



LUND UNIVERSITY

Flight speeds and climb rates of Brent Geese: mass-dependent differences between spring and autumn migration

Green, Martin; Alerstam, Thomas

Published in:
Journal of Avian Biology

DOI:
[10.1034/j.1600-048X.2000.310213.x](https://doi.org/10.1034/j.1600-048X.2000.310213.x)

2000

[Link to publication](#)

Citation for published version (APA):
Green, M., & Alerstam, T. (2000). Flight speeds and climb rates of Brent Geese: mass-dependent differences between spring and autumn migration. *Journal of Avian Biology*, 31(2), 215-225. <https://doi.org/10.1034/j.1600-048X.2000.310213.x>

Total number of authors:
2

General rights

Unless other specific re-use rights are stated the following general rights apply:
Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal

Read more about Creative commons licenses: <https://creativecommons.org/licenses/>

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

LUND UNIVERSITY

PO Box 117
221 00 Lund
+46 46-222 00 00

Flight speeds and climb rates of Brent Geese: mass-dependent differences between spring and autumn migration

Martin Green and Thomas Alerstam

Green, M. and Alerstam, T. 2000. Flight speeds and climb rates of Brent Geese: mass-dependent differences between spring and autumn migration. – J. Avian Biol. 31: 215–225.

Aerodynamic theories of bird flight predict that horizontal flight speed will increase with increasing load whereas vertical flight speed will decrease. Horizontal flight speed for birds minimizing overall time on migration is predicted to be higher than flight speed for birds minimizing energy expenditure. In this study we compare flight speeds of Brent Geese *Branta b. bernicla* recorded by tracking radar and optical range finder during spring and autumn migration in southernmost Sweden, testing the above-mentioned predictions. Geese passing Sweden in spring are substantially heavier than in autumn and there might also be a stronger element of time-selection in spring than in autumn. Recorded airspeeds were significantly higher in spring (mean 19.0 m s^{-1}) than in autumn (mean 17.3 m s^{-1}), the average difference being slightly larger than predicted due to the mass difference alone. The effects on airspeed of wind, vertical speed, flock size and altitude were also analysed, but none of these factors could explain the seasonal difference in airspeed. Hence, the results support the hypothesis of mass-dependent flight speed adjustment. The difference between the two seasons was not large enough to corroborate the hypothesis of a stronger element of time-selection in spring, but this hypothesis cannot be rejected. Vertical flight speeds were lower in spring than in autumn, supporting a negative effect of load on birds' flight power margin.

M. Green and T. Alerstam, Department of Animal Ecology, Lund University, Ecology Building, S-223 62 Lund, Sweden. E-mail: Martin.Green@zoekol.lu.se

On theoretical grounds birds are expected to adjust their flight speed in relation to a multitude of factors, e.g. depending on whether their flight is adapted to minimize power, energy cost per distance covered or total duration of the migratory journey. Flight speed will also be influenced by factors such as fuel load, wind, altitude, climb or descent and whether the birds are flying in flock formation (Pennycuik 1969, 1975, 1989, Tucker 1973, Hedenström and Alerstam 1995). To what extent do birds actually behave according to these theoretical predictions, and what is their ability to fine-tune their flight speed in relation to the different factors? Although there are a number of studies indicating that birds do indeed change their flight speed depending on wind and altitude (cf. Hedenström and Alerstam 1995), there is still little critical information on this, because of the uncertainties affecting quantitative predictions of flight speeds from the present aero-

dynamic theory for flapping flight in birds. Rather than trying to interpret measurements of absolute flight speeds in relation to theory, a more fruitful approach is to compare flight performance of the same species in different situations in a qualitative or semi-quantitative way, to test if differences are in accordance with theoretical expectation.

In this study we use this approach to compare the flight performance of Brent Geese *Branta bernicla bernicla* during spring and autumn migration. We made detailed measurements of flight speeds at two localities where Brent Geese leave the coast to fly across land in southernmost Sweden during their spring and autumn migratory passage, respectively. We test the predictions (i) that the birds have a higher airspeed but a lower rate of climb during spring than autumn migration because of their much larger fuel loads during the spring passage and, more speculatively, (ii) that they fly faster

during spring when migration may be more time-selected than during autumn (Alerstam and Lindström 1990, Hedenström and Alerstam 1995).

Prior to long migratory flights birds store fat and protein to be used as fuel on their journeys (Lindström and Piersma 1993). The increase in body mass is expected to affect flight performance in a number of ways (Hedenström 1992). Aerodynamic theories of bird flight (Pennycuick 1969, 1975, 1989, Tucker 1973, Greenewalt 1975, Rayner 1979) predict that airspeed (the birds' flight speed relative to the surrounding air) will increase with increasing mass. The positive relationship between load (extra mass) and airspeed is expected for all characteristic flight speeds irrespective of whether the bird flies to minimize energy per overall flight time (V_{mp}), minimize energy cost per distance travelled (V_{mr}) or minimize overall time spent on migration (V_{mt}) (Hedenström and Alerstam 1995). Based on the expected relationship between load and airspeed, Pennycuick (1978) predicted that cruising airspeed of a migrating bird should decrease during the flight as the bird gets lighter. This could be observed by measuring flight speeds of the same population of birds at two widely separated places along the route, as suggested by Pennycuick (1978) and Rayner (1990), but so far no such study has been made.

In fact, the only available empirical evidence about effects of load on flight speed come from experiments with trained birds and bats flying with artificially added mass. These experiments showed a reduction in flight speed with extra load (Videler et al. 1988, Videler 1995, Hughes and Rayner 1991), which is contrary to theoretical expectation. These results may be a consequence of the experimental situation and arrangement of the added mass (Rayner 1995), or to a flight situation of travelling between food patches (cf. Hedenström and Alerstam 1995). However, Videler (1995) suggested that an inverse correlation between load and airspeed might hold also for birds on migration, which is at odds with all traditional predictions.

By focusing on the migratory flights of Brent Geese with clearly different fuel loads on their spring and autumn passage, we will critically address this issue. Brent Geese conduct their migrations in long flights between traditional staging areas. In spring they fly directly from staging areas in the Wadden Sea, western Europe, to staging sites in the White Sea area, north-western Russia. In autumn they use the opposite route, from the White Sea to the Wadden Sea. Southernmost Sweden is situated at the beginning of the 2500 km flight in spring, relatively close to (300–500 km) the Wadden Sea, and at the end of the flight in autumn. Thus, autumn birds passing Sweden will have consumed more of their fuel stores than spring birds and therefore be considerably lighter. This is

also validated by spring and autumn body masses measured in the Wadden Sea (Ebbinge 1989).

