Burning the engine: a time-marching computation of fat and protein consumption in a 5420-km non-stop flight by great knots, *Calidris tenuirostris*

C. J. Pennycuick and Philip F. Battley

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Samples of great knots (*Calidris tenuirostris*) were collected in an earlier project, before and after a 5420-km migration stage from Australia to China (believed to be flown non-stop) to determine the mass of fat consumed, and also the mass of protein withdrawn from the flight muscles and other organs. The flight was simulated by a "time-marching" computation, which calculated the fuel energy required, and allowed different hypotheses to be tried for the consumption of protein. The simulation predicted that the great knots would take about 4 days to cover the distance, in agreement with field estimates. Realistic predictions of the consumption of fat and protein were obtained by setting the conversion efficiency to 0.23 and the body drag coefficient to 0.10, withdrawing sufficient protein from the flight muscles to keep the specific work in the myofibrils constant throughout the flight, and taking enough additional protein from other tissues to bring the energy derived from oxidising protein to 5% of the total energy consumed.

The same computation was applied to published data on the pre-migration body composition of bar-tailed godwits (*Limosa lapponica*), which are said to migrate over 10 000 km from Alaska to New Zealand. The computed range for a sample killed by collision with an obstruction, while actually departing from Alaska, was sufficient to reach the South Pole. A second sample, shot before departure from New Zealand, would have run out of fat before reaching Alaska, but could easily have reached northern Australia, where these godwits stage on their northbound migration. The higher range estimate for the Alaskan birds was not due to higher fat mass (only 5% difference) but to a higher fat fraction, which they had achieved by reducing the mass of other organs before departure.

Some recent observations of high chemical power, observed in wind tunnel experiments, have been interpreted as being due to much lower conversion efficiency than the value of 0.23 assumed here, but this interpretation is flawed. Measurements of mechanical power from another wind tunnel project were also unexpectedly high, suggesting that unsteady flight by wind tunnel birds increases their power requirements, both mechanical and chemical, with no implications for efficiency. The calculated power is for "steady horizontal flight", meaning that a valid test of predicted power requires birds to be trained to hold a constant position in the test section, while maintaining a steady wingbeat frequency and amplitude. This has not been achieved in recent experiments, and is hard to achieve when using physiological methods, because of the long periods of continuous flight needed. Measurements of mechanical rather than chemical power require shorter flight times, and offer better prospects for reliable power measurements.

C. J. Pennycuick, School of Biological Sciences, Univ. of Bristol, Woodland Road, Bristol BS8 1UG UK (c.pennycuick@bristol.ac.uk). – P. F. Battley, Australian School of Environmental Studies, Griffith Univ., Nathan, Queensland 4111, Australia.

Predicting the energy requirements of a migrating bird depends on calculating a "power curve" from a theory embodying some underlying physical and physiological assumptions. Values have to be assigned to a number of variables, some of which are easier to measure than others (Pennycuick 1989). Conversely, laboratory or field observations can be compared with these predictions, and any discrepancies can, in principle, be traced to wrong assumptions, or inaccurate values assigned to variables used in the calculation. The most direct way to test a calculated power curve is to measure the power itself in wind tunnel experiments, by mechanical or physiological means, and some discrepancies have recently been reported in experiments of this kind. Measurements of chemical power in red knots (*Calidris canutus*) flying in a wind tunnel yielded estimates about twice those predicted, which the authors (Kvist et al. 2001) attributed to an anomalously low value (0.1 or even less) for the efficiency with which the muscles convert fuel energy into work. If the power were really so high in migrating red knots (as opposed to wind tunnel birds), there would be some difficulty in accounting for their known migration performance, and also for that of some related species that are known or believed to fly extremely long distances non-stop.

In this paper we try another type of test, in which the amount of fat required by great knots (*Calidris tenuirostris*) to migrate from Australia to China, predicted from a computer simulation, was compared with measurements from birds collected before departure and after arrival. We also simulated the consumption of protein from the flight muscles and other organs, according to various alternative hypotheses. The evidence from field observations and ringing recoveries indicates that the great knots are capable of flying this leg of their northward migration non-stop, although they may take a more indirect route, with intermediate stops, on the southward return flight (Tulp et al. 1994).

