



HAL
open science

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

► To cite this version:

C. J. Pennycuick, L. R. Griffin, Kendrew Colhoun, Richard Angwin. A trial of a non-statistical computer program for monitoring fuel reserves, response to wind and other details from GPS tracks of migrating geese. *Journal für Ornithologie = Journal of Ornithology*, 2010, 152 (S1), pp.87-99. 10.1007/s10336-010-0633-6 . hal-00652645

HAL Id: hal-00652645

<https://hal.science/hal-00652645>

Submitted on 16 Dec 2011

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20

**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. Pennycuick¹, L. R. Griffin², Kendrew Colhoun³ and Richard Angwin⁴

¹School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG,
U.K.

²Wildfowl and Wetlands Trust, Caerlaverock Wetlands Centre, Eastpark Farm, Dumfries
DG1 4RS, U.K.

³Wildfowl and Wetlands Trust, Castle Espie Wetlands Centre, Ballydrain Road, Comber,
County Down, Northern Ireland, U.K.

⁴Weather Desk, Broadcasting House, Whiteladies Road, Bristol BS8 2LR, U.K.

Corresponding author: c.pennycuick@freeuk.com

21

Summary

22 GPS transmitters were used with the Argos satellite system to track two Brent Geese from
23 Iceland to Arctic Canada, three Greenland White-fronted Geese from Scotland to west
24 Greenland, and two Barnacle Geese from Scotland to Spitsbergen. Each goose's wing span
25 was measured at the time of tagging, and its body mass and fat fraction were estimated at the
26 time of departure. This was the starting point for the *Flight* program's time-marching
27 simulation, which is a non-statistical procedure based on flight mechanics. The ground speed
28 was measured between each GPS fix and the previous one, and combined with a wind
29 estimate to find the air speed. The program calculated the power, using the air density from
30 the GPS altitude. The rates of consumption of fat and muscle tissue were calculated from the
31 power, and used to update the body mass and composition. The total air distance flown by
32 each bird was not consistently less than the ground distance, and there was no indication that
33 the birds could select their routes, or even their timing, so as to bias the wind in their favour.
34 Rates of climb when ascending the Greenland Ice Cap were very low in the Brent Geese, in
35 relation to the maximum rate of climb of which the flight muscles were expected (on
36 mechanical grounds) to be capable of supporting. The Brent Geese stopped often during the
37 ice crossing, suggesting that they could not sustain sufficient aerobic power for continuous
38 flight. The White-fronts' fat fractions were lower across the ice cap, and they climbed faster
39 and stopped less often. Energy height was used as a species-independent measure of energy
40 reserves. All seven northbound geese arrived in their nesting areas at estimated energy
41 heights exceeding 200 km (around 350 km for the two Brent Geese). All of the geese
42 achieved average energy gradients of at least 11, including short stops, meaning that their
43 arrival energy heights were sufficient to fly a further 2200 – 4000 km. We propose that these
44 reserves represent the energy height needed to initiate successful breeding in these arctic
45 habitats, with an element of insurance against contrary winds.

46

47

48 **Keywords:** bird migration, computer simulation, flight mechanics, energy height

49

50

51

Introduction

52 Throughout most of 2008, the BBC ran a series of weekly radio programmes under the title
53 "World on the Move", following the migrations of a wide variety of animals. These included
54 a number of geese, which we tracked by the Argos satellite system, using GPS-based

55 transmitters, deployed under an existing, conservation-oriented Wildfowl and Wetlands Trust
56 research programme. The background to this programme has been described by Griffin
57 (2008), along with recent results, and current activities are reported at
58 www.wwt.org.uk/research/tracking/maps.asp. We followed three species whose likely
59 destinations were already known from previous satellite tracking, as were the approximate
60 distances and expected timing of the spring migration. We used the *Flight* program, which
61 was developed by one of us (CJP), to run a computer simulation of each individual flight,
62 based on flight mechanics rather than statistics, to see whether we could quantitatively
63 account for each goose's consumption of fat and protein while migrating, and for its energy
64 reserves on arrival in the nesting area. The program is freely available on the internet, and we
65 present the results as a demonstration of what it can do, and also to point out measurements
66 which future observers could make, to check the program's predictions, and improve their
67 accuracy.

68 As we had a professional meteorologist among the authors (RA), we were able to take
69 account of the wind at every point of each flight, to estimate the bird's air speed, which in
70 turn allowed us to generate running estimates of a number of variables, including the amounts
71 of fat and protein that each goose consumed, and the reserves remaining, hour by hour
72 throughout the flight. The calculations are based on aeronautical concepts, and we use the
73 conventional terminology from aeronautics wherever possible, as biological terms which
74 have been introduced independently are seldom directly equivalent, and often insufficiently
75 precise. The program works by first estimating the bird's average air speed for each leg of the
76 flight (between each two successive GPS fixes) and then estimating the chemical power, i.e.
77 the rate at which fuel energy is consumed during the leg. The power is multiplied by the
78 duration of the leg to get the amount of energy used, and this in turn is used to estimate the
79 mass of fat and protein consumed. The body mass is revised downwards, before calculating a
80 new power estimate at the start of the next leg. The aeronautical theory, on which the
81 calculations are ultimately based, is set out in such texts as Anderson (1991), but the program
82 takes account of some features that are specific to birds, especially the progressive
83 consumption of protein from the flight muscles and other organs, and its use as
84 supplementary fuel (Lindström & Piersma 1993, Piersma & Gill 1998). It is not practical to
85 give full explanations of the program's operation in a research paper, but references are given
86 in the text to paragraph numbers in a book (Pennycuick 2008), which explains the theory that
87 underlies the program, and also attempts to bridge the gap between the somewhat different
88 concepts and terminology to which aeronautical engineers and biologists are accustomed. The

89 *Flight* program can be downloaded free from <http://www.bio.bristol.ac.uk/people>
90 [/pennycuick.htm](http://pennycuick.htm), or from <http://books.elsevier.com/companions/7780123742995>, which is
91 the publisher's companion page for the book. Readers who have installed it will find further
92 information in the online manual.

93

94 [Fig. 1 here]

95

96

Methods

97 Geese

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

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

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

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

121

122 Wing measurements

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

135

136 [Table 1 here]

137

138 Starting body mass

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

150

151 Estimating fat fraction from body mass

152 The distance that any bird can fly without feeding is determined by the fat *fraction* at
153 departure, i.e. by the ratio of the mass of stored fat to the total body mass, not by the fat mass
154 as such (Pennycuick 2008, 8.1.1). An increase of the fat fraction results in increased range,
155 whether it is achieved by adding fat, or by reducing the mass of other body components, or
156 both. Measuring the fat fraction directly is impractical as it involves killing the bird, but if the

157 bird belongs to a population from which samples have been trapped and weighed over a
158 period of years, as our geese did, it is possible to use the *Flight* program to estimate the fat
159 fraction from the body mass. Past records were scanned for the lowest mass ever recorded, a
160 statistical outlier representing a goose that had lost its way, or arrived late in the stopover area
161 after all the food had been eaten, or been caught in head winds, and was weighed before it
162 had time to start recovering. Table 1 lists the estimated departure mass for each bird, and also
163 the lowest mass previously reported in each species, for a bird that was thin but apparently
164 healthy. It is assumed that the difference between a bird's current mass and this minimum
165 mass represents the combined mass of fat and protein that is available to be consumed as fuel.
166 Each bird's mass was set to the estimated departure value, and the starting fat fraction was
167 varied in repeated runs of the *Flight* program, until a value was found by trial and error that
168 ran down to zero when the body mass was equal to the reported minimum mass (Pennycuick
169 2008, Box 8.4). The division of the energy requirement between fat and protein is taken
170 account of by the program (below). In practice it takes a couple of minutes to estimate the
171 starting fat fraction by this method, and the Excel output of the program can then be used to
172 generate a table or graph that shows the fat fraction corresponding to any mass between the
173 minimum and the starting mass, for that individual bird. The logic does not exclude the
174 possibility that the reported minimum mass refers to a bird that has not completely exhausted
175 its fat, but still has a small reserve remaining. This does not affect the calculations of distance
176 flown or other variables, down to the assumed minimum mass. It might terminate the
177 simulation at a point where the bird could in reality have flown a little further, but this did not
178 happen in any of our simulations.

179

180 Transmitters

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

189

190 Data processing

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

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

213 The GPS variant is included in the published program from *Flight* 1.20 onwards,
214 together with the Excel template with the macros, and a set of example files from one of the
215 Greenland White-fronted Geese that feature in this paper. Detailed output from a program run
216 can be generated as an Excel spreadsheet, whose format is the same as the output for
217 programmed migration. It shows the time from start and the ground distance flown at each fix
218 (and 29 other variables), but does not show the GPS positions. Optionally, the program will
219 also generate another spreadsheet, the "Progress Update", which shows the latitude, longitude
220 and height of each fix, together with a reduced set of output variables, originally intended for
221 broadcasters. Another option (used in the preparation of Fig. 1) generates a "kml" file, which
222 plots the track if its icon is dragged and dropped into an open Google Earth window.