The difference in body mass between spring and autumn might not be the only factor creating a difference in airspeeds between the seasons. If optimization criteria differ between spring and autumn migration we would expect an even larger difference in flight speeds than the one caused by body mass alone. Migrating birds have traditionally been expected to fly with speeds that minimize energy expenditure per distance covered (V_{mr}). However, Alerstam and Lindström (1990) pointed out that in order to minimize overall time spent on migration, including refuelling at stopovers, birds should fly faster than V_{mr} . A stronger element of time-selection in spring than in autumn seems likely in arctic-nesting birds like Brent Geese, which have to reach the breeding areas within certain time limits to be able to breed successfully in the short arctic summer.

In order to make a critical evaluation of differences in flight speeds between spring and autumn migration with respect to fuel load and, possibly, time-selection, we must control for a number of additional factors. Migrating birds are expected to adjust flight speed to prevailing winds by increasing airspeed in headwinds and reducing it in tailwinds (Pennycuick 1978). Sidewinds may also affect flight speeds and optimal speeds are expected to be even higher in sidewinds, especially in strong sidewinds, than in due headwinds (Liechti et al. 1994). There is an expected trade-off between horizontal airspeed and vertical speed (climb rate), airspeeds decreasing with increasing climb rate (Hedenström and Alerstam 1992). Flying in flock formation is expected to be associated with an optimal airspeed that decreases with increasing flock size (Hummel 1983), although the reverse relationship between airspeed and flock size has been observed in waders (Noer 1979). Characteristic airspeeds increase with increasing altitude due to the decrease in air density (Pennycuick 1975).

According to flight mechanical theory the relative power margin, i.e. the difference between power that can be produced by the flight muscles and the power required to fly, becomes reduced with increasing body mass. This happens because power required to fly increases faster with body mass than does power available from the muscles (Pennycuick 1969, 1989). Assuming that climbing capacity is limited by the available power margin, an increased load will reduce the maximum climbing capacity (Hedenström and Alerstam 1992). We will therefore analyse not only flight speeds but also vertical speeds of climbing flocks of Brent Geese, testing the prediction that the heavier spring birds show lower climb rates than the lighter autumn birds.

Methods

Predicted flight speeds were calculated according to Pennycuik (1975, 1989: prog. 1), with modified assumptions about profile power ratio ($= 8.4/AR$, where AR is aspect ratio; Pennycuik 1995). Recent wind tunnel studies have suggested that the coefficient of body drag (C_{db}) is considerably lower than previously thought (Pennycuik et al. 1996). In our calculations we used both the original estimate of C_{db} (0.25) and the suggested new, lower one (0.10; Pennycuik et al. 1996). Data on wing span and body mass of Brent Geese were taken from Ebbinge and Spaans (1995) and Ebbinge (1989). Spring body mass was taken as the mean of mid May

body masses of all birds (both sexes). This value represents a conservative estimate of departure mass since departure from the Wadden Sea staging areas, for the flight over Sweden towards the Arctic, takes place in late May. Autumn body mass was taken as mean body mass of birds in the Wadden Sea in October, just after arrival from the flight over Sweden. As lean body mass we used the lowest monthly average mass during the year from Ebbinge (1989). For wing area we used the value from Ebbinge and Spaans (1995) corrected to include the body area between the wings as defined by Pennycuik (1989). Predicted flight speeds were calculated for sea level conditions with an air density of 1.23 kg m^{-3} .

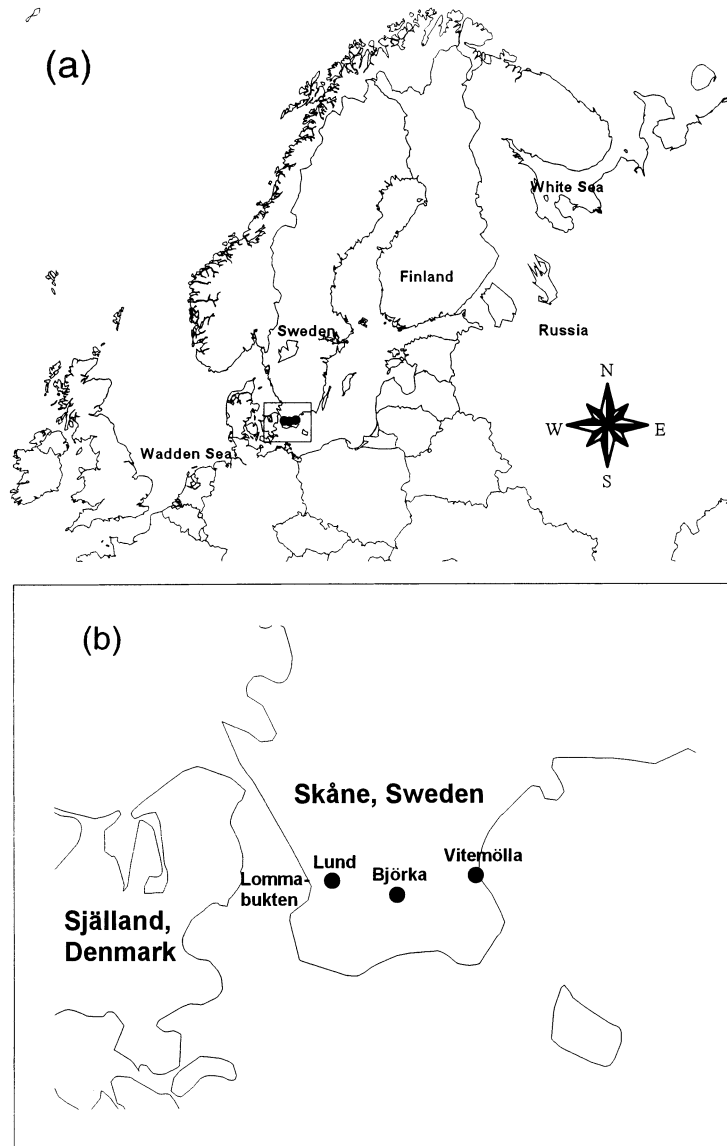


Fig. 1. Maps over north-western Europe showing main staging areas Wadden Sea and White Sea (a) and southernmost Sweden (b) showing study sites Lund, Vitemölla and Björka.