Predicting the range: limitations of the Breguet equation

The power is expected to decrease by a large amount in the course of a long migratory flight, and the speed may also vary (Pennycuick 1989). The amount of fuel energy consumed is estimated by integrating the chemical power (to find the energy) and the speed (to find the distance), with respect to time. The integration can be performed analytically, but only by making some simplifying assumptions, which are more appropriate to fixed-wing aircraft than to birds. The classical "Breguet equation" gives the distance (Y) that an aircraft can fly as:

$$Y = (e\eta N/g) \ln[1/(1 - F)]. \tag{1}$$

Eq. (1) makes the point that the range does not depend on the size of the aircraft (or bird), but rather on the "fuel fraction" (F) at departure. Any aircraft, large or small, that departs with a fuel fraction of (say) 0.2, meaning that 20% of the departure mass consists of fuel, should travel the same distance, provided that the values of the other four variables in Eq. (1) are the same. Breguet (1922) expressed Eq. (1) in this form, in order to draw the attention of aircraft designers of the time to the importance of maximising the lift:drag ratio (N), by eliminating sources of drag in the aircraft structure. The other variables are the energy density of the fuel (e), the conversion efficiency (η) and the acceleration due to gravity (g).

Eq. (1) gives the range, provided that e, η, N and g can be assigned values that do not change throughout the flight. This is possible, or at least imaginable, in a fixed-wing aircraft, in which the maximal value of N can (in principle) be held constant throughout the flight, provided that the aircraft's external shape does not change, and the pilot progressively reduces speed to match the progressively declining maximum range speed (V_{mr}). However, these restrictions are not realistic for a migrating bird. Even if the fuel is assumed to consist of fat only, the consumption of fat alters the morphology, and this in turn changes N. Pennycuick (1989) resolved this in a somewhat crude way by assuming that the bird reduces speed progressively so as to maintain the maximum range speed (V_{mr}) throughout the flight, and then using the mean of two values of N, from different power curves at the beginning and end of the flight. It was still assumed that the fuel was fat only, and that the values for e, η and g remained constant throughout the flight.

This approach became obsolete when it was realised that long-distance migrants are able to consume protein from the flight muscles and other organs in flight, and replace it quickly during stopovers (Piersma 1998, Lindström et al. 2000). Unlike an aircraft, a migrating bird can "burn" part of its engine and airframe in flight, and use the material (protein) as supplementary fuel. Obviously e cannot be regarded as constant when the bird is using a variable combination of two different fuels, with different power densities. There are in any case reasons (below) why the bird needs to be free to select its cruising speed, without regard to holding N constant. Breguet's equation cannot be used in these circumstances, and it is not practical to formulate a more elaborate analytical solution, that would remove the restrictions on its use. It is unfortunately not possible to simulate the consumption of fat and protein in a migrating bird by any such simple "range equation"

as Eq. (1). A different approach is needed for a realistic simulation.

Time-marching computation

Instead of attempting an analytical solution, power and speed can be integrated numerically over time, using a "time-marching" computation (Pennycuick 1998). This works by calculating the amounts of fat and protein consumed in a short period (6 min) during which all variables, including the power and speed, are assumed to remain constant. The power and speed are then recalculated for the next 6-min period, taking account of the small amounts of fat and protein consumed in the previous period. This is repeated until the bird either covers the required distance, or runs out of consumable fat. With this approach, N need not be assumed to be constant, because it is recalculated at each step, and no restrictions are necessary on the speed at which the bird is assumed to fly. Not only the fat remaining at the end of the flight, but also the remaining mass of flight muscles and other body parts, can be predicted and compared with field observations. Different hypotheses can be tried for assigning the amounts of protein to be withdrawn from the flight muscles and airframe as supplementary fuel, to see which best predicts the field results.

Methods

Field observations

One of us (PFB) collected a sample of 10 great knots (7 males and 3 females) at Broome, on the north-west coast of Australia (18° 00′ S, 122° 22′ E) on 21 March 1998, while the birds were preparing to migrate to their breeding grounds in northern Asia. A further 10 great knots (6 males and 4 females) were collected shortly after arrival at Chongming Island, at the mouth of the Yangtse River, China (30° 48′ N, 121° 27′ E) between 1–9 April 1998. This stage of the migration is believed to be normally flown non-stop (Battley et al. 2000). The fresh mass and wing span of each specimen were recorded in the field. Wing tracings were taken from some specimens, from which the wing area was later measured, and used to get a mean value for the aspect ratio (Pennycuick 1999). The flight muscles (pectoralis and supracoracoideus of both sides) were weighed fresh, then dried for 3 days at 60°C to remove water, then fat-extracted in a Soxhlet apparatus using petroleum ether as the solvent. "Flight muscle mass" refers to the fresh muscle mass minus the mass of fat extracted. Other organs were processed in the same way, and the total fat mass was summed for the entire body.