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

225

226 Muscle burn criterion

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

240

241

Results and Discussion

242 Starting fat fraction

243 Although the maximum fat fractions that are possible for different birds are not well known,
244 there is definitely a trend for the upper limit to decline in larger birds. Values above 0.5 have
245 been reported in various passerines and medium-sized waders, meaning that all the other
246 body parts have to be squeezed into less than half of the all-up mass. This includes the heart
247 and lungs, which most probably have to be enlarged to support the aerobic muscle power
248 needed to lift and propel the whole package. It is unlikely that any goose could fly with a fat
249 fraction of 0.5, but our two Brent Geese (the smallest species of the three) both left Iceland
250 with estimated fat fractions of 0.44. They are likely to have been constrained by limitations of
251 muscle power, or oxygen availability, or both, and we looked for signs of this when they
252 crossed the Greenland ice cap (below). They also had the longest distance to cover without
253 stopovers, about 2800 km from Iceland to Ellesmere Island. The White-fronted Geese and
254 Barnacle Geese started with fat fractions in the range 0.29-0.33, but they only had to cover
255 distances up to about 1700 km without stopovers. It will be seen later that all of the
256 northbound geese departed after each stopover with generous fuel reserves.

257

258 Minimum power speed

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

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

280

281 [Fig. 2 here]

282

283 The effects of altitude and body mass can be seen in Fig. 2, which was plotted from
 284 the Progress Updates for the seven northbound geese, and shows the current estimate of V_{mp}
 285 for each goose against the total ground distance covered so far. Both Brent Geese showed a
 286 hump in the V_{mp} curve, from below 17 to 18.5 m s^{-1} , as they climbed to 2500 m or so over
 287 Greenland. The three White-fronted Geese stopped for three weeks in Iceland, about 1400 km
 288 out from Scotland, during which they moved only a short distance while their estimated mass,
 289 and also their V_{mp} , built up to near the original departure levels. They too showed a
 290 pronounced hump in the curve as they crossed Greenland by different routes that involved
 291 climbing to heights of between 2500 and 3000 m. The Barnacle Geese flew low over the sea
 292 for most of their migration, with V_{mp} declining gradually along with their body mass. Their

293 feeding stopover consisted of 2-3 weeks moving slowly up a 350-km section of the
 294 Norwegian coast, with their mass and their V_{mp} building up progressively.

295

296 [Fig. 3 here]

297

298 Ratio of average air speed to V_{mp}

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

308 Although both Brent Geese set off from Iceland with the same high fat fraction (0.44),
 309 JV stopped frequently while crossing the icecap and took two days to get across, while DZ
 310 stopped less and got across in less than a day. Both Brent Geese flew continuously for long
 311 periods during the 1100-km transit of Baffin Bay, their mass being well down by then. The
 312 three White-fronted Geese stopped on the water shortly before reaching Iceland, and also
 313 earlier, during the crossing from Scotland. They stopped on the water near the east coast of
 314 Greenland, around 2300 km from the start, and then flew intermittently up the east slope of
 315 the ice. Two of the three flew continuously once they reached the top, while the third (V4A)
 316 stopped frequently while crossing the ice. The two Barnacle Geese flew continuously across
 317 the North Sea, and also on the crossing from Norway to Spitsbergen, except for the first part
 318 of the crossing, where they were still heavy from the stopover.

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

327

328 [Fig. 4 here]

329

330 Head winds and tail winds

331 If migrating birds were somehow able to plan their routes so as to take advantage of tail
332 winds on one side or another of a moving weather system, the result would be that the air
333 distance flown would be less than the ground distance covered. This was easily tested from
334 our data, as we had the ground distance for each leg directly from the GPS, and we also had
335 the air speed, and the airborne time taking account of stops (above), which were multiplied
336 together to give the air distance for each leg. Fig. 4 shows the total air distance plotted against
337 the ground distance for 8 entire flights, including the southbound flight of Barnacle DDT.
338 Each point would lie on the diagonal line if there was no wind throughout the flight, or if
339 periods of tail wind were balanced by periods of head wind, whereas if the bird managed to
340 bias the result in favour of tail winds, the point would lie below the line. Actually, only
341 Barnacle DUC is well below the line, and the other seven geese are either on the line, or just
342 above it. This does not support the idea that the geese were taking advantage of tail winds in
343 a non-random manner.

344

345 [Fig. 5 here]

346

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

349

350
$$\text{Tail Wind Ratio} = (\text{Ground Distance} - \text{Air Distance}) / \text{Ground Distance}.$$

351

352 This ratio is positive for a tail wind, and negative for a head wind. It can take a large negative
353 value if the bird is flying against a strong head wind that makes its ground speed very small,
354 as happened to Brent Goose JV on the last part of his flight from Ellesmere Island to Amund
355 Ringnes Island. One of the Barnacle Geese (DLT) also persevered against persistent head
356 winds on the crossing from Norway to Spitsbergen, while the other one (DUC) made the
357 same crossing on a different day and got neither help nor hindrance from the wind.
358 Otherwise, each goose got tail winds in some parts of its route, but flew on against head
359 winds in others, with no obvious pattern. There is no indication that any of the geese selected
360 their routes to take advantage of wind patterns, or even that they timed their departures to

361 take advantage of tail winds. Two of the White-fronted Geese (V1A and V2A) actually
362 departed from Scotland (together) in head winds that persisted for most of the way across to
363 Iceland.

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

374

375 [Fig. 6 here]

376

377 Altitude and rate of climb

378 Hedenström and Ålerstam (1992) introduced the idea that a bird's maximum rate of climb
379 depends on its *power margin*, that is the excess of the maximum power available from the
380 flight muscles over the power required to fly level at V_{mp} , and they applied this to radar
381 observations of migrating birds. This principle, in a more general form, is incorporated in the
382 *Flight* program, and we used it to maintain, for each of our geese, a running estimate of its
383 maximum rate of climb at any point in the flight. This is a mechanical limit, imposed
384 ultimately by the maximum stress that the flight muscles are capable of exerting in an
385 isometric contraction, and the active strain at maximum power (Pennycuick 2008, Box 7.5).
386 In aerobic flight, a lower limit may be imposed by oxygen availability. If the aerobic limit
387 comes down below the power required to fly level at V_{mp} , owing to reduced air density at
388 high altitude, then the bird is reduced to proceeding in short hops, with rest periods to recover
389 the resulting oxygen debt. Migration over the Greenland ice cap involves a steep climb to
390 2500 m or more, followed by some hours of level flight at that altitude, and we were
391 especially interested to examine the five tracks that crossed Greenland for signs of both types
392 of limit.

393 The lower graphs in Figs. 6 and 7 show each bird's GPS altitude versus ground
394 distance, for the Brent Geese and the White-fronted Geese respectively, while the upper

395 graphs show the average rate of climb (negative for descent) for each leg of the flight, found
 396 by dividing the height change during the leg by the time. In the case of legs with an average
 397 air speed less than V_{mp} , meaning that the bird was only flying for part of the time (above), the
 398 rate of climb was corrected by dividing by the proportion of the leg time that was spent
 399 airborne. This gives the rate of climb during the time that the bird was actually flying, rather
 400 than the average for the whole leg. In all five geese, the highest rates of climb were seen
 401 during the ascent of the eastern slope of the Greenland ice cap. These observed rates of climb
 402 are plotted in Fig. 8 against the mechanical limit for each goose, as calculated by the “Power
 403 Curve” section of the *Flight* program, using the estimated body mass for each goose at the
 404 time it started the ascent. The points for all five geese were well below the diagonal line in
 405 the diagram, meaning that the observed rates of climb were below the calculated mechanical
 406 limit.

407

408 [Fig. 7 here]

409

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

418 The theory next requires a value for the maximum isometric stress that the flight
 419 muscles can exert, which is expected to be constant in all vertebrate skeletal muscles. The
 420 default value in the *Flight* program (560 kN m^{-2}) comes from observations of whooper swans,
 421 whose performance is constrained by their large size (Pennycuick 2008, 7.3.7). This leads in
 422 turn to an upper limit for the specific work in the myofibrils, which is estimated to be around
 423 41 J kg^{-1} (Pennycuick 2008, 7.3.1). The margin of power available for climbing is determined
 424 by the difference between this limit and the specific work required to fly level, which was
 425 around 17 J kg^{-1} in the Brent Geese, and 20 J kg^{-1} in the White-fronted Geese, the difference
 426 being due mainly to the smaller size of the Brent Geese. The Brent Geese, with their wider
 427 margin, should be capable of a higher rate of climb than the White-fronted Geese (X-axis in
 428 Fig. 8). However, the observed rate of climb (Y-axis) was up to three-quarters of the

429 maximum in the White-fronted Geese, but a much smaller fraction in the Brent Geese, and
430 also less in absolute terms.

