ORIGINAL ARTICLE

A trial of a non-statistical computer program for monitoring fuel reserves, response to wind and other details from GPS tracks of migrating geese

C. J. Pennycuick · L. R. Griffin · Kendrew Colhoun · Richard Angwin

Abstract GPS transmitters were used with the Argos satellite system to track two Light-bellied Brent Geese (*Branta bernicla hrota*) from Iceland to Arctic Canada, three Greenland White-fronted Geese (*Anser albifrons flavirostris*) from Scotland to west Greenland, and two Barnacle Geese (*Branta leucopsis*) from Scotland to Spitsbergen. Each goose's wing span was measured at the time of tagging, and its body mass and fat fraction were estimated at the time of departure. This was the starting point for the *Flight* program's time-marching simulation, which is a non-statistical procedure based on flight mechanics. The ground speed was measured between each GPS fix and the previous one, and combined with a wind estimate to find the air speed. The program calculated the power, using the air density from the GPS altitude. The rates of consumption of fat and muscle tissue were calculated from the power, and used to update the body mass and composition. The total air distance flown by each bird was not consistently less than the ground distance, and there was no indication that the birds could select their routes, or even their timing, so as to bias the wind in their favour. Rates of climb when ascending the Greenland Ice Cap were very low in the Brent Geese, in relation to the maximum rate of climb of which the flight muscles were expected (on mechanical grounds) to be capable of supporting. The Brent Geese stopped often during the ice crossing, suggesting that they could not sustain sufficient aerobic power for continuous flight. The fat fractions of the White-fronted Geese were lower across the ice cap, and they climbed faster and stopped less often. Energy height was used as a species-independent measure of energy reserves. All seven northbound geese arrived in their nesting areas at estimated energy heights exceeding 200 km (around 350 km for the two Brent Geese). All of the geese achieved average energy gradients of at least 11, including short stops, meaning that their arrival energy heights were sufficient to fly a further 2,200–4,000 km. We propose that these reserves represent the energy height needed to initiate successful breeding in these arctic habitats, with an element of insurance against contrary winds.

Keywords Bird migration · Computer simulation · Flight mechanics · Energy height

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Introduction

Throughout most of 2008, the BBC ran a series of weekly radio programmes under the title *World on the Move*, following the migrations of a wide variety of animals. These included a number of geese, which we tracked by the Argos satellite system, using GPS-based transmitters, deployed under an existing, conservation-oriented Wildfowl and Wetlands Trust research programme. The background to

this programme has been described by Griffin (2008), along with recent results, and current activities are reported at http://www.wwt.org.uk/research/tracking/maps.asp. We followed three species whose likely destinations were already known from previous satellite tracking, as were the approximate distances and expected timing of the spring migration. We used the *Flight* program, which was developed by one of us (C.J.P.), to run a computer simulation of each individual flight, based on flight mechanics rather than statistics, to see whether we could quantitatively account for each goose's consumption of fat and protein while migrating, and for its energy reserves on arrival in the nesting area. The program is freely available on the internet, and we present the results as a demonstration of what it can do, and also to point out measurements which future observers could make, to check the program's predictions and to improve their accuracy.

As we had a professional meteorologist among the authors (R.A.), we were able to take account of the wind at every point of each flight, to estimate the bird's air speed, which in turn allowed us to generate running estimates of a number of variables, including the amounts of fat and protein that each goose consumed, and the reserves remaining, hour by hour throughout the flight. The calculations are based on aeronautical concepts, and we use the conventional terminology from aeronautics wherever possible, as biological terms which have been introduced independently are seldom directly equivalent, and often insufficiently precise. The program works by first estimating the bird's average air speed for each leg of the flight (between each two successive GPS fixes) and then estimating the chemical power, i.e. the rate at which fuel energy is consumed during the leg. The power is multiplied by the duration of the leg to get the amount of energy used, and this in turn is used to estimate the mass of fat and

protein consumed. The body mass is revised downwards, before calculating a new power estimate at the start of the next leg. The aeronautical theory, on which the calculations are ultimately based, is set out in such texts as Anderson (1991), but the program takes account of some features that are specific to birds, especially the progressive consumption of protein from the flight muscles and other organs, and its use as supplementary fuel (Lindström and Piersma 1993; Piersma and Gill 1998). It is not practical to give full explanations of the program's operation in a research paper, but references are given in the text to paragraph numbers in a book (Pennycuick 2008), which explains the theory that underlies the program, and also attempts to bridge the gap between the somewhat different concepts and terminology to which aeronautical engineers and biologists are accustomed. The *Flight* program can be downloaded free from http://www.bio.bristol.ac.uk/people/pennycuick.htm, or from http://books.elsevier.com/companions/7780123742995, which is the publisher's companion page for the book. Readers who have installed it will find further information in the online manual.

Methods

Geese

Complete spring tracks were obtained from seven adult male geese of three species, listed in Table 1, as they migrated from wintering areas in the British Isles or spring staging areas in Iceland to different arctic breeding areas, whose approximate locations were already known from previous satellite tracking studies. Figure 1 shows one track of each species. There were no major differences between the tracks of different birds of the same species.

Table 1 Data for transmitter birds

Species	Migration direction	Start mass (kg)	Min mass (kg)	Fat fraction	Start energy height (km)	Wing span (m)	Aspect ratio	L/D from Power Curve	
								Departure	Arrival
Barnacle DLT	N-bound	2.33	1.4	0.29	349	1.35	8.13	13.9	14.7
Barnacle DUC	N-bound	2.52	1.4	0.328	410	1.41	8.13	14.2	15.1
Barnacle DDT[a]	S-bound	(2.1)	1.4	(0.245)	(282)	(1.42)	8.13	15.1	16.7
Whitefront V1A	N-bound	3.04	1.8	0.299	363	1.44	7.86	13.5	14.5
Whitefront V2A	N-bound	2.91	1.8	0.296	358	1.42	7.86	13.5	14.3
Whitefront V4A	N-bound	2.95	1.8	0.292	352	1.47	7.86	13.9	15.1
Brent DZ	N-bound	2.27	0.9	0.441	634	1.24	8.45	13.2	15.1
Brent JV	N-bound	2.27	0.9	0.444	641	1.17	8.45	12.5	14.3

Barnacle Barnacle Goose (*Branta leucopsis*), *Whitefront* Greenland White-fronted Goose (*Anser albifrons flavirostris*), *Brent* Light-bellied Brent Goose (*Branta bernicla hrota*)