Table 1. Body mass, morphological data and predicted flight speeds from flight mechanical theory (Pennycuik 1975, 1989) for Brent Geese on spring and autumn migration in South Sweden. Aspect ratio is the ratio of wing span to mean chord of the wing, calculated as $(\text{wing span})^2/(\text{wing area})$. Predicted flight speeds are shown both for coefficient of body drag (C_{db}) = 0.25 (a) and for C_{db} = 0.10 (b).

	Spring		Autumn	
Lean body mass (kg)	1.25		1.25	
Total body mass (kg)	1.60		1.35	
Wing span (m)	1.20		1.20	
Wing area (m ²)	0.146		0.146	
Aspect ratio	9.9		9.9	
V_{mp} (m s ⁻¹)	12.0 ^a	15.1 ^b	11.3 ^a	14.3 ^b
V_{mr} (m s ⁻¹)	18.7 ^a	23.6 ^b	17.8 ^a	22.4 ^b

Flight speeds of migrating Brent Geese were recorded mainly at two sites in Skåne, South Sweden (Fig. 1). Spring migrating birds were tracked at Lund (55°42'N, 13°12'E) by using an optical range finder (WILD, 80 cm, 11.25 ×) with azimuth and elevation scales, from the roof terrace of the Ecology Building (83.5 m asl) in late May–early June of 1995 and 1996 and by using a tracking radar (X-band, 200 kW peak power, pulse duration 0.25 μs, pulse repeat frequency 500 Hz, 1.5° pencil beam width, antenna 91.5 m asl) in late May–early June of 1997 and 1998. Autumn migrating birds were tracked with a mobile tracking radar (X-band, 40 kW peak power, pulse duration 0.3 μs, pulse repeat frequency 1800 Hz, 2.2° pencil beam width) at Vitemölla (radar antenna 30 m asl) at the Baltic Sea coast (55°42'N, 14°12'E) in September and October of 1980–1982. In addition a few (4) radar trackings were made at Björka (radar antenna 45 m asl), in South Central Skåne (55°39'N, 13°37'E) in October of 1986 and 1989. The topography of the different main localities are somewhat similar with land rising from sea level to about 100 m asl. On a smaller scale there is a small difference as land rises gently from sea level towards Lund while it rises quite steeply from sea level up to 30 m asl at Vitemölla. Thereafter the relief of the landscape is a gently rising one also at Vitemölla, comparable to the situation at Lund.

The optical range finder trackings were made at distances of 300 m–3 km and fixes were normally read every 20 s. Previous calibration measurements to fixed objects at known distances indicate that the accuracy of range measurements was ± 10 m at 500 m, ± 20 m at 1 km and ± 100 m at 2 km (Hedenström and Alerstam 1994).

The radar trackings were made at distances ranging from 300 m up to 30 km. All flocks passed initially within 0.3–5 km, even the ones later tracked for very long distances. Range, azimuth and elevation were recorded by a computer every 2 s (Lund, spring), every 10 s (autumn trackings in 1981–1989) or every 60 s (autumn trackings in 1980, n = 14). Maximum tracking error for a radar target in high speed motion 1 km

away is 0.7° in elevation and azimuth and 12 m in range (Hedenström and Alerstam 1992). To determine airspeeds of the flocks, wind direction and speed were measured by tracking hydrogen- or helium-filled weather balloons, released within an hour of bird tracking. Airspeeds were then calculated by vector subtraction of wind velocity at the altitude where the birds were flying from the birds' flight tracks (track direction and groundspeed). For climbing flocks flying through several altitude strata, wind measurements from the relevant strata were used and airspeed calculated as the average of all airspeed calculations during the entire tracking.

For analyses of vertical speed (climb rate) we selected sequences showing steady ascent of at least 0.2 m s⁻¹ for more than 120 s. In spring several flocks passing Lund were climbing very slowly, at rates intermediate between level flight and true climbing (climb rates between 0 and 0.2 m s⁻¹). These flocks have been omitted from the analysis of climb rate since we were only interested in flocks expected to use maximum sustainable power during the climb. For flocks with several climbing phases during a tracking, or with intervals of different rates of ascent during the climb, we selected the sequence with the highest climb rate, provided it lasted at least 120 s. All trackings refer to visually identified, migrating flocks. The radar used in autumn was equipped with 9 × and 18 × binoculars for identification of radar targets. In spring, Brent Goose flocks were spotted and counted with 10 × binoculars or a 30 × telescope and subsequently located and tracked with the range finder or by radar.

Results

Predicted flight speeds of Brent Geese

Predicted characteristic airspeeds of Brent Geese are shown in Table 1. Here we show values for both minimum power speed (V_{mp}) and for maximum range speed (V_{mr}). The main purpose of calculating predicted characteristic airspeeds is not to present their absolute values but the expected difference in speed between spring and autumn based on the body mass difference. The predicted differences due to mass are 0.7–0.9 m s⁻¹ with C_{db} = 0.25 and 0.8–1.2 m s⁻¹ with C_{db} = 0.10. Hence, we predict that the Brent Geese fly faster by c. 1 m s⁻¹ on their passage in spring than in autumn, if they adjust airspeed in relation to their mass according to flight mechanical theory. Should there be a considerably larger difference in speed between spring and autumn, this would indicate that the geese adapt their flight speed in response to time-selection to a higher degree in spring than in autumn because time-selected flight speeds are faster than energy-selected speeds as shown by Alerstam and Lindström (1990) and Hedenström and Alerstam (1995, 1997).

Tracking data

The general situation during which the trackings were made was similar between spring and autumn. In spring, the geese fly inland at Lommabukten west of Lund (Fig. 1) and the majority of flocks was either climbing or in level flight. Some of the longer radar tracks contained phases of both climb and level flight. In autumn, most tracks were of flocks flying inland at Vitemölla (Fig. 1) either with an initial phase of climb followed by level flight or climbing throughout the tracking. In addition, some flocks in autumn were tracked in level flight low over the Baltic Sea ($n = 10$) or at higher altitude over central Skåne ($n = 4$). Omitting the low altitude flocks flying over the Baltic Sea did not change any of the results so they remain included in the analysis.

