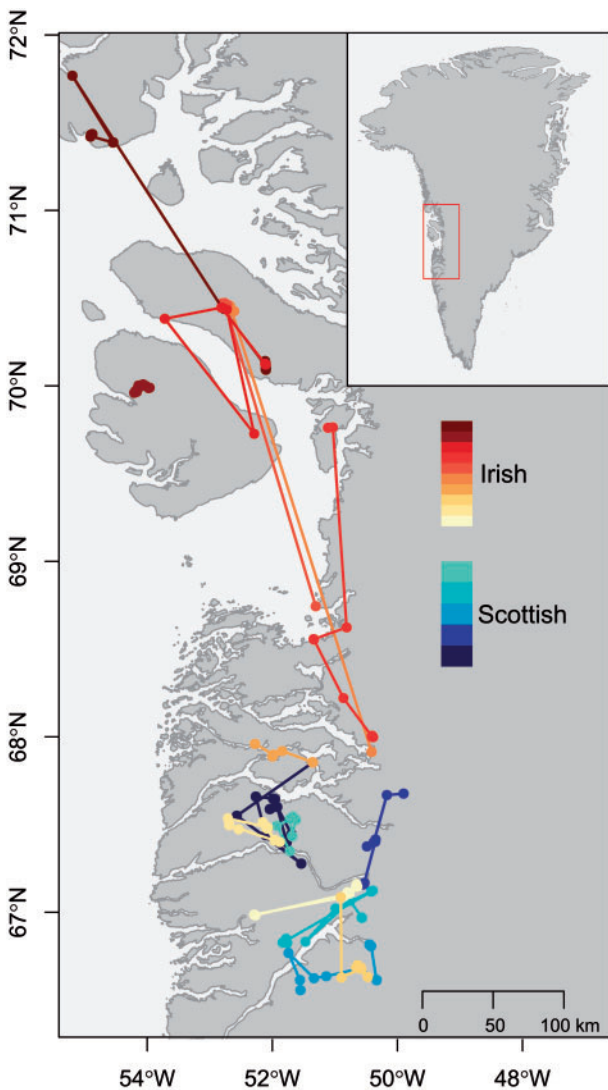
Figure 4. Individual tracks of 15 Greenland white-fronted geese during the first 14 days on breeding areas in Greenland. Of these, 5 individuals were tagged in Scotland (each track is an individual with unique shade of blue) and 10 individuals were tagged in Ireland (each track is an individual with unique shade of yellow, orange, or red). GPS–ACC devices measured one GPS location per day. Map of Greenland inset.

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