Body mass components and fractions

For computation purposes, the total body mass was subdivided into three components, fat mass, flight muscle mass and "airframe mass", defined as the total body mass, minus the sum of the fat mass and the flight muscle mass. The "fat fraction" is defined as the fat mass divided by the total mass. We also recognised a "flight muscle fraction" and an "airframe fraction", defined relative to the total body mass, in the same manner as the fat fraction. Under these definitions, the fractions for the different components always add up to 1, however many body components are recognised, and whatever withdrawals of material contribute to the fuel. We do not use the concept of "lean mass". For range calculations, the fat fraction as defined here corresponds to the "fuel fraction" (F in the Breguet equation) and was used in that sense by Pennycuick (1969). It is not helpful to redefine the fat fraction relative to the lean mass, rather than to the total mass, as some authors have done.

Computer simulation

The simulation program was described by Pennycuick (1998). A more recent Windows version (http://detritus.inhs.uiuc.edu/wes/pennycuick.html), has some additional features (below), which were used in the present project. Variables needed in the computation, and the values assigned to them, are listed in Table 1. Bad values for any of these variables may cause a discrepancy between the observed and computed fuel consumption, and conversely, it may be possible to trace any discrepancies to variables whose values are not accurately known, such as the body drag coefficient, and (perhaps) the conversion efficiency. The computation estimated the chemical power, using the current values of the body mass and frontal area, as a "snapshot", calculated for one moment in the flight by the method of Pennycuick (1989). This value of the

Table 1. Variable values used in the simulation for both the great knot and the bar-tailed godwit.

Body drag coefficient	0.10
Induced power factor	1.2
Profile power ratio	0.973
Air density (kg m^{-3})	0.91
Acceleration due to gravity (m s^{-2})	9.81
Ratio air speed: minimum power speed at start	1.2
Fat energy density (J kg^{-1})	3.90×10^7
Dry protein energy density (J kg^{-1})	1.83×10^7
Ratio water lost: protein consumed	2.2
Conversion efficiency	0.23
Circulation and respiration factor	1.1
Density of muscle (kg m^{-3})	1060
Mitochondria inverse power density (m^3 W^{-1})	1.2×10^{-6}

power was assumed to apply for a short period (6 min), during which all variables were assumed to remain constant. The fuel energy consumed during the 6-minute period was assigned to fat or protein, according to criteria which formed part of the assumptions under test. The masses of different body components were then revised, along with other variables such as the body frontal area and the wingbeat frequency, before calculating a new snapshot for the next 6-minute period. This was continued, in 6-minute steps, until the bird either covered the required distance, or ran out of fat.

Burning the engine

The computation allowed for protein from the flight muscles to be consumed, so as to reflect the decreasing demands on the muscles, as the mass declines. ''Burning the engine'' in this way reduces the power required to fly by reducing the total mass, and also contributes fuel energy by consuming protein. The addition of this feature results in higher range estimates than were obtained in earlier calculations (Pennycuick 1989), when only fat was recognised as fuel, and the flight muscle mass was assumed (wrongly) to remain constant. The criterion for determining the amount of protein to be withdrawn from the flight muscles was that the specific work (work done by unit mass of contractile tissue in each contraction) should be held constant. This was identified by Pennycuick (1998) as the most realistic of three ''muscle burn criteria'' that were originally tried. At the molecular level, ''constant specific work'' means that each remaining myosin filament is required to do a fixed amount of work in each contraction, throughout the flight. We subdivided the flight muscles into myofibrils and mitochondria, and treated these two components separately in the simulation, neglecting other components. First, we estimated the volume fraction of mitochondria from the specific power for the whole muscle (Pennycuick and Rezende 1984). We defined the specific work relative to the mass of myofibrils, rather than to the mass of the whole muscle, and held it constant by reducing the mass of the myofibrils only. We reduced the mass of mitochondria separately, by an amount sufficient to hold the specific power within the mitochondria constant. This appears to be consistent with the observations of Bauchinger and Biebach (2001), although the way they represent the muscle components is somewhat different.

In successive time periods, the cycle work (work done in each contraction) declines as the all-up mass declines, even though the wingbeat frequency also declines. If the mass of myofibrils in the flight muscles were to remain constant, the specific work would decline, but we offset this by reducing the mass of myofibrils after each 6-minute interval, by an amount sufficient to restore the specific work to the value that it had at the beginning of the flight. Fuel energy corresponding to the mass of dry protein consumed was deducted from the energy that would otherwise have been taken from the consumption of fat. The flight muscle mass (and the total mass) was reduced by the mass of hydrated protein consumed.