Number and duration of tracks are shown in Table 2 a and b for the complete sample of trackings and the climbing sequences, respectively. Most tracks were of 2–10 min duration (72% in both seasons); 13% (spring) and 28% (autumn) were of more than 10 min duration. Both data sets thus represent long continuous trackings of migratory flight. The climbing sequences were of similar duration in spring and autumn with the majority between 2 and 5 min.

Effect of wind, climb rate, flock size and flight altitude on airspeed

In Table 3 a we present summary statistics for flight speeds and factors that might affect flight speeds during spring and autumn. Groundspeeds and airspeeds were significantly higher in spring than in autumn (ground-speed: t -test, $p < 0.001$, $df = 132$; airspeed: $p < 0.001$, $df = 132$).

Before considering the differences in flight speeds between spring and autumn, we will present the analyses of factors that might affect observed flight speeds. Wind situations differed slightly but significantly between spring and autumn, with a higher proportion of tailwind tracks in spring and of headwind tracks in autumn (Table 3 a). In both seasons there was a significant negative relationship between airspeed and wind effect (speed decrement/increment due to wind, measured as groundspeed minus airspeed; Table 4, Fig. 2). The change in airspeed with wind effect was the same in spring and autumn (Fig. 2).

Dividing the material in headwind and tailwind situations (wind effect < 0 resp. > 0) and analysing the effect of wind, revealed that the change in airspeed seemed to be confined to headwind situations only. In headwinds the geese increased airspeed with increasing wind speed whereas no significant relationship was found with increasing tailwinds. The regression equations in headwinds were: $Y = 18.4 - 0.46 X$ ($r = 0.43$, $n = 36$, $p = 0.01$) in spring, and $Y = 15.1 - 0.64 X$ ($r = 0.47$, $n = 32$, $p = 0.01$) in autumn, where Y is airspeed and X is wind effect (groundspeed minus airspeed).

The regression coefficients indicate a somewhat greater change of airspeed during autumn, but the 95% confidence intervals of the slopes overlapped broadly (-0.13 to -0.79 in spring vs -0.19 to -1.09 in autumn). The mean airspeed in tailwinds was 18.5 m s^{-1} (s.d. 2.8 m s^{-1} , $n = 40$) in spring and 16.8 m s^{-1} (s.d. 2.1 m s^{-1} , $n = 26$) in autumn. Mean airspeed in headwinds was 19.5 m s^{-1} (s.d. 2.7 m s^{-1} , $n = 36$) in spring and 17.7 m s^{-1} (s.d. 3.2 m s^{-1} , $n = 32$) in autumn.

Strong sidewinds, with an angle between track and heading exceeding 30° (cf. Liechti et al. 1994) occurred on very few occasions during the trackings, on none in

Table 2. Summary of number of tracks, track duration and total tracking time for the total material (a) and for the selected climbing sequences (b).

a. Total material		Spring	Autumn
No. of tracks	Optical range finder	42	0
	Tracking radar	34	58
	Total	76	58
Track duration (s)	Mean	355	523
	Range	42–2120	120–1330
Total tracking time (s)		26 976	30 320
b. Climbing sequences		Spring	Autumn
No. of tracks	Optical range finder	17	0
	Tracking radar	10	37
	Total	27	37
Track duration (s)	Mean	276	272
	Range	120–1000	120–1020
Total tracking time (s)		7465	10 064

Table 3. Summary statistics of flight speeds and factors that might influence flight speeds of Brent Geese on spring and autumn migration in South Sweden for the total material (a) and for selected climbing sequences (b). Wind effect is expressed as Groundspeed minus Airspeed. Differences between spring and autumn were tested with Student's t-test for groundspeed, airspeed, wind effect, climb rate and with Mann-Whitney U-test for flock size and flight altitude. Levels of significance: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, ns = non significant.

a. Total material	Spring (n = 76) Mean (\pm s.d.)	Autumn (n = 58) Mean (\pm s.d.)	Difference	Level of significance
Groundspeed (m s^{-1})	19.7 (3.9)	16.0 (3.9)	3.7	***
Airspeed (m s^{-1})	19.0 (2.8)	17.3 (2.8)	1.7	***
Wind effect (m s^{-1})	0.7 (3.8)	-1.3 (3.8)	2.0	**
Climb rate (m s^{-1})	0.11 (0.31)	0.14 (0.28)	-0.03	ns
Flock size (no. of birds)	280 (278)	76 (84)	204	***
Flight altitude (m agl)	341 (163)	215 (172)	126	***
b. Climbing sequences	Spring (n = 27) Mean (\pm s.d.)	Autumn (n = 37) Mean (\pm s.d.)	Difference	Level of significance
Groundspeed (m s^{-1})	19.9 (4.6)	13.9 (3.4)	6.0	***
Airspeed (m s^{-1})	18.4 (3.1)	15.4 (2.8)	3.0	***
Wind effect (m s^{-1})	1.4 (3.4)	-1.5 (4.0)	2.9	***
Climb rate (m s^{-1})	0.46 (0.27)	0.62 (0.27)	-0.16	*
Flock size (no. of birds)	272 (254)	60 (76)	212	***
Flight altitude (m agl)	446 (199)	241 (192)	205	***

Table 4. Coefficients of correlation between airspeed and some factors that might affect airspeeds for Brent Geese on spring and autumn migration in South Sweden. * $p < 0.05$, ** $p < 0.01$, ns = non significant.

	Spring (n = 76)	Level of significance	Autumn (n = 58)	Level of significance
Wind effect	-0.31	**	-0.31	*
Climb rate	-0.22	ns (p = 0.06)	-0.14	ns
Log Flock size	-0.08	ns	0.25	ns (p = 0.06)
Flight altitude	0.01	ns	0.26	*

spring and only four in the autumn. Thus we did not analyse the possible effect of sidewinds any further.