[a] The southbound Barnacle Goose DDT was tagged in the previous year. His wing span was not measured, and there were no data to gauge his mass and fat fraction on departure from Spitsbergen
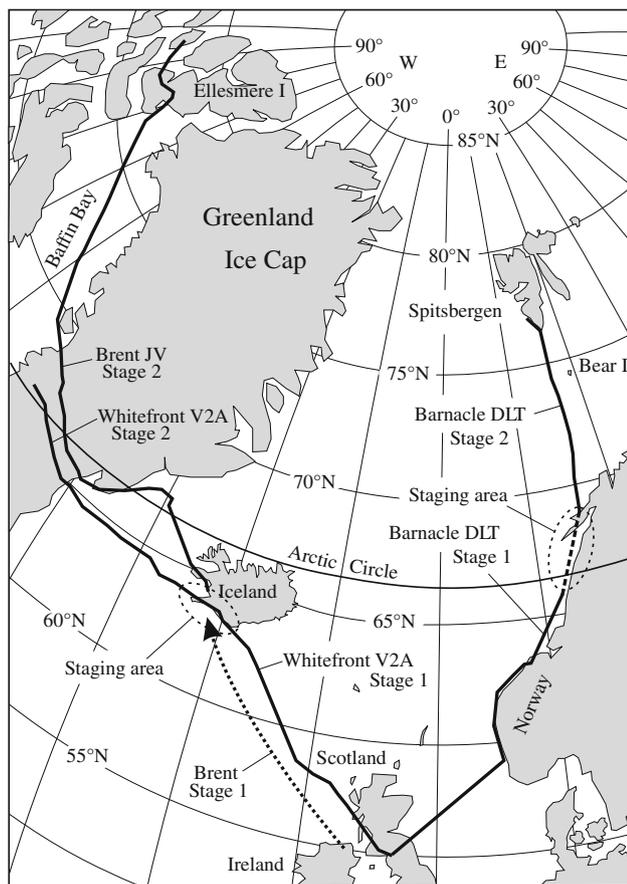
Fig. 1 The study area with the tracks of one goose of each of the three species tracked. *Barnacle* Barnacle Goose (*Branta leucopsis*), *Whitefront* Greenland White-fronted Goose (*Anser albifrons flavirostris*), *Brent* Light-bellied Brent Goose (*Branta bernicla hrota*). The Brent Geese wintered in Northern Ireland but their tracks begin in Iceland, where they were tagged

Two Light-bellied Brent Geese (*Branta bernicla hrota*), which had wintered in Northern Ireland, were tagged during their main feeding stopover in Iceland, and tracked from there over a route that was first described by Gudmundsson et al. (1995), across Greenland, then up the whole length of Baffin Bay to the south end of Ellesmere Island. The one shown in Fig. 1 (Brent Goose JV) stopped there for 10 days, presumably feeding, before continuing further west to Amund Ringnes Island, while the other Brent Goose (DZ) continued a shorter distance to the Bear Peninsula in south-west Ellesmere Island.

Three Greenland White-fronted Geese (*Anser albifrons flavirostris*) were tagged in southern Scotland, and tracked to a feeding stopover in Iceland, after which they crossed to Greenland and climbed over the ice cap to the breeding area in West Greenland, just above the Arctic Circle. This route was described from satellite tracks by Glahder et al. (1999).

Two Barnacle Geese (*Branta leucopsis*) were tagged in southern Scotland, and tracked to Spitsbergen, with a feeding stopover in Norway, along a route previously studied by Griffin (2008). A third Barnacle Goose (DDT) is also included in Table 1, although this goose was tagged in 2007, and we had to estimate its wing span. DDT's solar-powered transmitter was still working in the autumn of 2008, as it completed its second round trip to Spitsbergen, giving us some insights into strategy differences between the spring and autumn migrations, which we did not get from any of the 2008 birds.

Wing measurements

The program simulates the flight of an individual bird (not of the mean of a sample), and it was therefore run separately for each individual in Table 1. Ideally, a complete set of measurements is needed for each individual. The most important measurement determining speed, power and fuel consumption is the wing span, and we measured this for each goose when it was caught and tagged. The wing area is also needed, but is less important in terms of the effect of errors on the accuracy of the result. We estimated the wing area from the span, using a fixed value for the aspect ratio, measured from a sample of adult birds of each species (Pennycuick 2008, Boxes 1.3–1.4). Captive samples of 12 White-fronted Geese and 8 Brent Geese were measured for this purpose at Slimbridge, while the Barnacle Geese were a cannon-netted sample of 14 wild birds, which included one of the transmitter birds. As the wing span had not been measured on Barnacle DDT, it was assigned the average wing span for adult males in the measured sample.

Starting body mass

We could not measure each bird's body mass at departure, and had to resort to statistical methods to estimate this, after which changes in mass were calculated by the program, by estimating the power required to fly at the observed height and air speed. Each bird was weighed at the time it was tagged, and the mass values were adjusted upwards to allow for feeding between tagging and initial departure. For the Barnacle Geese and White-fronted Geese, this was based on statistical analysis of birds caught and weighed at various dates in previous years. The masses of the Brent Geese were extrapolated to the departure date by assuming that energy was acquired by feeding at a net rate based on an estimate of the bird's (increasing) basal metabolic rate. This somewhat crude procedure is explained in the *Flight* program's manual, and was automatically invoked by the program to estimate the mass of

fat and protein gained whenever a bird stopped within a known feeding area.

Estimating fat fraction from body mass

The distance that any bird can fly without feeding is determined by the fat *fraction* at departure, i.e. by the ratio of the mass of stored fat to the total body mass, not by the fat mass as such (Pennycuick 2008, 8.1.1). An increase of the fat fraction results in increased range, whether it is achieved by adding fat, or by reducing the mass of other body components, or both. Measuring the fat fraction directly is impractical as it involves killing the bird, but if the bird belongs to a population from which samples have been trapped and weighed over a period of years, as our geese did, it is possible to use the *Flight* program to estimate the fat fraction from the body mass. Past records were scanned for the lowest mass ever recorded, a statistical outlier representing a goose that had lost its way, or arrived late in the stopover area after all the food had been eaten, or been caught in head winds, and was weighed before it had time to start recovering. Table 1 lists the estimated departure mass for each bird, and also the lowest mass previously reported in each species, for a bird that was thin but apparently healthy. It is assumed that the difference between a bird's current mass and this minimum mass represents the combined mass of fat and protein that is available to be consumed as fuel. Each bird's mass was set to the estimated departure value, and the starting fat fraction was varied in repeated runs of the *Flight* program, until a value was found by trial and error that ran down to zero when the body mass was equal to the reported minimum mass (Pennycuick 2008, Box 8.4). The division of the energy requirement between fat and protein is taken account of by the program (below). In practice, it takes a couple of minutes to estimate the starting fat fraction by this method, and the Excel output of the program can then be used to generate a table or graph that shows the fat fraction corresponding to any mass between the minimum and the starting mass for that individual bird. The logic does not exclude the possibility that the reported minimum mass refers to a bird that has not completely exhausted its fat but still has a small reserve remaining. This does not affect the calculations of distance flown or other variables, down to the assumed minimum mass. It might terminate the simulation at a point where the bird could in reality have flown a little further, but this did not happen in any of our simulations.