Minimum percentage energy from protein

The computation also recognised that the metabolic machinery requires some minimum percentage of the energy to be derived from oxidising protein (Jenni and Jenni-Eiermann 1998). If the metabolism of protein from the flight muscles for mechanical reasons (above) is not enough to satisfy this metabolic requirement, then additional protein has to be withdrawn from the airframe, meaning any organ other than the flight muscles. In our simulation, the minimum percentage of the energy to be taken from oxidising protein was 5% by default, but other values could be set. If the minimum was set to zero, protein was consumed from the flight muscles only, to keep the specific work constant as above, and in that case we found that the resulting consumption of protein contributed 2.29% of the total energy used, using the variable values in Table 1. If we set the minimum to any value higher than this, additional protein was taken from the airframe, and less fat was consumed, to compensate for the energy released.

Flight altitude and air speed

The altitude and speed at which the great knots fly are unknown, so we had to assign reasonable values. We set the air density to 0.91 kg m^{-3}, corresponding to a flight altitude of about 3000 m ASL. Although the choice of flight altitude has only a small effect on the range, flying higher (i.e. at a lower air density) increases the speed and reduces the flight time, at the expense of higher values of specific work and specific power, and heavier demands on the respiratory and circulatory systems. We did not perform a separate calculation for the initial climb, assuming in effect that the bird is already at its selected cruising height when it starts migrating. The minimum power speed (V_{mp}) was calculated for the fully loaded bird, in the departure configuration, at the selected flight altitude. The true air speed (V) was initially set to 1.2V_{mp}. After that the absolute value of V (in m s^{-1}) was held constant for the remainder of the flight. As V_{mp} declined later in the flight, owing to the consumption of fuel, the ratio of V to V_{mp} progressively increased. The computation method does not impose any restrictions on the selection of speed, but practical restrictions are imposed by

Table 2. Wing measurements for the great knot: body components and mass fractions before and after a flight of 5420 km ground distance.

Wing span (m)	0.586	(SD = 0.0146, n = 20)		
Wing area (m²)	0.0397	(SD = 0.00183, n = 7)		
Aspect ratio	8.65			

	Before migration		After migration	
	Mass (g)	Fraction	Mass (g)	Fraction
Fat	89.8	0.385	10.7	0.086
Flight muscle	33.6	0.144	25.5	0.204
Airframe	110	0.472	88.8	0.710
Total	233	1	125	1

the mechanics of the bird, and its aerobic capacity. Although this particular speed program does not represent any theory of optimal migration, it probably is actually close to a practical optimum (below).

Results

Observed body composition

Table 2 and Fig. 1 show the difference in body composition between the departing and arriving birds, in terms of the three mass components, airframe, flight muscle and fat. Although consumption of fat represented the largest component of mass loss, as expected, substantial amounts of mass were also lost from the flight muscles and from the airframe. Further details and statistical analyses of the field data were given by Battley et al. (2000). Although one can never be sure that a bird collected prior to migration was fully fuelled and ready to depart, the mean mass of the Australian females was near the departure mass given by Higgins and Davies (1996) and the males were only slightly lighter. We tried running simulations separately for males and females, but found only small differences in

the predictions. The results are based on mean values of variables, for both sexes combined, as listed in Table 2.

Computed body composition

Fig. 2 shows the body mass as observed after arrival (left), and as predicted by the computer simulation under four alternative assumptions (right), subdivided in each case into airframe, flight muscle and fat. The assumption that 5% of the total energy consumed must come from protein (second prediction from left) most closely matched the observed values for fat and flight muscle mass on arrival (far left). These predictions represent the hypothesis that sufficient protein is withdrawn from the flight muscles to hold the specific work in the myofibrils constant throughout the flight, and this leads to somewhat more flight muscle being consumed than was observed (grey band). The alternative assumption that specific power was held constant (not shown) would result in even more flight muscle being consumed, whereas if no muscle tissue were consumed, then much more would remain at the end of the flight than was observed (Pennycuick 1998). The total protein consumed, from both the flight muscles and the airframe, accounted for approximately 5% of the energy, as assumed.
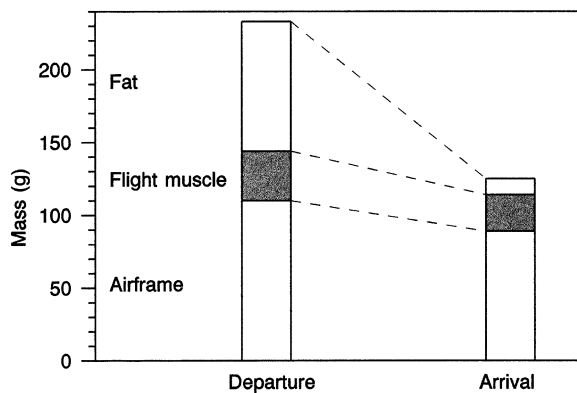