Overall climb rates did not differ between spring and autumn for the total sample (Table 3 a). Airspeed was not significantly correlated with climb rate in any of the two seasons, although a tendency towards a negative relationship was found in spring (Table 4). Flock sizes were much larger in spring than in autumn (Table 3 a, Fig. 3). During both seasons most tracks were of flocks ranging from several tens up to several hundreds of birds. In these intervals we do not expect any large impact of increasing flock size on airspeed. For aerodynamic reasons the largest effect should be found between birds flying singly and in flocks of up to about 10–15 birds (Lissaman and Shollenberger 1970, Hummel 1983). No significant correlations were found between flock size and airspeed, but there was a tendency towards increasing airspeed with increasing flock size in autumn (Table 4). Flight altitudes in spring were higher than in autumn (Table 3 a, Fig. 4), but the majority of tracks was below 500 m where only a limited effect on airspeed is expected due to decreasing air density. Still, in autumn airspeed increased slightly with increasing altitude (Table 4).

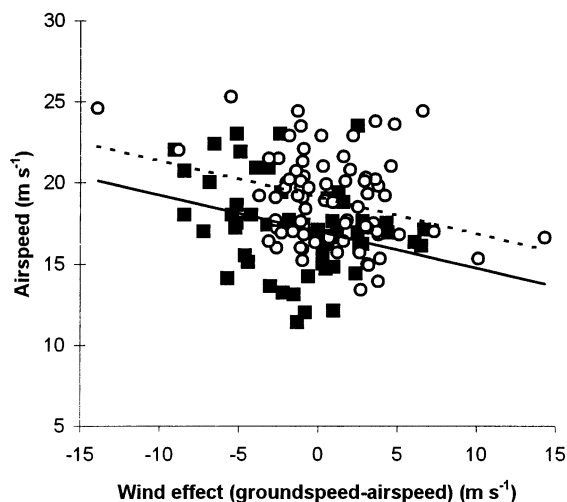


Fig. 2. Linear regressions of recorded airspeeds in relation to wind effect (groundspeed minus airspeed) of Brent Geese on spring (open circles) and autumn (filled squares) migration over southernmost Sweden. Regression equations are $Y = 19.1 - 0.23 X$ ($r = -0.31$, $n = 76$, $p = 0.01$) in spring (dotted line) and $Y = 17.0 - 0.23 X$ ($r = -0.31$, $n = 58$, $p = 0.02$) in autumn (solid line) where Y is airspeed and X is wind effect.

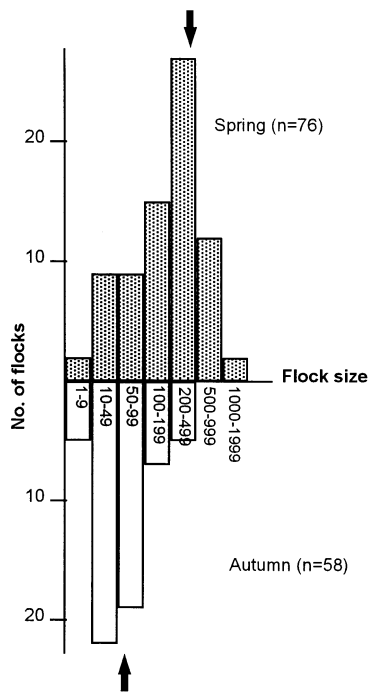


Fig. 3. Distribution of flock sizes in the total sample of trackings of Brent Geese on spring and autumn migration in southernmost Sweden. Arrows show means.

Flight speeds in spring and autumn

Groundspeed and airspeed were higher in spring than in autumn (Table 3 a, Fig. 5 a and b). Part of the difference in groundspeed was explained by a larger proportion of tailwind tracks during spring, but an important part was also due to significantly different airspeeds between the seasons. The overall difference in mean airspeeds was 1.7 m s^{-1} . For the mean airspeeds in Table 3 a, the 95% confidence intervals were $18.3\text{--}19.6 \text{ m s}^{-1}$ in spring and $16.6\text{--}18.0 \text{ m s}^{-1}$ in autumn. The intercepts of the regression lines in Fig. 2 show that the average airspeeds at zero wind were 19.1 m s^{-1} in spring and 17.0 m s^{-1} in autumn, with 95% confidence intervals of $18.5\text{--}19.7 \text{ m s}^{-1}$ in spring and $16.2\text{--}17.7 \text{ m s}^{-1}$ in autumn.

Climbing sequences

Vertical speeds during climbing flight were significantly lower in spring than in autumn (Table 3 b, Fig. 6). The general differences between spring and autumn in horizontal flight speeds (groundspeed and airspeed), wind effect, flock size and altitude were very similar to those described for the total material (Table 3 a, b), as the climbing sequences make up a subsample of the total tracking material. Neither horizontal flight speeds nor

any of the other factors (wind effect, flock size, flight altitude) had any significant effect on climb rates (Table 5), although there was a tendency towards increasing climb rates with increasing altitude in autumn ($r = 0.32$, $p = 0.06$).

Considering only the climbing flights, airspeeds showed a significant negative correlation with wind effect in autumn but not in spring (Table 6). No effect of climb rate on airspeed was found, but average airspeeds in climbing flight (18.4 m s^{-1} in spring and 15.4 m s^{-1} in autumn) were slightly lower than overall mean airspeeds (19.0 m s^{-1} and 17.3 m s^{-1}). Comparing airspeeds between climbing sequences and phases of level flight of the same flocks showed significantly lower airspeed during climb than level flight in autumn (means: 14.2 m s^{-1} vs 18.7 m s^{-1} ; paired t-test, $p = 0.0001$, $df = 19$). In spring sample size was too small for a meaningful analysis. Flock size and flight altitude showed no significant correlation with airspeed during climb (Table 6).