Transmitters

Solar-powered, 45-g PTT-100 GPS transmitters, manufactured by Microwave Telemetry, were used on the Barnacle and Greenland White-fronted Geese, while the Brent Geese (and Barnacle DDT) carried 30 g transmitters of otherwise similar specification. All were programmed to log GPS fixes, including altitude, at 2-h intervals during the migration period, although there were some longer gaps. The birds were caught by cannon-netting in winter feeding areas, or at spring stopover sites in the case of the Brent Geese, and the transmitters were attached to the middle of the back using elastic straps which allowed for variation in body circumference (Griffin 2008).

Data processing

The *Flight* program's migration simulation is not a statistical exercise, but a physical computation which runs separately for each bird, using the individual data from Table 1. The original version (still the default) requires the bird's wing measurements and its starting mass and fat fraction, sets rules for the bird to select its height and speed, and computes the power required from the muscles, which in turn determines the rate of consumption of fuel energy. The program then initiates a time-marching computation in which the bird's mass, and the power, is updated 10 times per hour until all of its fat has been consumed. A new GPS variant was developed for this project, which begins with a GPS track, and estimates the bird's fuel consumption between each GPS fix and the previous one. At the end of the GPS data, it reverts to the original programmed simulation, and extrapolates the track until all the fat has been consumed.

The raw Argos data were loaded into an Excel spreadsheet incorporating a macro that calculated and filled in the ground speed and track direcion for each leg, and the position, time and height of the mid-point of the leg. The spreadsheet was then passed to the meteorologist (R.A.) who interpolated the wind speed and direction at the mid-point of each leg, using synoptic weather observations where available. Forecast Met Office low-level aviation charts were also used along with isobaric charts to estimate geostrophic winds, and additional charts were obtained from http://www.weatherpage.se. Winds from radiosonde balloon data were particularly useful in otherwise data-sparse regions, where some interpolation of data was required. Average air speeds were calculated by a second macro from the ground speeds and wind speeds for each leg, and the completed spreadsheet then became the input source for the *Flight* program.

The GPS variant is included in the published program from *Flight* 1.20 onwards, together with the Excel template with the macros, and a set of example files from one of the Greenland White-fronted Geese that feature in this paper. Detailed output from a program run can be generated as an Excel spreadsheet, whose format is the same as the output

for programmed migration. It shows the time from start and the ground distance flown at each fix (and 29 other variables), but does not show the GPS positions. Optionally, the program will also generate another spreadsheet, the "Progress Update", which shows the latitude, longitude and height of each fix, together with a reduced set of output variables, originally intended for broadcasters. Another option (used in the preparation of Fig. 1) generates a "kml" file, which plots the track if its icon is dragged and dropped into an open Google Earth window.

Flight's default values were used throughout for variables used in the program, unless otherwise stated.

Muscle burn criterion

It has been known for many years that birds consume protein from their flight muscles and other organs when they migrate, and use it, in effect, as supplementary fuel (Lindström and Piersma 1993; Piersma and Gill 1998). The program needs a rule that determines how much muscle tissue to take in each calculation cycle. Previous studies have shown that maintaining "constant specific work" accounts for field observations of varying flight muscle mass, better than other criteria that have been tried (Pennycuick 1998). This is not a statistical procedure. It means that, as the body mass declines, enough muscle tissue is consumed to keep the work done by unit mass of muscle tissue in each contraction constant (Pennycuick 2008, 8.2.3). Further protein is then withdrawn if necessary from the "airframe" (the body excluding flight muscles and fat) to bring the energy derived from oxidising protein to 5% of the total energy consumption for all purposes, including basal metabolism. This is because the metabolic pathways for oxidising fat require about 5% of the energy released to come from protein (Jenni and Jenni-Eiermann 1998).

Results and discussion

Starting fat fraction

Although the maximum fat fractions that are possible for different birds are not well known, there is definitely a trend for the upper limit to decline in larger birds. Values above 0.5 have been reported in various passerines and medium-sized waders, meaning that all the other body parts have to be squeezed into less than half of the all-up mass. This includes the heart and lungs, which most probably have to be enlarged to support the aerobic muscle power needed to lift and propel the whole package. It is unlikely that any goose could fly with a fat fraction of 0.5, but our two Brent Geese (the smallest species of the three) both left Iceland with estimated fat fractions of 0.44. They are likely

to have been constrained by limitations of muscle power, or oxygen availability, or both, and we looked for signs of this when they crossed the Greenland ice cap (below). They also had the longest distance to cover without stopovers, about 2,800 km from Iceland to Ellesmere Island. The White-fronted Geese and Barnacle Geese started with fat fractions in the range 0.29–0.33, but they only had to cover distances up to about 1,700 km without stopovers. It will be seen later that all of the northbound geese departed after each stopover with generous fuel reserves.

Minimum power speed

One of the variables tracked by the program is the minimum power speed (V_{mp}), which is the air speed at which work is required from the flight muscles at the lowest rate. A slower air speed than V_{mp} is unstable in level flight, because if the bird happens to speed up slightly, the power requirement drops, and it tends to speed up more, until it meets the rising part of the power curve above V_{mp} (Pennycuick 2008, 3.3). Also, there is an energetic advantage in flying faster than V_{mp}, because the distance covered per unit of work done increases up to the maximum range speed (V_{mr}), which is about 1.6 V_{mp} in geese (Pennycuick 2008, 3.3). On the other hand, flying slower than V_{mp} not only requires more power but also results in lower fuel economy in relation to distance. It is safe to say that no migrating bird cruises at a speed below V_{mp}. Hence, if the observed average air speed between two GPS fixes is less than V_{mp}, the bird must have stopped for part of the time.

The *Flight* program maintains a running estimate of the bird's current V_{mp}, using a simple and robust formula which has been validated by field observation (Pennycuick 2001), and also by wind tunnel experiments (Pennycuick et al. 1996a). The formula involves seven variables, four of which are treated by the program as having values that are fixed for a particular bird. These are the bird's wing span, the acceleration due to gravity, the induced power factor and the drag coefficient of the body. The other three are the mass and frontal area of the body, both of which decrease as fuel is used up, and the air density, which decreases if the bird climbs to a higher altitude, as five of the seven geese were obliged to do, in order to get over Greenland. Decreasing mass causes V_{mp} to decrease, while decreasing frontal area causes V_{mp} to increase, as does lower air density.