Fig. 1. Subdivision of great knot body mass into airframe, flight muscle and fat components, before and after a non-stop flight of 5420 km ground distance. The total height of each bar represents the fresh mass, as measured in the field.
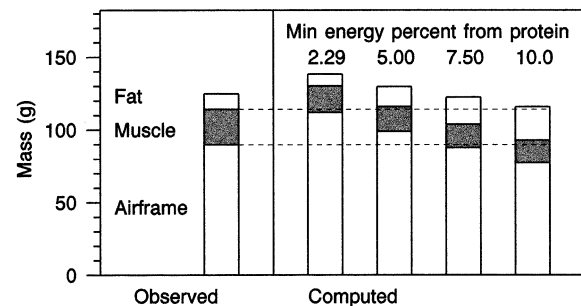

Fig. 2. Predicted great knot mass distribution on arrival, with alternative lower limits for the percentage of the total energy to be derived from oxidising protein. The computed flight muscle mass (grey) is lower than observed, but could be increased by changing the method of air speed selection (see text).

Discussion

Predicted range and flight time

Although it is not certain that the great knots fly non-stop to Shanghai, the simulation predicted that they should be able to fly the distance in about 95 h (just under 4 days), which agrees well with the estimate of 3.5–4 days given by Higgins and Davies (1996). According to the simulation, they departed from Australia with enough fat to fly 7040 km without refuelling, which is sufficient to reach a latitude nearly 15° north of their destination near Shanghai (Fig. 3). No special assumptions had to be made. The notion that following winds would be necessary (Tulp et al. 1994) probably

arose from the use of early estimates of the body drag coefficient (C_{Db}), which were unduly high (0.25–0.40). Later wind tunnel experiments (Pennycuick et al. 1996b) showed that these high values are an artifact due to boundary layer separation from wingless, frozen bodies. This apparently does not occur to the same degree in living birds, for which values in the region of 0.10, as used here (Table 1), are more realistic. Fig. 4 shows the strong effect that the assumed value of the body drag coefficient has on predictions of both the distance flown and the flight time. A great knot with $C_{Db} = 0.25$ would be off the right-hand side of Fig. 4, and would run out of fat long before arriving in China.

Comparison with the bar-tailed godwit

In another test of the simulation, the body mass, fat fraction and flight muscle fraction were set to published values for the Alaskan bar-tailed godwit (*Limosa lapponica*) from Piersma and Gill (1998). The wing span and aspect ratio (Table 3) were estimated from wing tracings supplied by R.E. Gill (pers. comm.). The remaining variables in the simulation were assigned the same values as for the great knot (Table 1). These bar-tailed godwits migrate between Alaska and the North Island of New Zealand, a great circle distance of 10 260 km. They are thought to be capable of flying this route non-stop, as only small numbers are seen staging during the southward migration at islands such as Kiribati, Tuvalu, Fiji and the Kermadec Islands (Piersma and Gill 1998). No observations of arriving birds were made in this study, but samples of departing birds were obtained at both ends of the migration. The
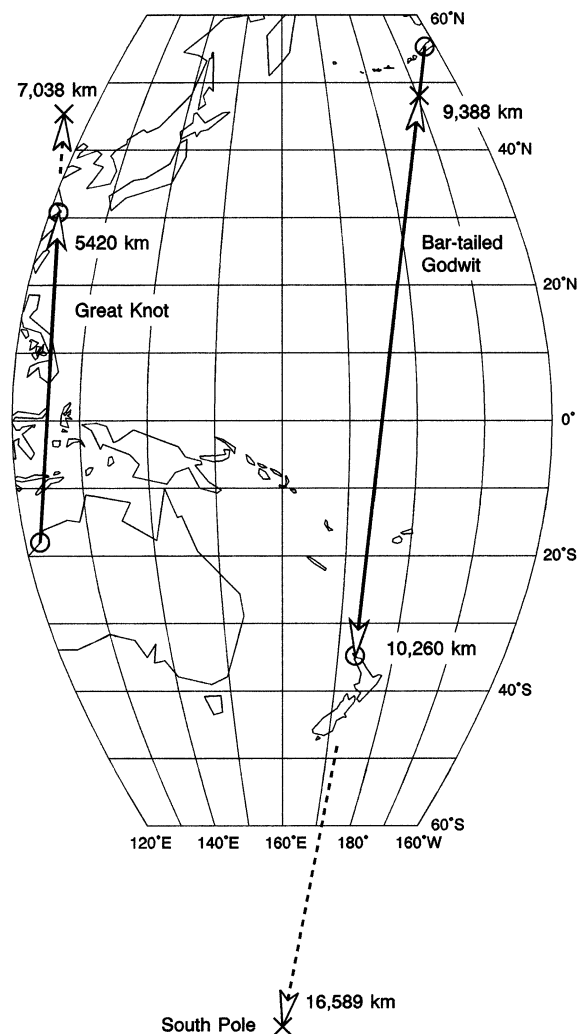