Discussion

Difference in airspeeds

Even if airspeeds of migrating Brent Geese were quite variable between flocks, ranging between 13 and 25 m s^{-1} (with a similar degree of variation in spring and autumn, Fig. 5), their mean airspeed was clearly faster during spring than autumn (Table 3 a, Fig. 5). Recorded airspeeds were close to predicted V_{mr} calculated with $C_{db} = 0.25$ and fell between predicted V_{mp} and V_{mr} calculated with $C_{db} = 0.10$ (Table 1, Table 3 a). The difference between mean spring and autumn airspeeds was 1.7 m s^{-1} , i.e. about 10% of the overall mean. Airspeed was significantly correlated with wind during both spring and autumn migration, but the difference between seasons remained irrespective of the

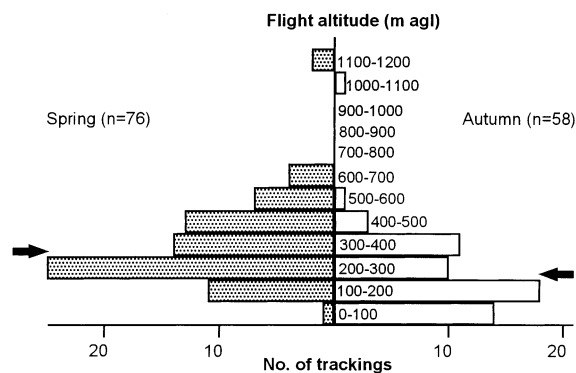


Fig. 4. Distribution of flight altitudes in the total sample of trackings of Brent Geese on spring and autumn migration in southernmost Sweden. Arrows show means.

wind effect (Fig. 2) and was on average 2.1 m s^{-1} when accounting for the wind effect by calculating the airspeeds at zero wind (corresponding to the intercepts in Fig. 2).

Vertical speed (climb/descend rates) did not differ between the two seasonal total samples of tracks (Table 3 a), so this factor cannot explain the difference between spring and autumn airspeed. Average flock size

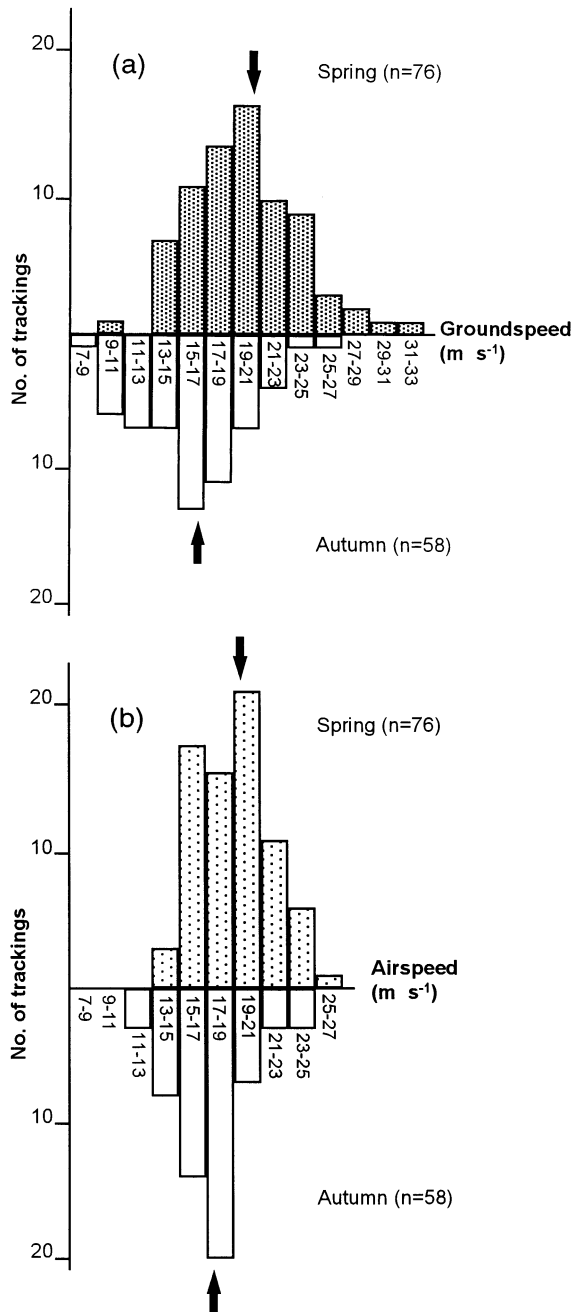


Fig. 5. Distribution of groundspeeds (a) and airspeeds (b) of the total sample of Brent Geese on spring and autumn migration in southernmost Sweden. Arrows show means.

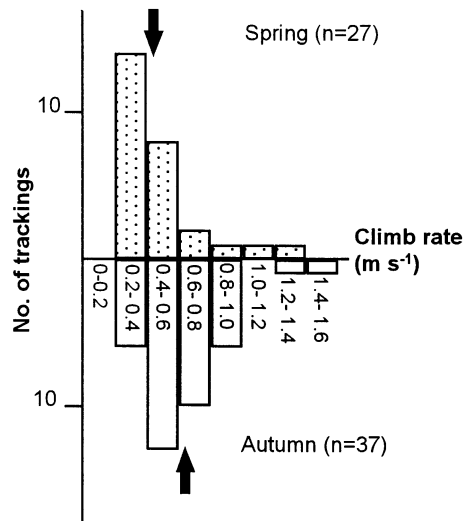


Fig. 6. Distribution of vertical flight speeds, climb rates, for selected climbing sequences of Brent Geese on spring and autumn migration in southernmost Sweden. Arrows show means.

and altitude, however, differed significantly between the two seasons (Table 3 a), but for two reasons it is highly unlikely that the difference in airspeed was due to any of these factors: (1) The theoretically expected effects would be minor (affecting airspeed by less than 1%) compared with the observed seasonal difference in airspeed (cf. Lissaman and Shollenberger 1970, Hummel 1983, Pennycuik 1975). By way of example, characteristic flight speeds are expected to increase by a mere 5% per 1000 m increase in altitude (calculated from Pennycuik 1975) because of the reduction in air density. (2) There was no significant correlation between flock size and airspeed in either season, and only a weak correlation between altitude and airspeed in autumn (Table 4).

Differences in weather (barometric pressure) and age composition are two further factors with a potential influence on airspeed, but we think that also these factors are highly unlikely to provide an explanation for the observed seasonal difference in airspeed. If spring tracks were consistently recorded in low pressure situations and autumn tracks in high pressure situations we would expect airspeeds in spring to be higher than in autumn. However, the difference in air density between low and high pressures is relatively small and would give differences in airspeeds of only about 1% (Pennycuik 1975, 1989). Furthermore, tracks in both spring and autumn were made in varying weather conditions, with a dominance of high pressure situations in both seasons.

The presence or absence of juvenile birds might affect airspeeds. Juvenile Brent Geese are structurally smaller and lighter than adult birds (Cramp 1977), and may therefore fly more slowly than adults. Brent Geese migrate family-wise during autumn and if adult birds

Table 5. Coefficients of correlation between climb rate and some factors that might affect climb rates for Brent Geese on spring and autumn migration in South Sweden, selected climbing sequences. ns = non significant.