The effects of altitude and body mass can be seen in Fig. 2, which was plotted from the Progress Updates for the seven northbound geese, and shows the current estimate of V_{mp} for each goose against the total ground distance covered so far. Both Brent Geese showed a hump in the V_{mp} curve, from below 17 to 18.5 m s^{-1}, as they climbed to 2,500 m or so over Greenland. The three White-fronted
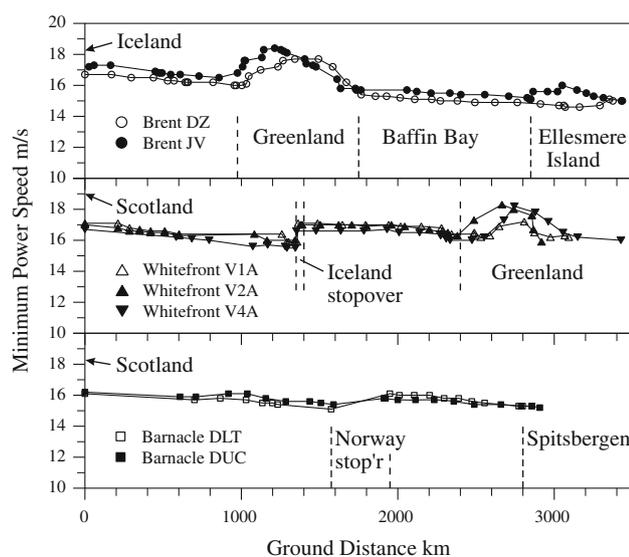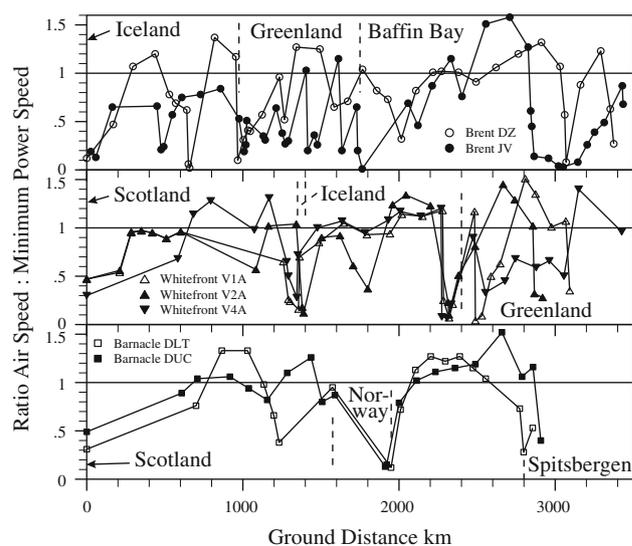
Fig. 2 Running estimates of the minimum power speed of each goose, plotted against ground distance covered

Fig. 3 Ratio of the average air speed for each leg to the current value of the minimum power speed. If this ratio is less than 1 (*horizontal line* in each graph), the goose must have stopped during the leg

Geese stopped for 3 weeks in Iceland, about 1,400 km out from Scotland, during which they moved only a short distance, while their estimated mass, and also their V_{mp}, built up to near the original departure levels. They too showed a pronounced hump in the curve as they crossed Greenland by different routes that involved climbing to heights of between 2,500 and 3,000 m. The Barnacle Geese flew low over the sea for most of their migration, with V_{mp} declining gradually along with their body mass. Their feeding stopover consisted of 2–3 weeks moving slowly up a 350-km section of the Norwegian coast, with their mass and their V_{mp} building up progressively.

Ratio of average air speed to V_{mp}

It is obvious that a bird has stopped if two or more consecutive GPS fixes are in the same place, but our air speed measurements (only possible with detailed wind data) showed that all of the geese also made short stops between fixes, more often than had been suspected. The average air speed (V_a) at which the bird flew between two GPS fixes was taken at face value if it exceeded the current estimate of the minimum power speed (V_{mp}). If V_a was less than V_{mp}, then the program assumed that the bird actually flew at V_{mp}, but only for a fraction V_a/V_{mp} of the time between the fixes, and sat on the ground or water for the rest of the time. Figure 3 shows different patterns in the different individuals, when the ratio V_a/V_{mp} is plotted against ground distance covered.

Although both Brent Geese set off from Iceland with the same high fat fraction (0.44), JV stopped frequently while crossing the icecap and took 2 days to get across, while DZ

stopped less and got across in less than a day. Both Brent Geese flew continuously for long periods during the 1,100-km transit of Baffin Bay, their mass being well down by then. The three White-fronted Geese stopped on the water shortly before reaching Iceland, and also earlier, during the crossing from Scotland. They stopped on the water near the east coast of Greenland, around 2,300 km from the start, and then flew intermittently up the east slope of the ice. Two of the three flew continuously once they reached the top, while the third (V4A) stopped frequently while crossing the ice. The two Barnacle Geese flew continuously across the North Sea, and also on the crossing from Norway to Spitsbergen, except for the first part of the crossing, where they were still heavy from the stopover.

Figure 3 also shows that air speeds during periods of continuous flight were mostly in the region of 1.0–1.3 times V_{mp}, but that at least one goose of each species reached an average air speed exceeding 1.5 V_{mp} for at least one leg, near the end of the flight, when the mass was low. This would be near enough to the maximum range speed (V_{mr}) for the fuel economy (air distance flown/fuel energy consumed) to be near its maximum value. The power required from the flight muscles, and also from the heart and lungs, would be considerably higher than when flying at V_{mp}, but flying faster results in the goose using less fuel in total, and arriving sooner.

Head winds and tail winds

If migrating birds were somehow able to plan their routes so as to take advantage of tail winds on one side or another of a moving weather system, the result would be that the air
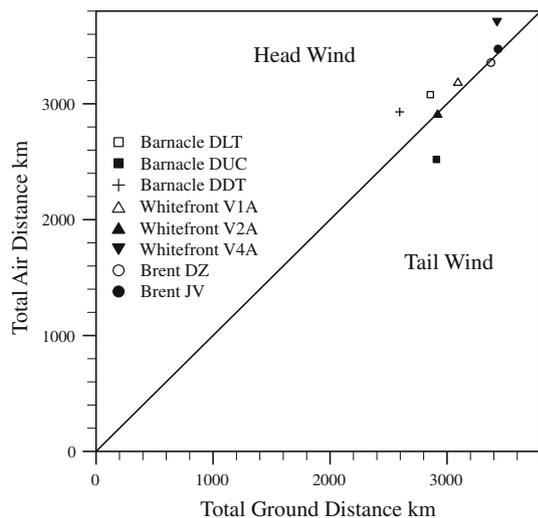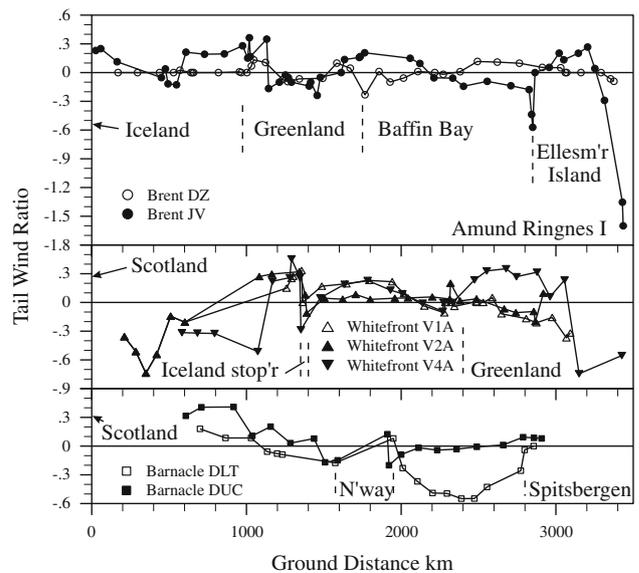
Fig. 4 Total air distance flown versus total ground distance covered by each goose. If a point is below the *diagonal line* (air distance < ground distance), the goose had a net tail wind component