Fig. 3. Map of the western Pacific Ocean showing the migration routes of great knots (left) and bar-tailed godwits (right). Circles mark the points where samples of birds were collected, crosses mark the computed distances at which birds would have run out of fat. The map projection preserves distances but not directions. The straight lines shown do not accurately represent great circle tracks.
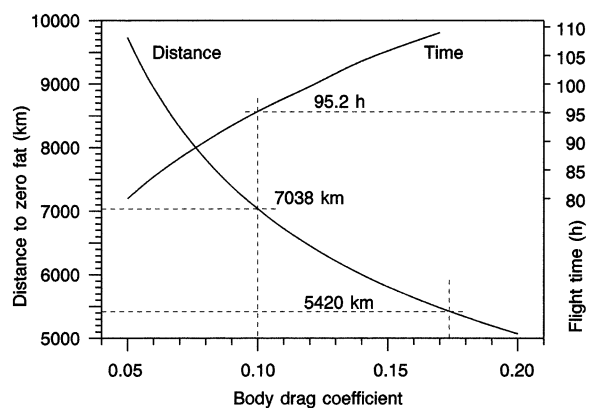

Fig. 4. Effect of varying the great knot's body drag coefficient on the air distance flown until all fat is exhausted, and on the flight time required for the distance (5420 km). With the assumed value of $C_{db} = 0.10$, the bird can cover 30% more than the ground distance (7040 km), but it would not be able to cover the distance if the value of C_{db} were in the range measured in wind tunnel tests of frozen bodies. These values begin at 0.25, and are off the right-hand end of the graph.

Table 3. Wing measurements for the bar-tailed godwit, from tracings supplied by R. E. Gill: pre-migration measurements of fresh mass from Piersma and Gill (1998).

Wing span (m)	0.748	(SD = 0.0148, n = 3)			
Wing area (m^2)	0.0568	(SD = 0.00233, n = 3)			
Aspect ratio	9.85				
Mass before departure from:	Alaska			New Zealand	
	Mass (g)	Fraction		Mass (g)	Fraction
Fat	201	0.548		191	0.427
Flight muscle	55	0.150		62	0.140
Airframe	111	0.302		193	0.433
Total	367	1		446	1

birds in the southbound sample were thought to be actually on their way, when they were killed by colliding with a radar tower on the Alaskan Peninsula, whereas the New Zealand birds had been illegally shot, and were confiscated from a poacher.

According to the simulation, the southbound birds would have reached New Zealand after flying for 175 h (7.3 days), with enough fat remaining to carry on to the South Pole, whereas the northbound sample would have run out of fat about 800 km before reaching the Alaskan Peninsula (Fig. 3). The huge difference in predicted range between the two samples was not due to a corresponding shortage of fat in the New Zealand birds (Table 3). Their average fat mass (191 g) was only 5% less than that of the Alaskan birds (201 g). However the range is not determined by the fat mass as such, but by the fat fraction (Pennycuick 1969). The fat fraction of the New Zealand birds was only 0.427, as compared to 0.548 for the Alaskan birds. After completing the accumulation of fat, the Alaskan birds had increased their fat fraction further by reducing the mass of other organs, as described in detail by Piersma and Gill (1998). It would appear that the New Zealand birds had accumulated nearly the same amount of fat, but had not reduced the mass of the digestive system, liver and other organs, and that it is essential for a bar-tailed godwit to do this before setting off on the 10 260 km direct flight. However, the New Zealand birds had ample fuel to reach northern Australia, where substantial numbers of bar-tailed godwits stage on the northward migration. It is possible that they normally depart from New Zealand without reducing their body organs to the extreme degree seen before they leave Alaska on the direct southward migration.