431

432 [Fig. 8 here]

433

434 Gudmundsson et al. (1995) noted that their Brent Geese took a long time to get up on
435 to the ice cap, and suggested that this was due to aerobic limitations. We speculate further
436 that the maximum rate of climb is limited by aerobic capacity to a value below the
437 mechanical limit, and that the high fat fractions taken on by the Brent Geese result in their
438 aerobic power margin for climb being smaller than that of White-fronted Geese. Both of our
439 Brent Geese had sufficient mechanical power to fly level at the top of the ice cap, but only
440 one of them (DZ) was able to fly continuously once he reached the top. According to the
441 simulation, this implies that DZ was able to maintain aerobically a chemical power level of
442 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} .
443 This is a minimum estimate of his aerobic capacity at that air density. The other Brent Goose
444 (JV) required a slightly lower level of chemical power (121 W) at a similar stage of the flight,
445 but was only able to maintain this intermittently, with frequent stops, meaning that his
446 aerobic capacity was insufficient to maintain continuous level flight. Regrettably, there is no
447 quantitative theory from which the aerobic capacity of the heart and lungs can be calculated
448 as a function of air density, although it is known that bird lungs, being organised differently
449 from those of mammals, are more effective at extracting oxygen when the air density is low
450 (Tucker 1968, Pennycuik 2008, Box 7.7). Our results reveal wide variations between
451 individuals in their ability to sustain continuous flight over the top of the ice cap, in both
452 Brent and White-fronted Geese, but we do not see any likely explanation for this.

453

454 [Fig. 9 here]

455

456 Body mass and the wingbeat-frequency fuel gauge

457 The program estimated that each goose's body mass declined while the goose was flying, and
458 increased during feeding stopovers. That much, but little else, can be seen in Fig. 9, which
459 shows running estimates of body mass for all the northbound geese. However the fat fraction
460 can be estimated from the body mass, as noted in the section (above) on estimating the fat
461 fraction at departure, and if the body mass could be measured remotely, this could be used, in
462 effect, as a fuel gauge. This might be possible in a bird like a goose, which flaps steadily

463 along for most of the time when migrating, by taking a wingbeat count from an
 464 accelerometer, in a timed interval just before each scheduled GPS fix, and transmitting the
 465 count as one byte of data, along with the fix. To illustrate the principle, Fig. 10 shows the
 466 *Flight* program's running estimate of Brent Goose JV's wingbeat frequency. The estimate
 467 declines from 6.2 Hz on leaving Iceland with a full load of fat to 5.2 Hz at Ellesmere Island,
 468 then jumps to 5.4 Hz following the assumed feeding stop, before declining to 5.0 Hz during
 469 the last 500 km, in which the goose had to fly against a strong head wind as he neared Amund
 470 Ringnes Island. If the wingbeat frequencies in Fig. 10 had been measured rather than
 471 estimated, the calculation could have been inverted to replace JV's mass curve in Fig. 9, so
 472 providing a check on the estimated body mass. It would also have shown whether JV actually
 473 did feed during his stop at Ellesmere Island as assumed, and if so, how much mass (and fat)
 474 he gained. Such a fuel-gauge calculation would have to take account of the altitude, as the air
 475 density also affects the wingbeat frequency.

476

477 [Fig. 10 here]

478

479 Energy height and range

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

486 There is a very direct way to represent the range calculation, and that is to begin by
 487 converting the starting fat fraction into an "energy height", at which the bird starts its flight
 488 (Pennycuick 2008, 8.3). The goose comes "down" from this virtual starting height on a
 489 gradient, which reflects the rate at which it uses fuel. As in a glider, the flatter the gradient,
 490 the further the goose goes from a given starting height. The gradient on which a glider comes
 491 down is simply its lift-to-drag ratio, while for the goose, the *Flight* program calculates and
 492 continuously updates the "effective lift-to-drag ratio", which is the equivalent measure of
 493 aerodynamic efficiency in flapping flight. It depends mostly on the wing span and the body
 494 drag, and corresponds directly to the lift-to-drag ratio of a glider or fixed-wing aircraft. The
 495 effective lift-to-drag ratio increases slightly as the flight proceeds, because of the body's
 496 decreasing frontal area, which in turn reduces its drag. It is affected by the air speed, the

497 gradient being flattest if the goose flies at its current maximum range speed (V_{mr}), and steeper
498 if lack of power forces it to fly more slowly, near V_{mp} .

499

500 [Fig. 11 here]

501

502 The starting energy height is tabulated for each goose in Table 1. It is calculated from
503 the starting fat fraction (Pennycuick 2008, Box 8.3), and also takes account of the conversion
504 efficiency of the flight muscles, and the acceleration due to gravity. Fig. 11 shows the
505 remaining energy height, calculated by the *Flight* program for each goose, plotted against the
506 *air* distance flown (unlike the earlier graphs, which have ground distance on the X-axis). The
507 two Brent Geese started from Iceland at energy heights around 650 km, and arrived in their
508 respective nesting areas with about 350 km remaining, one (JV) with a late stopover, and the
509 other (DZ) without. The Barnacle Geese and White-fronted Geese all started from energy
510 heights around 350 km, except for Barnacle DUC, who stayed longer in Scotland and fuelled
511 up to 410 km before departing. All five geese replenished their energy height during
512 stopovers in Iceland or Norway, and followed much the same gradient on the second stage of
513 their migration, arriving in the breeding area with around 200 – 250 km of energy height in
514 hand.

515

516 Autumn migration of Barnacle DDT

517 The dotted line at the bottom of Fig. 11 is the southbound flight of Barnacle DDT, for which
518 the calculation is somewhat conjectural, as he was tagged in the previous year, and some
519 items of data were lacking. We assigned him the average wing span for an adult male
520 Barnacle Goose (1.42 m). As we had no recent information on his mass (or indeed on the
521 mass of any Barnacle Geese departing from Spitsbergen after nesting) we assumed that his
522 mass would be no higher than the upper limit for northbound birds when they leave the
523 Solway (about 2.5 kg), and probably less as he would have only recently completed his
524 moult. He left his nesting area in Reindalen, in the middle of Spitsbergen, on 25 September
525 2008, but spent the next four days moving intermittently south down the west coast, covering
526 a distance of 192 km. He would probably have lost some mass during this period, when
527 strong easterly winds ($15\text{-}20\text{ m s}^{-1}$) would have made the sea crossing to Norway
528 impracticable. We started the simulation when he left the southern tip of Spitsbergen on 29
529 September, and guessed his mass at that point to be 2.10 kg, corresponding to a fat fraction of
530 0.245, and an energy height just below 300 km, slightly lower than the northbound Barnacle

531 Geese departing from Scotland. His subsequent route was essentially the same as that of the
532 northbound birds, in the opposite direction, but without a stopover on the Norwegian coast.
533 According to the simulation, DDT flew an air distance of 2940 km between leaving
534 Spitsbergen on 29 September and crossing the coast of north-east England near Bamburgh on
535 1 October, and lost 257 km of energy height, making an average energy gradient of 11.4 for
536 the whole flight. Our estimate of his energy height on arrival (42 km) might, of course, be too
537 high or too low, reflecting the unknown error in our guess for his mass and energy height at
538 departure. However, it is safe to say that he was low on fat when he arrived, as local
539 observers reported that he spent the next four weeks feeding on stubble, moving up the coast
540 from Bamburgh to North Berwick, before joining the main wintering flock on the Solway on
541 29 October.

542

543 Average energy gradient and transmitter drag

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

552 There could also be another reason why the observed energy gradients appear to be on
553 the low side – the drag of the transmitter. It has long been suspected that a box-shaped
554 package, especially one with a right-angled rear end, might cause separation of the boundary
555 layer over the bird’s back, and that this could trigger separation over a larger area, causing a
556 massive increase in the body’s drag coefficient. The drag of a transmitter (as distinct from its
557 weight) is liable to decrease migration range by decreasing the lift-to-drag ratio, and hence
558 steepening the energy gradient. Concerns about this have been renewed by Gill et al. (2009),
559 who used two different types of transmitters to track Alaskan Bar-tailed Godwits migrating
560 extreme distances across the Pacific. The larger females were fitted with implanted
561 transmitters, which had a minimal effect on the bird’s external shape, and one of these birds
562 was tracked flying non-stop to New Zealand, and others to various Pacific islands. The males,
563 being smaller, were fitted with external back-pack transmitters, and none of these were

564 tracked over the full distance. It is unclear whether any of them ran out of fuel while still at
565 sea, but it seems possible that they did.

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

577

578 Fuel reserves

579 The energy heights of 200 km or more, at which the White-fronted Geese and Barnacle Geese
580 arrived at their spring destinations, would suffice to fly at least another 2200 km without
581 refuelling, if their effective lift-to-drag ratio averaged about 11, while the Brent Geese,
582 arriving at around 350 km, would have been able to fly nearly 4000 km further. These
583 reserves are far more generous than those required by aviation regulations for aircraft, but
584 there are two reasons why they probably are essential for arctic breeding geese.

585 The first is that, as noted above, the geese apparently were not able to anticipate head
586 winds along the route ahead. They did not stop when caught by head winds, but kept going
587 with very low ground speeds, and they did not even use such a simple expedient as to wait for
588 a favourable wind before departing. The cruising air speeds of these geese hardly ever
589 exceeded 20 m s^{-1} . As winds of similar speeds are not uncommon in spring and autumn, in
590 arctic and sub-arctic latitudes, delays are inevitable, and there is a real danger of being blown
591 off course, to a position from which a goose cannot recover. In the absence of any effective
592 means to avoid unfavourable winds, massive fuel reserves reduce this risk, although they do
593 not eliminate it entirely. Two out of four northbound Barnacle Geese that were tracked by
594 Griffin (2008) in the spring of 2006 reached Spitsbergen safely, but the other two, which left
595 Scotland later, perished at sea after being caught by a north-easterly gale in the Norwegian
596 Sea.