Fig. 5 Tail wind ratio, defined as (Ground Distance − Air Distance)/ Ground Distance, plotted against ground distance for each leg of each goose's flight. This can only be calculated from the second point in each track onwards. A point above the *zero line* means that the goose had a tail wind component on that leg, below the line means a head wind

distance flown would be less than the ground distance covered. This was easily tested from our data, as we had the ground distance for each leg directly from the GPS, and we also had the air speed and the airborne time taking account of stops (above), which were multiplied together to give the air distance for each leg. Figure 4 shows the total air distance plotted against the ground distance for eight entire flights, including the southbound flight of Barnacle DDT. Each point would lie on the diagonal line if there was no wind throughout the flight, or if periods of tail wind were balanced by periods of head wind, whereas if the bird managed to bias the result in favour of tail winds, the point would lie below the line. Actually, only Barnacle DUC is well below the line, and the other seven geese are either on the line, or just above it. This does not support the idea that the geese were taking advantage of tail winds in a non-random manner.

In Fig. 5, the "Tail Wind Ratio", is plotted against total ground distance for each flight. It is defined for each leg as

$$\text{Tail Wind Ratio} = (\text{Ground Distance} - \text{Air Distance})/$$
$$\text{Ground Distance}.$$

This ratio is positive for a tail wind, and negative for a head wind. It can take a large negative value if the bird is flying against a strong head wind that makes its ground speed very small, as happened to Brent Goose JV on the last part of his flight from Ellesmere Island to Amund Ringnes Island. One of the Barnacle Geese (DLT) also persevered against persistent head winds on the crossing from Norway to Spitsbergen, while the other one (DUC) made the same crossing on a different day and got neither help nor hindrance from the wind. Otherwise, each goose got tail winds

in some parts of its route, but flew on against head winds in others, with no obvious pattern. There is no indication that any of the geese selected their routes to take advantage of wind patterns, or even that they timed their departures to take advantage of tail winds. Two of the White-fronted Geese (V1A and V2A) actually departed from Scotland (together) in head winds that persisted for most of the way across to Iceland.

It is puzzling that geese continue to fly when caught by head winds, rather than stopping and waiting for the wind to change. A low-flying goose or swan should be able to detect visually that it is making little or no progress in the desired direction, when flying against a head wind whose strength is a substantial fraction of the bird's V_{mp}. However, Barnacle Goose DLT kept going on the crossing from Norway to Spitsbergen, despite a tail wind ratio of −0.5, and Brent Goose JV's tail wind ratio reached −1.6 during his approach to Amund Ringnes Island. On one 9-h leg, JV flew an air distance of 273 km, for a ground distance of only 116 km. Similar persistence was seen on two occasions in an earlier study, when Whooper Swans (*Cygnus cygnus*) kept going against head winds that were strong enough to force them far off course (Pennycuick et al. 1996b, 1999).
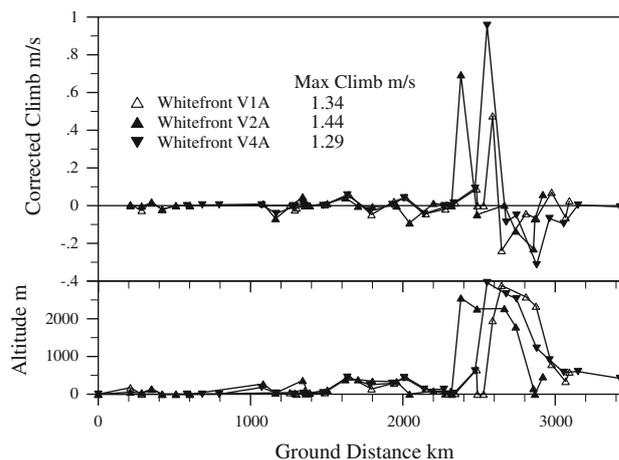
Altitude and rate of climb

Hedenström and Alerstam (1992) introduced the idea that a bird's maximum rate of climb depends on its *power*
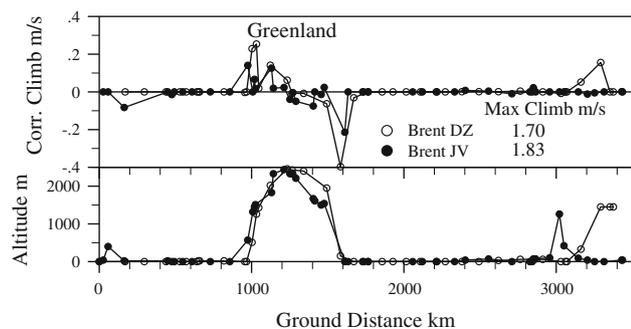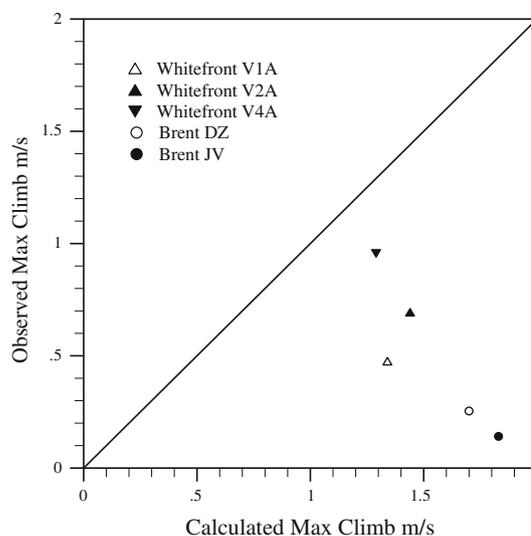
Fig. 6 *Lower graph* GPS altitude for the two Brent Geese. *Upper graph* corrected rate of climb. The correction was applied to legs in which the goose only flew for part of the time, and gives the average rate of climb during the time that the goose was airborne, rather than the overall average for the leg

Fig. 7 Altitude (*lower*) and corrected rate of climb (*upper*) as in Fig. 6, but for the three White-fronted Geese

Fig. 8 Observed rates of climb from Figs. 6 and 7, plotted against calculated mechanical upper limit for each goose

margin, that is the excess of the maximum power available from the flight muscles over the power required to fly level at V_{mp}, and they applied this to radar observations of migrating birds. This principle, in a more general form, is incorporated in the *Flight* program, and we used it to maintain, for each of our geese, a running estimate of its maximum rate of climb at any point in the flight. This is a mechanical limit, imposed ultimately by the maximum stress that the flight muscles are capable of exerting in an isometric contraction, and the active strain at maximum power (Pennycuick 2008, Box 7.5). In aerobic flight, a lower limit may be imposed by oxygen availability. If the aerobic limit comes down below the power required to fly level at V_{mp}, owing to reduced air density at high altitude, then the bird is reduced to proceeding in short hops, with rest periods to recover the resulting oxygen debt. Migration over the Greenland ice cap involves a steep climb to 2,500 m or more, followed by some hours of level flight at that altitude, and we were especially interested to examine the five tracks that crossed Greenland for signs of both types of limit.