Speed control program

The fuel margins predicted by the simulation did not depend on flying at the maximum range speed (V_{mr}), or at any supposedly "optimal" speed. It was noted by Pennycuick (1997) that practical considerations would usually favour flying at a slower speed than V_{mr}, even though a bird that is capable of maintaining V_{mr} throughout the flight would theoretically cover the greatest distance by doing that. It is always possible to estimate V_{mr} from a calculated power curve, but it does not follow that the bird is capable of flying at that speed, and it is unlikely that any long-distance migrant would be able to do so at departure. It is scarcely credible that a bird with an airframe fraction of only 0.3 (Table 3) can fly at all, when it is remembered that the airframe includes the structure (skeleton and feathers), the sensory and navigation systems, and the circulatory and respiratory systems needed to sustain aerobic power in the flight muscles. In the early stages of the flight, it is unlikely that a fully-loaded knot or godwit could fly much faster than the current value of the minimum power speed (V_{mp}). The "speed control program" incorporated in the simulation recognises this, and begins by calculating V_{mp} for the departure configuration, and setting the airspeed at 1.2 V_{mp}. This turned out to be 15.8 m s^{-1} for the great knot, and 16.3 m s^{-1} for the southbound bar-tailed godwit, both flying at 3000 m. The power at this speed would be only marginally above the minimum for each species. Thereafter, the absolute speed (in m s^{-1}) was held constant for the remainder of the flight. Although the selected cruising speed was initially well below our estimate of V_{mr}, the penalty in terms of decreased effective lift:drag ratio dwindled as V_{mp} progressively declined during the flight. The ratio of the fixed air speed to V_{mp} built up to 1.43 on arrival, where the range penalty would be small, as compared to flying at V_{mr}, which was estimated to be about 1.6V_{mp} for both species.

This "constant-speed" procedure is a simple way to allow the bird to start at almost minimum power when fully loaded, with only a minor sacrifice of range below the maximum theoretically obtainable. However, there are no constraints on hypothetical speed programs, and more complicated procedures are possible. For example, in the initial part of the flight, the specific work could be held constant without consuming any muscle tissue, by allowing the speed to increase, until it reached V_{mr}. After that, the speed would be progressively reduced to maintain V_{mr}, and protein would be consumed

from the flight muscles to hold the specific work constant. This would gain a little extra range and shorten the flight time, and might also reduce or eliminate the over-estimate seen in Fig. 2 of the amount of material withdrawn from the flight muscles. However, it is not useful to proliferate hypothetical speed control programs without field data on the air speeds actually selected by some long-distance migrant at different stages of a flight, and no such data are available as yet.

Need for reserves

The fuel margins predicted by the simulation for both the great knots and the southbound sample of bar-tailed godwits are more generous than aviation regulations would require, but are realistic for land birds flying such great distances over the ocean, without the benefit of weather forecasts. Birds can and do select favourable wind and weather conditions for departure, but they have no means of predicting what conditions they will encounter over a flight lasting several days, along a route of thousands of kilometres, other than on a statistical basis, from the typical conditions for the season. Pennycuick et al. (1996a) noted that satellite-tracked whooper swans (*Cygnus cygnus*) got into difficulties on several occasions when migrating over a relatively short sea crossing (800 km) between Scotland and Iceland, owing to failure to avoid unfavourable wind and weather conditions, which the human forecaster had predicted. There is no evidence that any bird is aware of or can predict weather beyond the distance that it can see, and this means that any long-distance migrant must have sufficient reserves to deal with adverse conditions which a human pilot, with access to weather services, would anticipate and avoid. Long over-water flights by land birds (even those that can rest on the water) need generous fuel reserves for an acceptable level of reliability. It is not a practical strategy to rely on tail winds.