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

606

607 Alternative strategies for spring migration

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

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

628

629 Validating the *Flight* model

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

647 Since the calculations are common to all species, their accuracy can also be checked
648 on different species. The program has already been used to account successfully for changes
649 in body composition before and after a migratory flight of over 5000 km by Great Knots
650 (Pennycuik and Battley, 2003). No changes were needed to the program, before applying it
651 to geese in the present study. More exact tests of the accuracy of the program's predictions
652 will depend on the ingenuity of observers in devising checks specifically for that purpose. For
653 example if a way could be found to weigh a tagged individual immediately before departure,
654 and again immediately after arrival, then fuel consumption could be checked more accurately.
655 In-flight measurements of wingbeat frequency could also be used for the same purpose, as
656 suggested above. If consistent discrepancies are found, there is plenty of scope in the program
657 for correcting erroneous output, by adjusting the default values assigned to variables used in
658 the calculation.

659

660 **Acknowledgements**

661 It is a pleasure to thank Julian Hector, Head of Radio Broadcasting in the BBC Natural
662 History Unit, Bristol, who devised and directed the *World on the Move* radio series, financed
663 the satellite tracking in conjunction with the Solway Coast Area of Outstanding Natural

664 Beauty Sustainable Development Fund, and co-ordinated the whole operation, and Baz
 665 Hughes who co-ordinated the Wildfowl and Wetlands Trust (WWT) side of the project. We
 666 are especially grateful to Guðmundur Guðmundsson of the Icelandic Institute of Natural
 667 History for allowing us to take part in the Brent Goose research project, to Nigel Jarrett of
 668 WWT for setting up the wing-measuring operation at Slimbridge and to Richard Hesketh,
 669 staff and volunteers at WWT Caerlaverock who, along with the North Solway Ringing
 670 Group, assisted with the barnacle goose catches. The activities described in this paper
 671 complied with United Kingdom and Iceland law.

672

673 **References**

674

675 Anderson, J.O. (1991): Fundamentals of Aerodynamics. McGraw Hill, New York.

676

677 Gill, R.E., Tibbitts, T.L., Douglas, D.C., Handel, C.M., Mulcahy, D.M., Gottschalck, J.C.,
 678 Warnock, N., McCaffery, B.J., Battley, P.F. & Piersma, T. (2009): Extreme endurance
 679 flights by landbirds crossing the Pacific Ocean: ecological corridor rather than barrier?
 680 Proc. R. Soc. Lond. B 276: 447-457.

681

682 Glahder, C.M., Fox, A.D. & Walsh, A.J. (1999): Satellite tracking of Greenland White-
 683 fronted Geese. Dansk Ornitologisk Forenings Tidsskrift 93: 271-276.

684

685 Griffin, L. R. (2008): Identifying the pre-breeding areas of the Svalbard Barnacle Goose
 686 *Branta leucopsis* between mainland Norway and Svalbard: an application of GPS
 687 satellite-tracking techniques. Vogelwelt 129: 226–232.

688

689 Gudmundsson, G.A., Benvenuti, S., Alerstam, T., Papi, F., Lilliendahl, K. & Åkesson, S.
 690 (1995): Examining the limits of flight and orientation performance: satellite tracking of
 691 Brent Geese migrating across the Greenland ice-cap. Proc. R. Soc. Lond. B 261,73-79.

692

693 Hedenström, A. & Alerstam, T. (1992): Climbing performance of migrating birds as a basis
 694 for estimating limits for fuel-carrying capacity and muscle work. J. Exp. Biol. 164: 19-
 695 38.

696

- 697 Jenni, L. & Jenni-Eiermann, S. (1998): Fuel supply and metabolic constraints in migrating
698 birds. *J. Avian Biol.* 29: 521-528.
699
- 700 Lindström, Å. & Piersma, T. (1993): Mass changes in migrating birds: the evidence for fat
701 and protein storage re-examined. *Ibis* 135: 70-78.
702
- 703 Obrecht, H.H., Pennycuick, C.J. & Fuller, M.R. (1988): Wind tunnel experiments to assess
704 the effects of back-mounted radio transmitters on bird body drag. *J. Exp. Biol.* 135: 265-
705 273.
706
- 707 Pennycuick, C.J. (1998): Computer simulation of fat and muscle burn in long-distance bird
708 migration. *J. Theoret. Biol.* 191: 47-61.
709
- 710 Pennycuick, C.J. (2001): Speeds and wingbeat frequencies of migrating birds compared with
711 calculated benchmarks. *J. Exp. Biol.* 204: 3283-3294.
712
- 713 Pennycuick, C.J. (2008): *Modelling the Flying Bird*. Elsevier, Amsterdam.
714
- 715 Pennycuick, C.J. & Battley, P.F. (2003): Burning the engine: a time-marching computation of
716 fat and protein consumption in a 5420-km flight by Great Knots (*Calidris tenuirostris*).
717 *Oikos* 103: 323-332.
718
- 719 Pennycuick, C.J., Klaassen, M., Kvist, A. and Lindström, Å. (1996a): Wingbeat frequency
720 and the body drag anomaly: wind tunnel observations on a Thrush Nightingale (*Luscinia*
721 *luscinia*) and a Teal (*Anas crecca*). *J. Exp. Biol.* 199: 2757-2765.
722
- 723 Pennycuick, C.J., Einarsson, O., Bradbury, T.A.M. and Owen, M. (1996b): Migrating
724 whooper swans (*Cygnus cygnus*): satellite tracks and flight performance calculations. *J.*
725 *Avian Biol.* 27: 118-134.
726
- 727 Pennycuick, C.J., Bradbury, T.A.M., Einarsson, Ó. and Owen, M. (1999): Response to
728 weather and light conditions of migrating Whooper Swans *Cygnus cygnus* and flying
729 height profiles, observed with the Argos satellite system. *Ibis* 141: 434-443.
730

731 Piersma, T. & Gill, R.E. (1998): Guts don't fly: small digestive organs in obese Bar-tailed
732 Godwits. *Auk* 115: 196-203.

733

734 Tucker, V.A. (1968): Respiratory physiology of house sparrows in relation to high-altitude
735 flight. *J. Exp. Biol.* 48: 55-66.

736

737 **Captions for figures**

738

739 **Fig. 1.** Map of the study area with the tracks of one goose of each of the three species
740 tracked. The Brent Geese wintered in Northern Ireland but their tracks begin in Iceland,
741 where they were tagged.

742

743 **Fig. 2.** Running estimates of the minimum power speed of each goose, plotted against ground
744 distance covered.

745

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

749

750 **Fig. 4.** Total air distance flown versus total ground distance covered by each goose. If a point
751 is below the diagonal line (air distance < ground distance), the goose had a net tail wind
752 component.

753

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

758

759 **Fig. 6.** Lower graph: GPS altitude for the two Brent Geese. Upper graph: corrected rate of
760 climb. The correction was applied to legs in which the goose only flew for part of the time,
761 and gives the average rate of climb during the time that the goose was airborne, rather than
762 the overall average for the leg.

763

764 **Fig. 7.** Altitude (lower) and corrected rate of climb (upper) as in Fig. 5, but for the three
765 White-fronted Geese.

766

767 **Fig. 8.** Observed rates of climb from Figs. 5 and 6, plotted against calculated mechanical
768 upper limit for each goose.

769

770 **Fig. 9.** Estimated body mass versus ground distance covered by the seven northbound geese.