The lower graphs in Figs. 6 and 7 show each bird's GPS altitude versus ground distance, for the Brent Geese and the White-fronted Geese, respectively, while the upper graphs show the average rate of climb (negative for descent) for each leg of the flight, found by dividing the height change during the leg by the time. In the case of legs with an average air speed less than V_{mp}, meaning that the bird was only flying for part of the time (above), the rate of climb was corrected by dividing by the proportion of the leg time that was spent airborne. This gives the rate of climb during the time that the bird was actually flying, rather than the average for the whole leg. In all five geese, the highest rates of climb were seen during the ascent of the eastern slope of the Greenland ice cap. These observed rates of climb are plotted in Fig. 8 against the mechanical limit for each goose, as calculated by the "Power Curve" section of the

Flight program, using the estimated body mass for each goose at the time it started the ascent. The points for all five geese were well below the diagonal line in the diagram, meaning that the observed rates of climb were below the calculated mechanical limit.

The theory from which the mechanical limits were calculated requires the flight muscle fraction, i.e. the ratio of the flight muscle mass to the body mass. This is not well known in geese, and cannot be determined without dissecting dead birds. The program started all the geese with a flight muscle fraction of 0.170 (*Flight*'s default value) and estimated that these values would have declined, by the time the geese started their climb up the ice slope, to values in the range 0.161–0.167. If the flight muscle fractions were really lower, then the mechanical limit to the rate of

climb would also be lower. However, improbably low flight muscle fractions would be needed to invalidate our conclusions.

The theory next requires a value for the maximum isometric stress that the flight muscles can exert, which is expected to be constant in all vertebrate skeletal muscles. The default value in the *Flight* program (560 kN m^{-2}) comes from observations of Whooper Swans, whose performance is constrained by their large size (Pennycuick 2008, 7.3.7). This leads in turn to an upper limit for the specific work in the myofibrils, which is estimated to be around 41 J kg^{-1} (Pennycuick 2008, 7.3.1). The margin of power available for climbing is determined by the difference between this limit and the specific work required to fly level, which was around 17 J kg^{-1} in the Brent Geese, and 20 J kg^{-1} in the White-fronted Geese, the difference being due mainly to the smaller size of the Brent Geese. The Brent Geese, with their wider margin, should be capable of a higher rate of climb than the White-fronted Geese (*X*-axis in Fig. 8). However, the observed rate of climb (*Y*-axis) was up to three-quarters of the maximum in the White-fronted Geese, but a much smaller fraction in the Brent Geese, and also less in absolute terms.

Gudmundsson et al. (1995) noted that their Brent Geese took a long time to get up on to the ice cap, and suggested that this was due to aerobic limitations. We speculate further that the maximum rate of climb is limited by aerobic capacity to a value below the mechanical limit, and that the high fat fractions taken on by the Brent Geese result in their aerobic power margin for climb being smaller than that of White-fronted Geese. Both of our Brent Geese had sufficient mechanical power to fly level at the top of the ice cap, but only one of them (DZ) was able to fly continuously once he reached the top. According to the simulation, this implies that DZ was able to maintain aerobically a chemical power level of about 130 W, in order to fly at V_{mp} (17.2 m s^{-1} at that point), at an air density of 0.96 kg m^{-3}. This is a minimum estimate of his aerobic capacity at that air density. The other Brent Goose (JV) required a slightly lower level of chemical power (121 W) at a similar stage of the flight, but was only able to maintain this intermittently, with frequent stops, meaning that his aerobic capacity was insufficient to maintain continuous level flight. Regrettably, there is no quantitative theory from which the aerobic capacity of the heart and lungs can be calculated as a function of air density, although it is known that bird lungs, being organised differently from those of mammals, are more effective at extracting oxygen when the air density is low (Tucker 1968; Pennycuick 2008, Box 7.7). Our results reveal wide variations between individuals in their ability to sustain continuous flight over the top of the ice cap, in both Brent
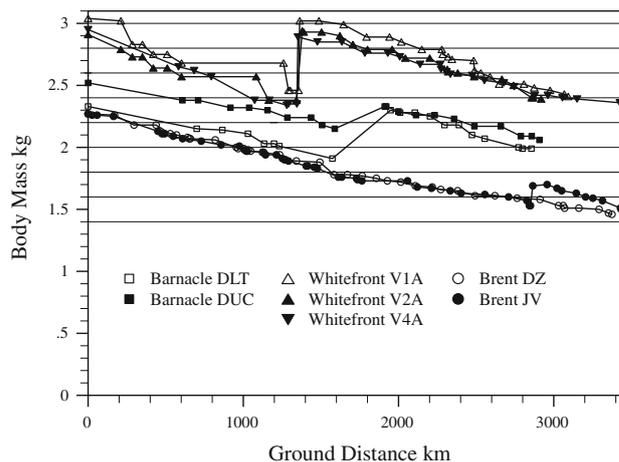
Fig. 9 Estimated body mass versus ground distance covered by the seven northbound geese
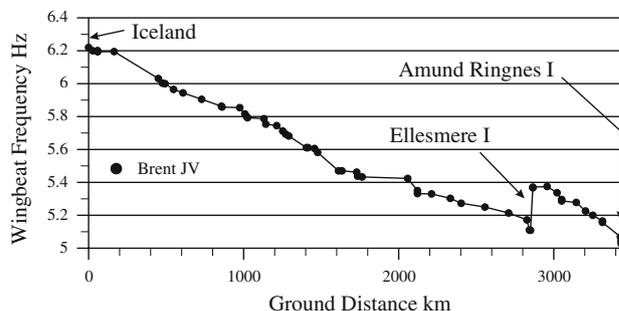
Fig. 10 Calculated wingbeat frequency for Brent JV versus ground distance covered. If the wingbeat frequency were measured remotely via the satellite link, this calculation could be inverted, and used to estimate the body mass as in Fig. 9. This would amount to a remote fuel gauge

and White-fronted Geese, but we do not see any likely explanation for this.