	Spring (n = 27)	Level of significance	Autumn (n = 38)	Level of significance
Airspeed	-0.04	ns	0.05	ns
Wind effect	0.30	ns	0.09	ns
Log Flock size	0.10	ns	0.15	ns
Flight altitude	0.01	ns	0.32	ns (p = 0.06)

adjust airspeed to that of the smaller juveniles (which is unknown if they do) and if our autumn trackings mainly consisted of families with young birds we would expect lower airspeeds in autumn. We do not know the age composition of our tracked flocks, but since our material spans several different spring and autumn seasons, and the breeding success of Brent Geese is characterized by seasons with almost no fledged juveniles alternating with seasons with up to 50% juveniles approximately every third year (Bergmann et al. 1994), we find it highly unlikely that we have tracked only family flocks with young. Furthermore, young birds are still lighter than adults in spring but heavier than young birds in autumn (Cramp 1977), so any effect of young birds would affect recorded spring airspeeds as well.

We conclude that there was a significant difference in airspeed between spring and autumn that cannot be explained by differences in wind situations, flock sizes, flight altitudes, weather (barometric pressure) or age composition of tracked flocks. The difference (2.1 m s^{-1} , $0.8\text{--}3.1 \text{ m s}^{-1}$ in a no wind situation) is reasonably close to what we expect from flight mechanical theory based on average differences in body mass between spring and autumn ($0.7\text{--}1.2 \text{ m s}^{-1}$). Our results are thus in agreement with the hypothesis that birds increase their airspeed with heavier fuel load according to traditional flight mechanical theory, but they are at variance with Videler's (1995) proposal that heavier birds decrease airspeed and instead increase lift by increasing wingbeat amplitude and inclination of body and tail, enlarging wing and tail area and increasing wingbeat frequency. The change in flight behaviour that Videler describes may occur for example when raptors carry food to their nests but probably not when migratory birds carry extra loads within their bodies as fat and protein. Furthermore, Videler's (1995) arguments are based on an assumed steep increase in flight cost with increasing speed. It is probably true that the flight

cost increases rather steeply at very high flight speeds, but wind tunnel studies have shown a relatively moderate increase within the speed intervals that birds actually use for cruising flight (reviewed in Norberg 1990, 1995). Thus, increasing airspeed with increasing mass might not be as costly as Videler assumes and, furthermore, migrating birds presumably build up their flight muscle mass before departing with heavy fuel loads (Pennycuik 1978, Piersma 1998).

The difference in airspeed between spring and autumn seemed to be slightly larger than predicted from the seasonal mass difference alone. Could this, in addition to a mass-dependent effect, be explained by an influence of a larger element of time-selection during spring as compared to autumn migration, according to our original hypothesis? We cannot rule out such an additional effect of time-selection, but there is no convincing evidence in favour of it since the discrepancy between the observed seasonal difference in airspeed and the predicted mass-dependent difference is not large enough to be statistically significant.

We consider it most likely that the seasonal difference in airspeed that we have recorded for migrating Brent Geese in southernmost Sweden is associated with the difference in load between the seasons, thus strongly supporting the hypothesis of mass-dependent flight-speed adjustment. The possibility of a more time-selected flight speed during spring than autumn migration must remain speculative.

Climbing performance

Observed maximum sustained climb rates in spring (0.46 m s^{-1}) were significantly lower than in autumn (0.62 m s^{-1}), as expected from the difference in average body mass between the seasons (Table 3 b). Our autumn climb rates were slightly higher than those previ-

Table 6. Coefficients of correlation between airspeed and factors that might influence airspeed for climbing sequences of Brent Geese on spring and autumn migration in South Sweden. *** $p < 0.001$, ns = non significant.

	Spring (n = 27)	Level of significance	Autumn (n = 38)	Level of significance
Wind effect	0.02	ns	-0.54	***
Climb rate	-0.04	ns	0.05	ns
Log flock size	-0.10	ns	0.01	ns
Flight altitude	0.23	ns	0.28	ns (p = 0.10)

ously reported based partly on the same material (0.53 m s^{-1} ; Hedenström and Alerstam 1992). The discrepancy is due to the fact that we used a shorter minimum tracking interval, 120 s, than Hedenström and Alerstam (1992) who selected sequences lasting at least 240 s. Several of the shorter trackings used in this study showed high climb rates. In both seasons there were a few sequences of very high climb rates, exceeding 1 m s^{-1} . In some of these cases the recorded climb rates might have been affected by vertical winds. If birds fly in rising air (thermals, slope winds or lee waves) their climb rates will of course increase. We have no means of controlling for the occurrence of vertical winds (cf. Hedenström and Alerstam 1992, 1994), but it is likely that such winds occur under certain circumstances at both our tracking sites. In spring the highest climb rates were recorded during late morning to early midday in clear weather, when the birds might have flown through areas of rising air in thermals and getting extra lift. In autumn both occasions with observed climb rates over 1 m s^{-1} (Fig. 6), occurred in easterly winds, when the relief of the coast probably can create slope winds at low altitudes (Hedenström and Alerstam 1992).

The climbing performance of the Brent Geese in this study may be compared with that of Light-bellied Brent Geese *Branta bernicla hrota* migrating from staging areas in Iceland across the Greenland ice-cap according to the satellite telemetry study of Gudmundsson et al. (1995). The Light-bellied Brents put on large fuel loads in Iceland to cover the flight over Greenland towards arctic Canada. Departure body masses are around or even exceed 2.0 kg (Gudmundsson et al. 1995). Apart from the difference in fuel loads these birds are morphologically very similar to the Brent Geese passing Sweden in spring and autumn (Cramp 1977, Gudmundsson et al. 1995). Birds flying over the Greenland ice-cap were found to have extremely low climb rates and slow forward flight speeds indicating that they actually had to land and rest intermittently while climbing up the slope of the Greenland ice. It seems that body masses of about 2.0 kg (54% extra load relative to lean body mass) are the largest Brent Geese can carry and still retain a (marginal) capacity to climb (Gudmundsson et al. 1995). Brent Geese departing from the Wadden Sea towards Siberia also put on large amounts of fat and protein (32%) but still, judging from this study, do not face any serious limitations of climbing capacity. These two studies in combination show that climbing capacity may be limited when birds carry very large fuel loads (Greenland birds) but also that relatively large birds, such as Brent Geese, can put on substantial amounts of fat and protein without facing any serious restrictions on climbing capacity (spring birds in South Sweden).