771

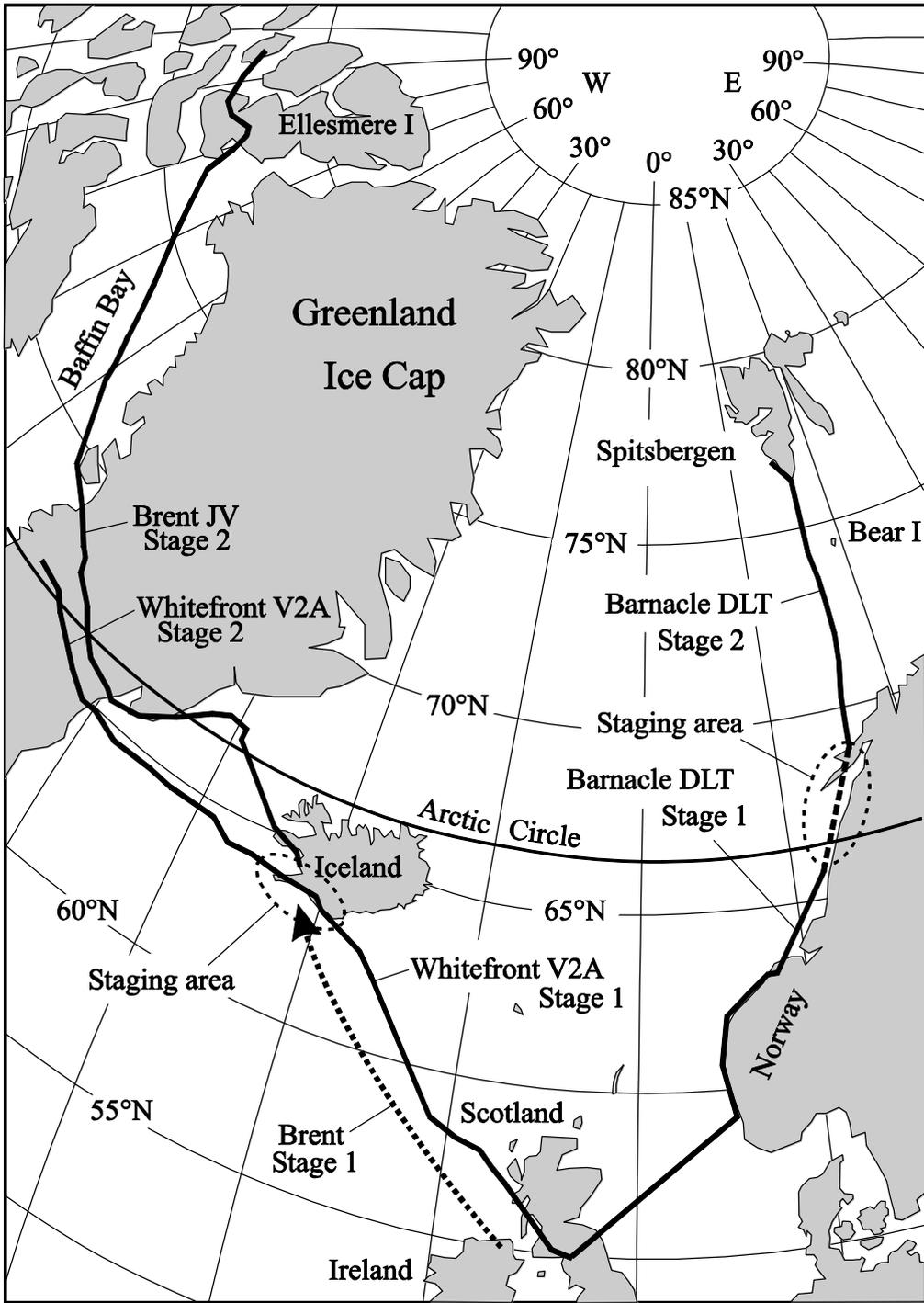
772 **Fig. 10.** Calculated wingbeat frequency for Brent JV versus ground distance covered. If the
773 wingbeat frequency were measured remotely via the satellite link, this calculation could be
774 inverted, and used to estimate the body mass as in Fig. 9. This would amount to a remote fuel
775 gauge.

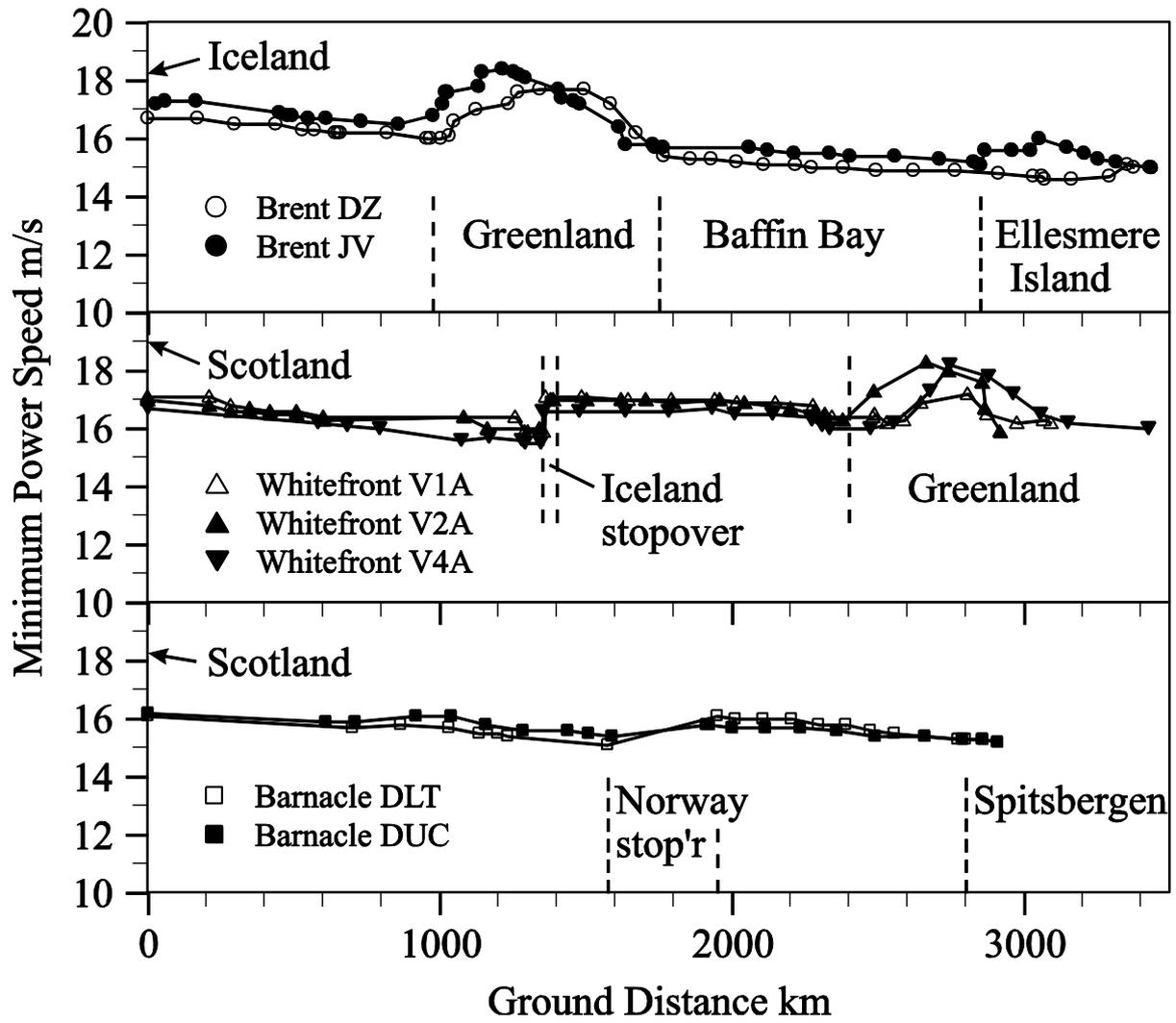
776

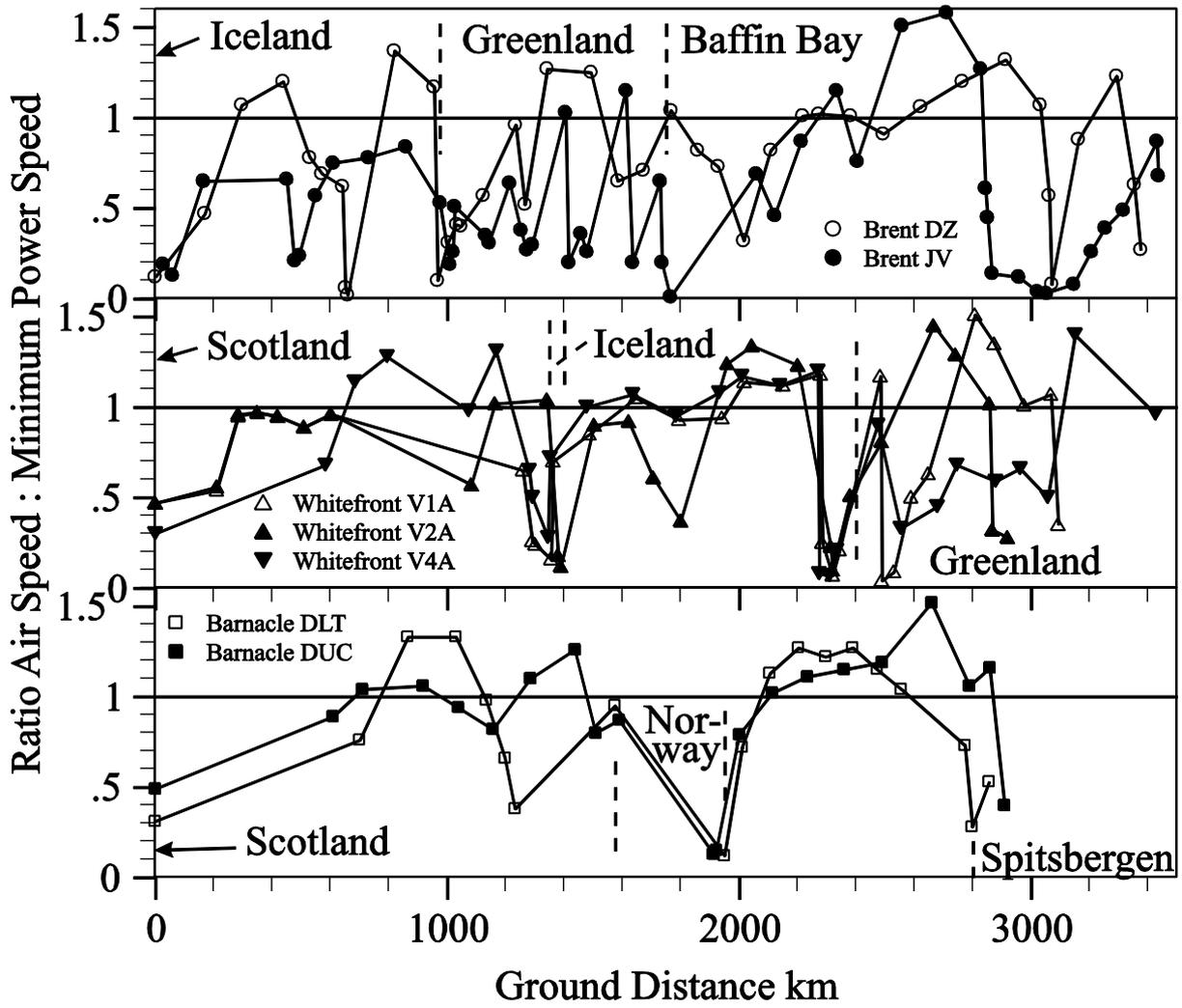
777 **Figure 11.** Energy height plotted against air distance flown. The dotted line at the bottom is
778 for the southbound Barnacle DDT, some of whose data had to be approximated. Energy
779 height curves for other species, large or small, would be directly comparable. Unlike curves
780 of body mass, they could be plotted on the same graph.