Body mass and the wingbeat-frequency fuel gauge

The program estimated that each goose's body mass declined while the goose was flying and increased during feeding stopovers. That much, but little else, can be seen in Fig. 9, which shows running estimates of body mass for all the northbound geese. However, the fat fraction can be estimated from the body mass, as noted in the section (above) on estimating the fat fraction at departure, and if the body mass could be measured remotely, this could be used, in effect, as a fuel gauge. This might be possible in a bird like a goose, which flaps steadily along for most of the time when migrating, by taking a wingbeat count from an accelerometer, in a timed interval just before each scheduled GPS fix, and transmitting the count as one byte of data, along with the fix. To illustrate the principle, Fig. 10

shows the *Flight* program's running estimate of Brent Goose JV's wingbeat frequency. The estimate declines from 6.2 Hz on leaving Iceland with a full load of fat to 5.2 Hz at Ellesmere Island, then jumps to 5.4 Hz following the assumed feeding stop, before declining to 5.0 Hz during the last 500 km, in which the goose had to fly against a strong head wind as he neared Amund Ringnes Island. If the wingbeat frequencies in Fig. 10 had been measured rather than estimated, the calculation could have been inverted to replace JV's mass curve in Fig. 9, so providing a check on the estimated body mass. It would also have shown whether JV actually did feed during his stop at Ellesmere Island as assumed, and if so, how much mass (and fat) he gained. Such a fuel-gauge calculation would have to take account of the altitude, as the air density also affects the wingbeat frequency.

Energy height and range

The Brent Geese had the lowest mass of all the geese in Fig. 9, but flew the longest distance. The body mass does not of itself tell us much about a bird's range, and neither does the fat mass, for the same reason, that both body mass and fat mass are bigger in a large bird than in a small one. The ratio of fat mass to body mass (the fat fraction) does directly determine the range, but only if a number of other measurements are also taken into account, and the most important of these is the wing span.

There is a very direct way to represent the range calculation, and that is to begin by converting the starting fat fraction into an "energy height", at which the bird starts its flight (Pennycuick 2008, 8.3). The goose comes "down" from this virtual starting height on a gradient, which reflects the rate at which it uses fuel. As in a glider, the flatter the gradient, the further the goose goes from a given starting height. The gradient on which a glider comes down is simply its lift-to-drag ratio, while for the goose, the *Flight* program calculates and continuously updates the "effective lift-to-drag ratio", which is the equivalent measure of aerodynamic efficiency in flapping flight. It depends mostly on the wing span and the body drag, and corresponds directly to the lift-to-drag ratio of a glider or fixed-wing aircraft. The effective lift-to-drag ratio increases slightly as the flight proceeds, because of the body's decreasing frontal area, which in turn reduces its drag. It is affected by the air speed, the gradient being flattest if the goose flies at its current maximum range speed (V_{mr}), and steeper if lack of power forces it to fly more slowly, near V_{mp}.

The starting energy height is tabulated for each goose in Table 1. It is calculated from the starting fat fraction (Pennycuick 2008, Box 8.3), and also takes account of the conversion efficiency of the flight muscles, and the
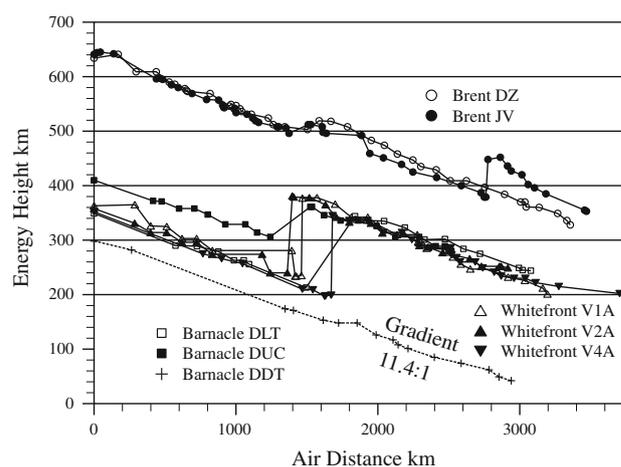
Fig. 11 Energy height plotted against air distance flown. The *dotted line* at the bottom is for the southbound Barnacle DDT, some of whose data had to be approximated. Energy height curves for other species, large or small, would be directly comparable. Unlike curves of body mass, they could be plotted on the same graph

acceleration due to gravity. Figure 11 shows the remaining energy height, calculated by the *Flight* program for each goose, plotted against the *air* distance flown (unlike the earlier graphs, which have ground distance on the *X*-axis). The two Brent Geese started from Iceland at energy heights around 650 km, and arrived in their respective nesting areas with about 350 km remaining, one (JV) with a late stopover, and the other (DZ) without. The Barnacle Geese and White-fronted Geese all started from energy heights around 350 km, except for Barnacle DUC, who stayed longer in Scotland and fuelled up to 410 km before departing. All five geese replenished their energy height during stopovers in Iceland or Norway, and followed much the same gradient on the second stage of their migration, arriving in the breeding area with around 200–250 km of energy height in hand.

Autumn migration of Barnacle DDT

The dotted line at the bottom of Fig. 11 is the southbound flight of Barnacle DDT, for which the calculation is somewhat conjectural, as he was tagged in the previous year, and some items of data were lacking. We assigned him the average wing span for an adult male Barnacle Goose (1.42 m). As we had no recent information on his mass (or indeed on the mass of any Barnacle Geese departing from Spitsbergen after nesting), we assumed that his mass would be no higher than the upper limit for northbound birds when they leave the Solway (about 2.5 kg), and probably less as he would have only recently completed his moult. He left his nesting area in Reindalen, in the middle of Spitsbergen, on 25 September 2008, but spent the next 4 days moving intermittently south down the

west coast, covering a distance of 192 km. He would probably have lost some mass during this period, when strong easterly winds (15–20 m s^{-1}) would have made the sea crossing to Norway impracticable. We started the simulation when he left the southern tip of Spitsbergen on 29 September, and guessed his mass at that point to be 2.10 kg, corresponding to a fat fraction of 0.245, and an energy height just below 300 km, slightly lower than the northbound Barnacle Geese departing from Scotland. His subsequent route was essentially the same as that of the northbound birds, in the opposite direction, but without a stopover on the Norwegian coast. According to the simulation, DDT flew an air distance of 2,940 km between leaving Spitsbergen on 29 September and crossing the coast of north-east England near Bamburgh on 1 October, and lost 257 km of energy height, making an average energy gradient of 11.4 for the whole flight. Our estimate of his energy height on arrival (42 km) might, of course, be too high or too low, reflecting the unknown error in our guess for his mass and energy height at departure. However, it is safe to say that he was low on fat when he arrived, as local observers reported that he spent the next 4 weeks feeding on stubble, moving up the coast from Bamburgh to North Berwick, before joining the main wintering flock on the Solway on 29 October.

Average energy gradient and transmitter drag

Table 1 includes estimates of the effective lift-to-drag ratio for each goose at the beginning and end of each flight, starting at 15.1 for DDT, and increasing to 16.7 at the end of his flight, owing to the reduction of frontal area caused by the decrease of body mass. These values come from the "Power Curve" section of the *Flight* program, and represent the energy gradient that this particular goose should be able to achieve, if he were to fly continuously at his maximum range speed (V_{mr}). The lower overall average for the whole flight (11.4) results from the goose flying more slowly than this, and also spending periods on the ground or water, when fuel was consumed (and energy height lost) but no progress was made.