Best estimate for conversion efficiency

The default value for the efficiency in Flight for Windows (0.23) is consistent with the results of classical exercise physiology on human athletes summarised by Wilkie (1968) and Margaria (1976). In round numbers, the conversion of fuel energy to ATP energy is around 60% efficient, and the conversion of ATP energy into work can be up to 40% efficient, depending on the mechanical conditions. That gives an overall conversion efficiency of 0.24. The only authors who have actually measured conversion efficiency in experiments on flying birds are Tucker (1972) and Bernstein et al. (1973), both of whom used an "incremental" method on different species of birds in the same wind tunnel. Having

allowed the bird to settle into steady flight, they tilted the tunnel by a small amount, so imposing a known small increment of mechanical power, and then measured the increment of chemical power. This technique is not susceptible to errors from effects that bias the mechanical or chemical power or both, because the total power is not used in the calculation of efficiency. The efficiency estimates averaged around 0.23 in both experiments, and this remains the best estimate available.

Reports of low conversion efficiency

Two recent papers have presented claims that the conversion efficiency in powered flight is lower than assumed here, around 0.18 according to Ward et al. (2001), and lower still, around 0.10, according to Kvist et al. (2001), based on wind tunnel experiments with starlings (*Sturnus vulgaris*) and knots (*Calidris canutus*) respectively. These low estimates would, if used in our simulation, lead to difficulty in accounting for the distances that field observers say that great knots and bar-tailed godwits fly non-stop. However, these efficiency estimates are flawed. To measure the conversion efficiency, both the chemical (metabolic) power and the mechanical power (rate of working by the flight muscles), or increments thereof, have to be measured simultaneously. Neither Ward et al. (2001) nor Kvist et al. (2001) did this, and consequently neither group had a valid basis for estimating efficiency. Both groups obtained unexpectedly high measurements of chemical power (only) by different physiological methods, involving hours of continuous flight, but neither measured mechanical power. Their estimates of efficiency came from comparing the measured chemical power with estimates (not measurements) of mechanical power.

Neither group published sufficient details to allow their calculations of mechanical power to be repeated. However, it appears that Kvist et al. (2001) used the same program that we used for the present paper (Flight for Windows) to estimate mechanical power, and that Ward et al. (2001) used a precursor of this program from Pennycuick (1989), which would have given the same results with the same input data. Ward et al.'s (2001) efficiency estimates were nearer than those of Kvist et al. (2001) to our "best estimate" of 0.23, probably because they made a compensating error in their calculation of mechanical power, by using estimates of the body drag coefficient based on measurements of the drag of dead bird bodies. This is known to over-estimate the drag because of massive boundary layer separation, as noted above, and this leads in turn to an over-estimate of the mechanical power.

It is possible that the conversion efficiency varies with changes of speed or body mass, as claimed without valid evidence by both Kvist et al. (2001) and Ward et al. (2001). However, any such effect is unlikely to be strong, as birds are able to vary the mechanical conditions in the flight muscles, by consuming flight muscle tissue and in other ways that would allow them to maximise the efficiency (Pennycuick 2001).

Implications for wind tunnel experiments

Both Ward et al. (2001) and Kvist et al. (2001) obtained estimates of chemical power that were higher than predicted by Flight for Windows, but it was not known whether the mechanical power was also higher than predicted. In another wind-tunnel experiment on a swallow (*Hirundo rustica*) Pennycuick et al. (2000) measured mechanical power (only), using a method that did not involve physiological methods of any kind, and these results also were around twice as high as predicted. By itself, this measurement of mechanical power implies nothing about efficiency, but when taken together with the physiological results, it suggests that something about the conditions of all three experiments caused the birds to work twice as hard as they would have, if the conditions of the experiment had corresponded to the assumptions underlying the computer program. A possible reason for this is unsteady flight in the wind tunnel. The computer program assumes that the bird flies along at a steady speed, whereas Ward et al. (2001) described their starlings repeatedly flying forwards and up to the top of the test section at the upstream end, and then gliding back and down to the bottom at the downstream end. Kvist et al.'s (2001) Knots flapped most or all of the time, but they too moved forward and back, and up and down in the test section. Pennycuick et al. (2000), observed much shorter flight sequences, but also commented on the swallow's erratic flight.

It would seem that more careful attention is needed to training birds to fly steadily, and maintain a constant position in the test section, when attempting to measure either mechanical or chemical power in wind tunnel experiments. This problem was anticipated by Rothe and Nachtigall (1987), who went to the trouble of selecting and breeding pigeons that spontaneously flew steadily before they attempted to make measurements of chemical power that required hours of continuous flight. The effect of intermittent speeding up and slowing down on the average power needs to be investigated, and this could best be done by measuring the mechanical power directly, as much shorter periods of steady flight are required for this type of measurement (Pennycuick et al. 2000). This is one of several sources of error that are difficult to eliminate in a flight that has to last for hours, because of the limitations of the physiological technique used to measure the power.

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