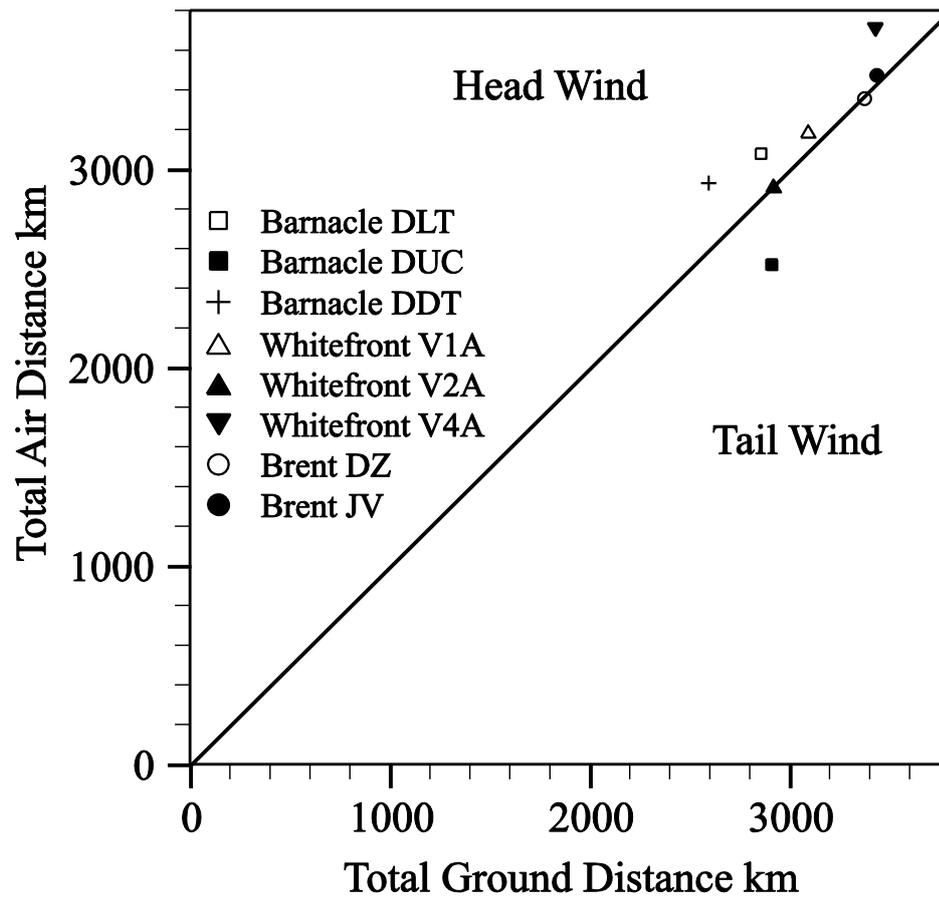
781

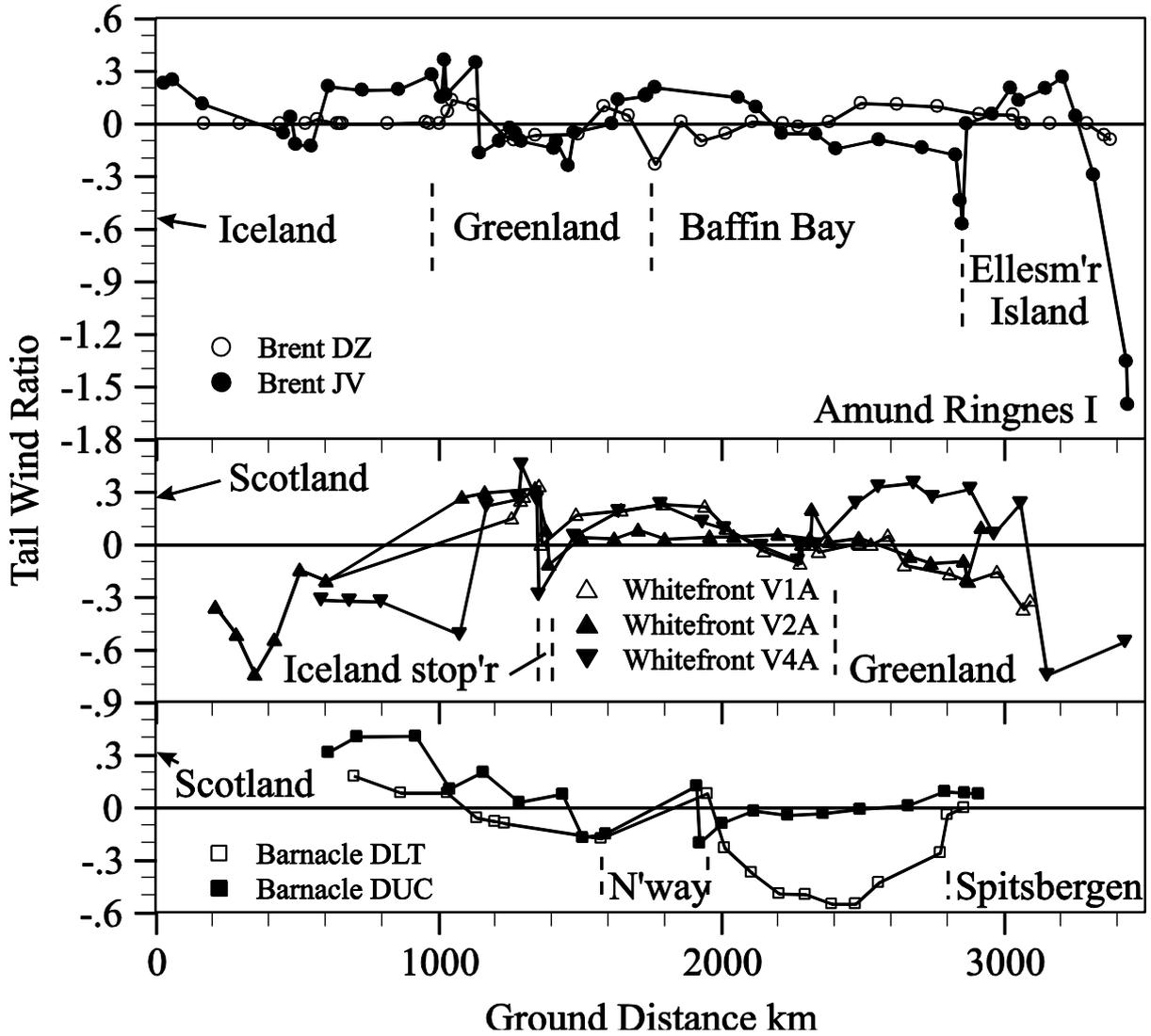
782



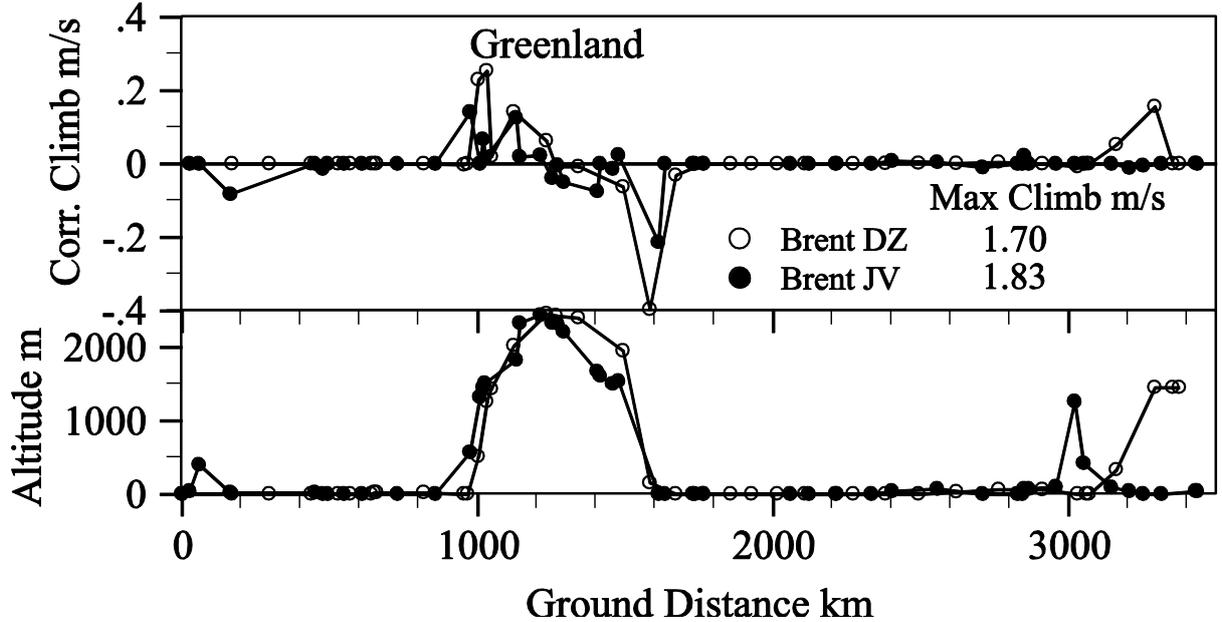




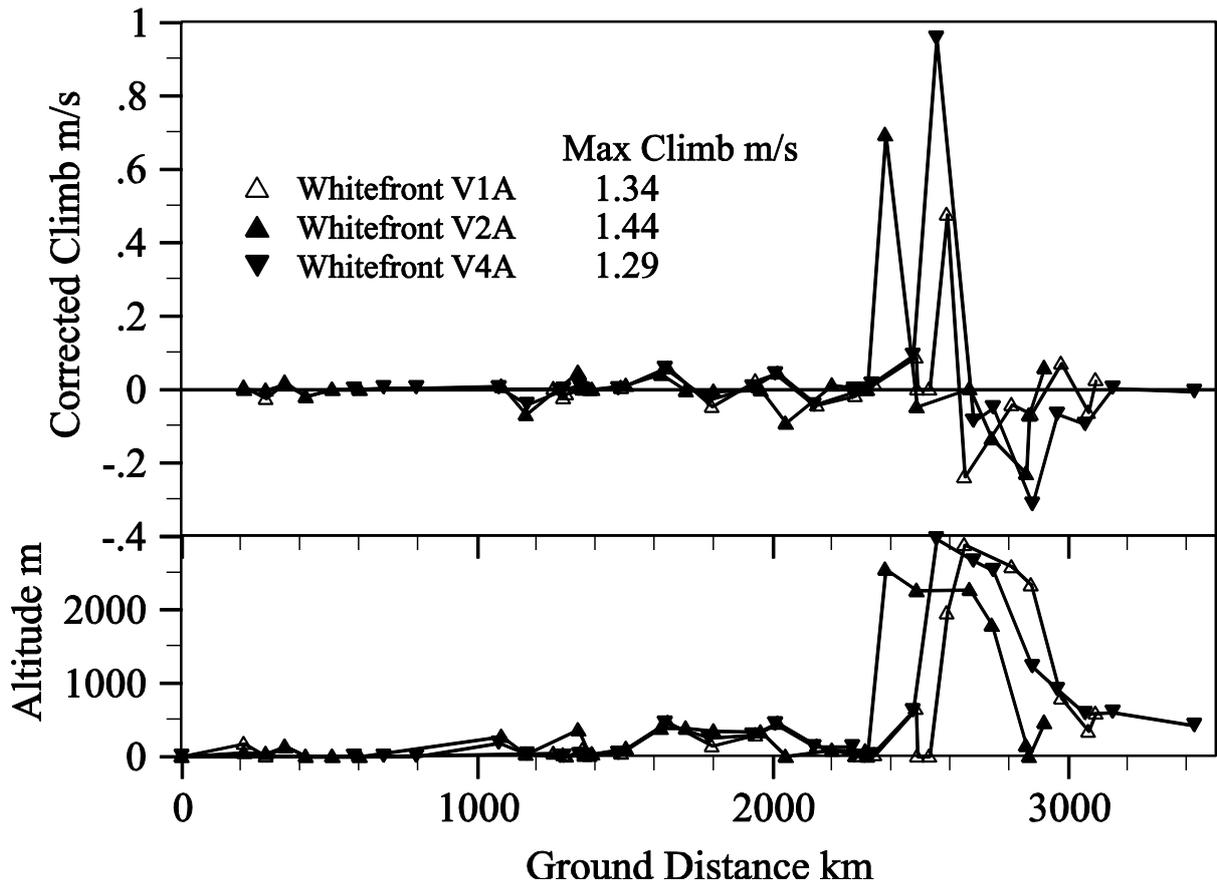




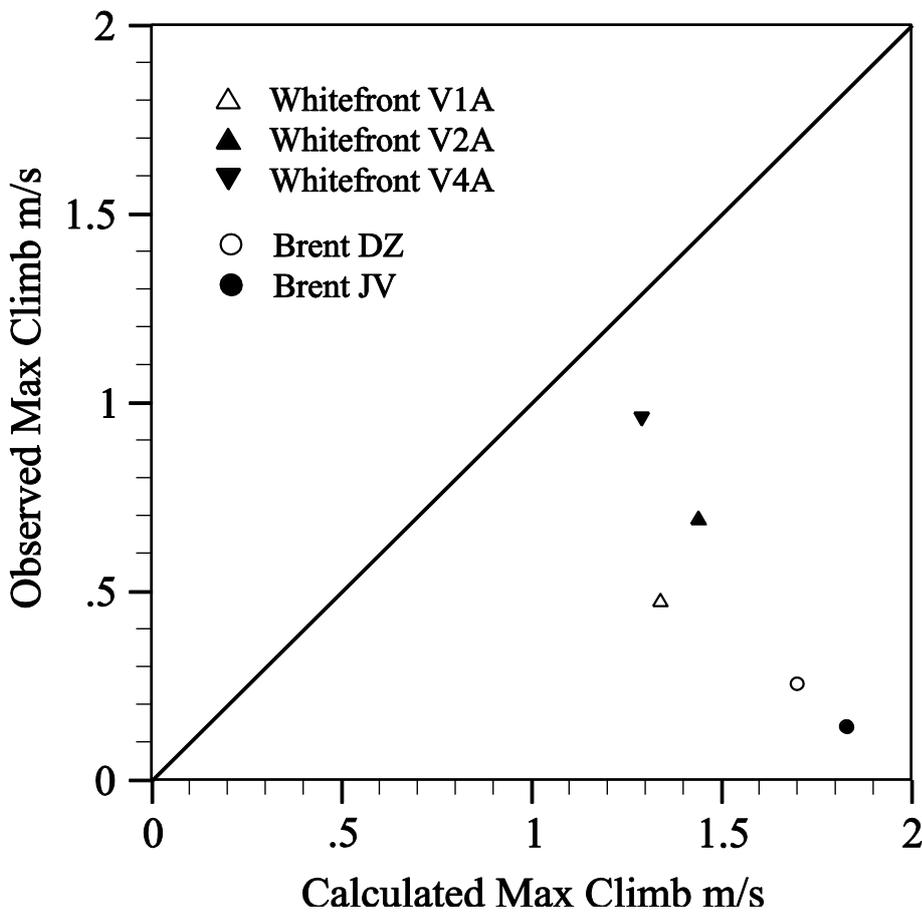
787



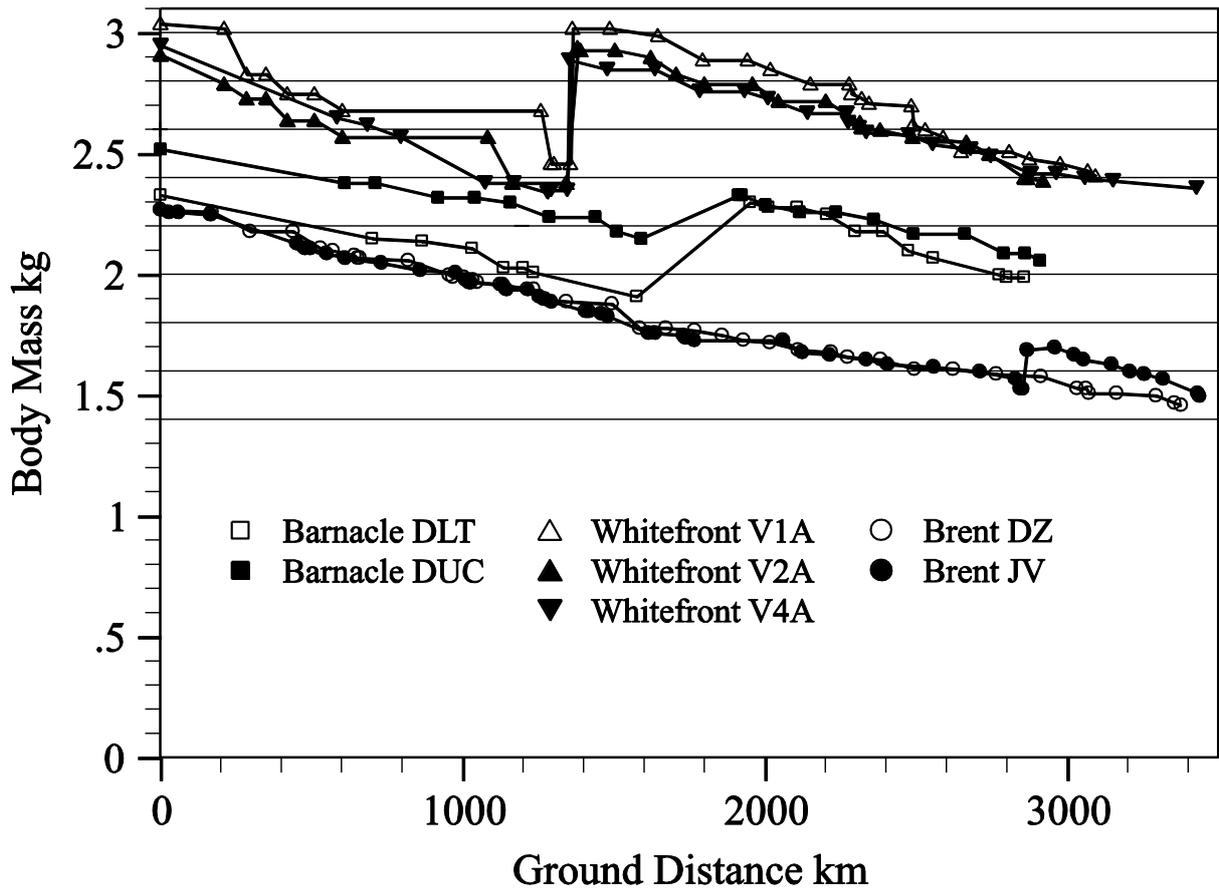
788



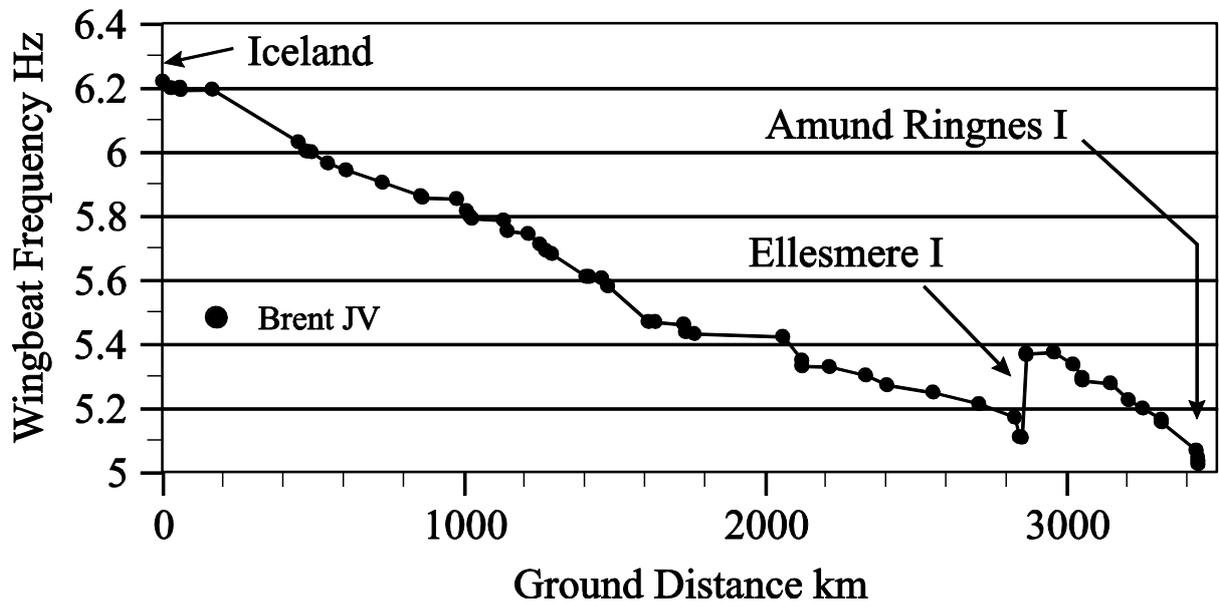
789



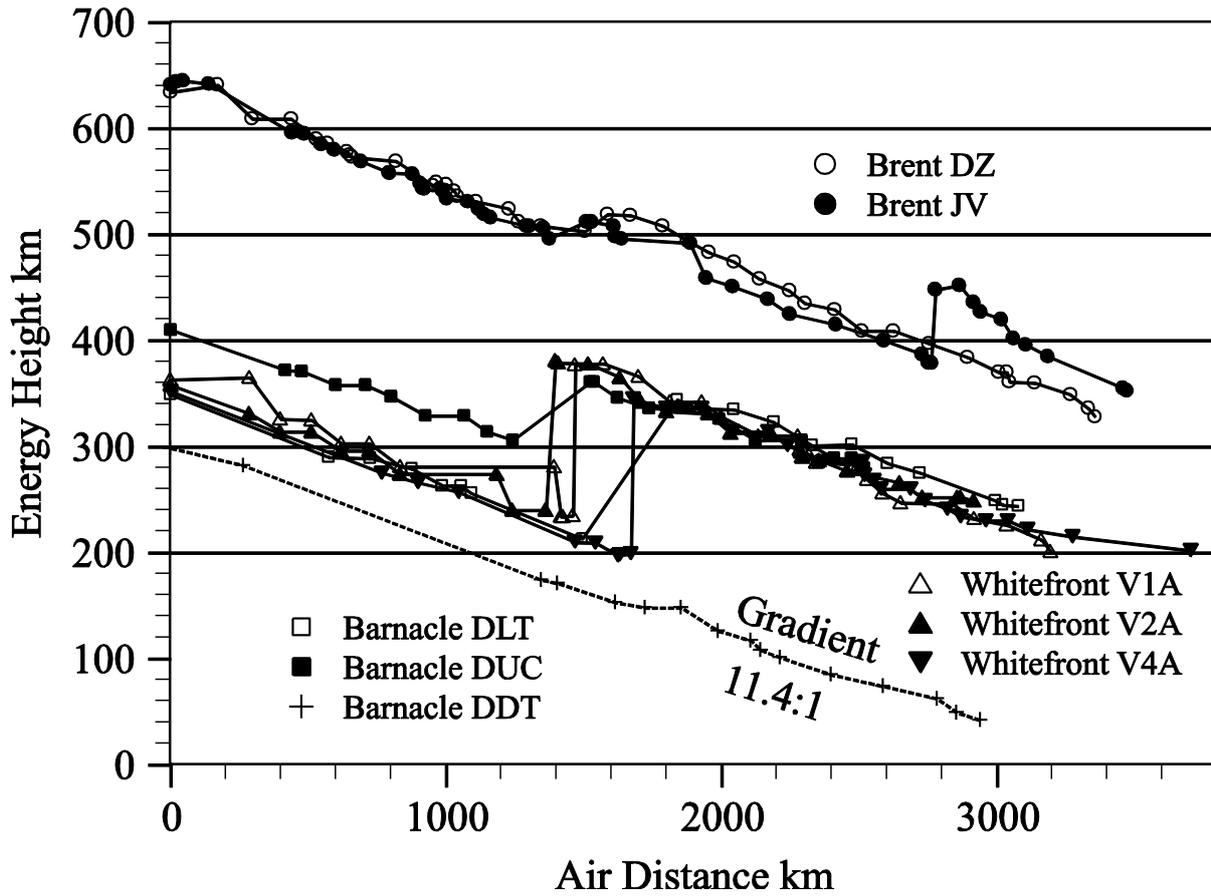
790



791



792



793

Air Distance km