There could also be another reason why the observed energy gradients appear to be on the low side—the drag of the transmitter. It has long been suspected that a box-shaped package, especially one with a right-angled rear end, might cause separation of the boundary layer over the bird's back, and that this could trigger separation over a larger area, causing a massive increase in the body's drag coefficient. The drag of a transmitter (as distinct from its weight) is liable to decrease migration range by decreasing the lift-to-drag ratio, and hence steepening the energy gradient. Concerns about this have been renewed by Gill et al. (2009), who used two different types of transmitters

to track Alaskan Bar-tailed Godwits (*Limosa lapponica*) migrating extreme distances across the Pacific. The larger females were fitted with implanted transmitters, which had a minimal effect on the bird's external shape, and one of these birds was tracked flying non-stop to New Zealand, and others to various Pacific islands. The males, being smaller, were fitted with external back-pack transmitters, and none of these were tracked over the full distance. It is unclear whether any of them ran out of fuel while still at sea, but it seems possible that they did.

The current version (1.22) of the *Flight* program provides a "payload drag factor" to allow for the effect of a transmitter on the body's drag coefficient, but it is not possible to use this feature at present as there are no experimental data. Obrecht et al. (1988) tried to investigate this effect by measuring the drag of frozen bird bodies in a wind tunnel, with and without dummy transmitters, but discovered only that the boundary layer will not remain attached to a frozen body, even without a transmitter, and consequently that the drag measurements were not valid. Pennycuick et al. (1996a) found a way to measure the (much lower) drag coefficient of a living bird's body, and their method could be used to measure the effect of external transmitters of different shapes. However, because of the sensitive nature of the flow, the method requires a low-turbulence wind tunnel for valid results, and there are other practical difficulties which have so far precluded experiments of this type.

Fuel reserves

The energy heights of 200 km or more, at which the White-fronted Geese and Barnacle Geese arrived at their spring destinations, would suffice to fly at least another 2,200 km without refuelling, if their effective lift-to-drag ratio averaged about 11, while the Brent Geese, arriving at around 350 km, would have been able to fly nearly 4,000 km further. These reserves are far more generous than those required by aviation regulations for aircraft, but there are two reasons why they are probably essential for arctic-breeding geese.

The first is that, as noted above, the geese apparently were not able to anticipate head winds along the route ahead. They did not stop when caught by head winds, but kept going with very low ground speeds, and they did not even use such a simple expedient as to wait for a favourable wind before departing. The cruising air speeds of these geese hardly ever exceeded 20 m s^{-1}. As winds of similar speeds are not uncommon in spring and autumn, in arctic and sub-arctic latitudes, delays are inevitable, and there is a real danger of being blown off course, to a position from which a goose cannot recover. In the absence of any effective means to avoid unfavourable winds, massive fuel

reserves reduce this risk, although they do not eliminate it entirely. Two out of four northbound Barnacle Geese that were tracked by Griffin (2008) in the spring of 2006 reached Spitsbergen safely, but the other two, which left Scotland later, perished at sea after being caught by a north-easterly gale in the Norwegian Sea.

The second reason for arriving with generous reserves is that the arctic nesting season is short, and a goose has to arrive sufficiently early to complete the nesting process, in time for the young to be capable of migrating south when the autumn sets in. On the other hand, arriving too early entails the risk that the habitat may still be frozen, and if that happens the bird may have to subsist on its stored reserves of fuel while it secures a territory and establishes a nest. The larger reserves carried by the Brent Geese may indicate that their high arctic habitat is more likely to suffer from this problem than the lower latitudes in Greenland where the White-fronted Geese nest, or the Barnacle Goose nesting area in western Spitsbergen, whose climate is influenced by the Gulf Stream.

Alternative strategies for spring migration

Our simulations indicated that Barnacle DDT could have arrived in Scotland at an energy height of around 100 km, if he had left Spitsbergen at the same energy height at which the two northbound Barnacle Geese, DLT and DUC, left Scotland. Conversely, it should be possible for northbound Barnacle Geese to arrive in Spitsbergen in the spring at a similar energy height, without a feeding stopover in Norway. Griffin (2008) noted that the wintering population left the Solway over a period of 2–4 weeks, and that some tagged birds that departed late completed the northbound migration without stopping long enough in Norway for significant replenishment of their reserves. This option may allow the birds to build up more reserves before leaving Scotland, and to arrive earlier in the breeding area than they could if they had to spend time competing with conspecifics in the Norwegian staging areas, but at the expense of arriving with less energy height in hand to survive late snow and frosts while initiating nesting. Climate change would no doubt affect the relative breeding success of birds adopting one strategy or the other, and thus drive the evolution of this aspect of migration.

No such constraints apply to a bird arriving in the wintering area. Barnacle DDT would have arrived in England with a minimal but safe reserve, following the modest energy height at which we guessed that he left Spitsbergen. He could also most probably have stopped in Norway if his fuel had been low when he passed through the usual northbound stopover area. The fact that he did not do that indicates that he had sufficient fuel to complete the migration without a stopover, as the *Flight* program indicates.

Validating the *Flight* model

The *Flight* program's calculations are based on the same body of theory that has been developed by aeronautical engineers over the past century or so, and exhaustively tested. The untested aspects are essentially adjustments that may apply differently to birds and to aircraft. The program predicts many different quantities which appear at first sight to be unconnected with one another, but they are not. They are all inter-connected, and this can exploited by using one prediction to test the accuracy of another. For example, one might suppose that there could be no way to check the estimates of chemical power for Brent Geese in transit over the ice cap, mentioned above—but these are the same estimates that are used by the program to calculate fat and protein consumption, and to update the body mass and the remaining fat. If the calculated power is too high or too low, then the estimates of fuel consumption will also be off in one direction or the other. The program accounts for a Barnacle Goose's ability to fly from Spitsbergen to northern England without a stopover, as observed, and also predicts that a stopover in Norway enables them to arrive in Spitsbergen with adequate reserves to start nesting, as field observers believe that they do. Between them, these two observations imply that the power estimates are in the right general area, which is a good start towards validating the program, as most of its predictions depend on the power calculation in one way or another.

Since the calculations are common to all species, their accuracy can also be checked on different species. The program has already been used to account successfully for changes in body composition before and after a migratory flight of over 5,000 km by Great Knots (*Calidris tenuirostris*) (Pennycuick and Battley 2003). No changes were needed to the program, before applying it to geese in the present study. More exact tests of the accuracy of the program's predictions will depend on the ingenuity of observers in devising checks specifically for that purpose. For example, if a way could be found to weigh a tagged individual immediately before departure, and again immediately after arrival, then fuel consumption could be checked more accurately. In-flight measurements of wingbeat frequency could also be used for the same purpose, as suggested above. If consistent discrepancies are found, there is plenty of scope in the program for correcting erroneous output, by adjusting the default values assigned to variables used in the calculation.

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