Acknowledgements – Financial support for this study was obtained from the Natural Science Research Council to T.A., and from Gustaf Danielsson's Foundation (Swedish Ornithological Society) to M.G. Felix Liechti and Åke Norberg gave valuable comments on the manuscript.

References

- Alerstam, T. and Lindström, Å. 1990. Optimal bird migration: the relative importance of time, energy and safety. – In: Gwinner, E. (ed.). *Bird Migration: Physiology and Ecophysiology*. Springer, Berlin pp. 331–351.
- Bergmann, H.-H., Stock, M. and ten Thoren, B. 1994. Ringelgänse. – AULA-Verlag, Wiesbaden.
- Cramp, S. (ed.). 1977. *Birds of the Western Palearctic*. – Oxford University Press, Oxford.
- Ebbinge, B. S. 1989. A multifactorial explanation for variation in breeding performance of Brent Geese *Branta bernicla*. – *Ibis* 131: 196–204.
- Ebbinge, B. S. and Spaans, B. 1995. The importance of body reserves accumulated in spring staging areas in the temperate zone for breeding in Dark-bellied Brent Geese *Branta b. bernicla* in the high Arctic. – *J. Avian Biol.* 26: 105–113.
- Greenewalt, C. H. 1975. The flight of birds. – *Trans. Am. Phil. Soc.* 65: 1–67.
- Gudmundsson, G. A., Benvenuti, S., Alerstam, T., Papi, F., Lilliendahl, K. and Åkesson, S. 1995. Examining the limits of flight and orientation performance: satellite tracking of brent geese migrating across the Greenland ice-cap. – *Proc. R. Soc. Lond. B* 261: 73–79.
- Hedenström, A. 1992. Flight performance in relation to fuel load in birds. – *J. theor. Biol.* 158: 535–537.
- Hedenström, A. and Alerstam, T. 1992. Climbing performance of migrating birds as a basis for estimating limits for fuel-carrying capacity and muscle work. – *J. Exp. Biol.* 164: 19–38.
- Hedenström, A. and Alerstam, T. 1994. Optimal climbing flight in migrating birds: predictions and observations of knots and turnstones. – *Anim. Behav.* 48: 47–54.
- Hedenström, A. and Alerstam, T. 1995. Optimal flight speeds in birds. – *Phil. Trans. R. Soc. Lond. B* 348: 471–487.
- Hedenström, A. and Alerstam, T. 1997. Optimum fuel loads in migratory birds: distinguishing between time and energy minimization. – *J. theor. Biol.* 189: 227–234.
- Hughes, P. M. and Rayner, J. M. V. 1991. Addition of artificial loads to long-eared bats *Plecotus auritus*: handicapping flight performance. – *J. Exp. Biol.* 161: 285–298.
- Hummel, D. 1983. Aerodynamic aspects of formation flight in birds. – *J. theor. Biol.* 104: 321–347.
- Liechti, F., Hedenström, A. and Alerstam, T. 1994. Effects of sidewinds on optimal flight speed of birds. – *J. theor. Biol.* 170: 219–225.
- Lindström, Å. and Piersma, T. 1993. Mass changes in migrating birds: the evidence for fat and protein storage re-examined. – *Ibis* 135: 70–78.
- Lissaman, P. B. S. and Shollenberger, C. 1970. Formation flight of birds. – *Science* 168: 1003–1005.
- Noer, H. 1979. Speeds of migrating waders Charadriidae. – *Dansk Orn. Foren. Tidskr.* 73: 215–224.
- Norberg, U. M. 1990. *Vertebrate Flight*. – Springer, Berlin.
- Norberg, U. M. 1995. Energetics of flight. – In: Carey, C. (ed.). *Avian Energetics and Nutritional Ecology*. Chapman & Hall, New York, pp. 199–249.
- Pennycook, C. J. 1969. The mechanics of bird migration. – *Ibis* 111: 525–556.
- Pennycook, C. J. 1975. Mechanics of flight. – In: Farner, D. S. and King, J. R. (eds). *Avian Biology*. Vol 5. Academic Press, New York, pp. 1–75.

- Pennycuik, C. J. 1978. Fifteen testable predictions about bird flight. – *Oikos* 30: 165–176.
- Pennycuik, C. J. 1989. *Bird Flight Performance: a Practical Calculation Manual*. – Oxford University Press, Oxford.
- Pennycuik, 1995. The use and misuse of mathematical flight models. – *Israel J. Zool.* 41: 307–319.
- Pennycuik, C. J., Klaasen, M., Kvist, A. and Lindström, Å. 1996. Wingbeat frequency and the body drag anomaly: Wind-tunnel observations on a thrush nightingale (*Luscinia luscinia*) and a teal (*Anas crecca*). – *J. Exp. Biol.* 199: 2757–2765.
- Piersma, T. 1998. Phenotypic flexibility during migration: optimization of organ size contingent on the risks and rewards of fuelling and flight? – *J. Avian Biol.* 29: 511–520.
- Rayner, J. M. V. 1979. A new approach to animal flight mechanics. – *J. Exp. Biol.* 80: 17–54.
- Rayner, J. M. V. 1990. The mechanics of flight and bird migration performance. – In: Gwinner, E. (ed.). *Bird Migration: Physiology and Ecophysiology*. Springer, Berlin, pp. 283–299.
- Rayner, J. M. V. 1995. Flight mechanics and constraints on flight performance. – *Israel J. Zool.* 41: 321–342.
- Tucker, V. A. 1973. Bird metabolism during flight: evaluation of a theory. – *J. Exp. Biol.* 58: 689–709.
- Videler, J. J. 1995. Consequences of weight decrease on flight performance during migration. – *Israel J. Zool.* 41: 343–353.
- Videler, J. J., Groenewegen, A., Gnodde, M. and Vossebelt, G. 1988. Indoor flight experiments with trained kestrels. The effect of added weight on flapping flight kinematics. – *J. Exp. Biol.* 134: 173–183.

(Received 5 January 1999, accepted 18 March 1999.)