794 Table 1. Data for transmitter birds. The southbound Barnacle Goose DDT was tagged in the previous year. His wing
 795 span was not measured, and there were no data to gauge his mass and fat fraction on departure from Spitsbergen.

796

797 Species	Migration direction	Start Mass kg	Min Mass kg	Fat Frac	Start Energy Height km	Wing Span m	Aspect Ratio	L/D from Power	Departure	Arrival
798 Barnacle DLT	N-bound	2.33	1.4	0.29	349	1.35	8.13	13.9	14.7	
800 Barnacle DUC	N-bound	2.52	1.4	0.328	410	1.41	8.13	14.2	15.1	
802 Barnacle DDT	S-bound	[2.1]	1.4	[0.245]	[282]	[1.42]	8.13	15.1	16.7	
804 Whitefront V1A	N-bound	3.04	1.8	0.299	363	1.44	7.86	13.5	14.5	
806 Whitefront V2A	N-bound	2.91	1.8	0.296	358	1.42	7.86	13.5	14.3	
808 Whitefront V4A	N-bound	2.95	1.8	0.292	352	1.47	7.86	13.9	15.1	
810 Brent DZ	N-bound	2.27	0.9	0.441	634	1.24	8.45	13.2	15.1	
812 Brent JV	N-bound	2.27	0.9	0.444	641	1.17	8.45	12.5	14.3	

809

810