

S36-2 The effect of size on water and energy balance during migratory flight: empirical data versus theory

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Abstract In the absence of sufficiently reliable empirical data, theoretical models for estimating the costs of flight have had to serve ecology. This has led to general insights, such as the finding that power requirements for flight increase rapidly with size. As maximum fuel loads decrease with size, potential flight range decreases too. Because water balance also needs to be maintained during flight, the potential problems for large migrants only seem to grow. This has significant implications for migratory flight. With every gram of fuel added, the more can returns in distance flown diminish. The physiological challenges of long flight in birds, however, can now be studied with greater accuracy than ever before because of the development of wind tunnels. Here, the latest findings are used to update previous predictions on energy and water use in migrating birds in relation to inter- and intra-specific variations in size. These findings are then placed into a more comprehensive ecological context by considering some of their consequences for avian migration strategies, stopover ecology and breeding performance.

Key words Flight, Migration, Energy, Water, Body size

1 Introduction

Although migration is widely associated with migratory flight, approximately 90% of migration time is actually spent going nowhere at stopover sites (Hedenström and Ålerstam, 1998). Thus, judged by time allocation, migration is more a matter of foraging. It is estimated that approximately one third of all energy expenditure during migration, however, is spent in the relatively short period of migratory flight (Hedenström and Ålerstam, 1998). Flight costs, therefore, loom large in the energy budget of migratory birds. This has caused much interest in energy levels, and in how flight costs change both across species and individuals of different mass and morphometry as they empty their fuel stores en route. To estimate flight costs empirically, nevertheless, is difficult, as a result of which many researchers have relied on aerodynamic theory and allometric equations for estimating the costs.

The preference for the aerodynamic model of Pennycuik (1989) as an explanant can be explained by the flexibility that it offers. Variations in flight altitude, body mass, morphometry, air density, etc., can all be taken into account in flight cost estimates. Unfortunately however, the choice of model, including the alternative empirical flight cost estimates model of Masman and Klaassen (1987), can lead to quite different outcomes. In Fig. 1, I provide an overview of empirical flight cost estimates in unrestrained birds during prolonged flight, and compare them with two aerodynamic predictions: one from Pennycuik's original 1989 model (Pen89) and another from the same model with a much lower body drag coefficient, after Pennycuik, Klaassen,

Kvist and Lindström (1996) (Pen96). Although the match on the depicted log-log scale may look impressive, predictions according to aerodynamic theory may vary considerably from empirical findings: on average 13% (range 50% to 99%) and 28% (range 66% to 51%) for Pen89 and Pen96 respectively.

Using repeated-measures ANCOVA, the effect of the model employed was significant ($F_{2,30} = 3.33, P < 0.05$). In a post-hoc comparison, this appeared to be due mainly to the large differences between Pen96 and the other estimates. Flight-power requirement estimates often serve an important role in "higher-order" models of migration, such as the prediction of flight range and optimal departure fuel loads from stopover sites. In this paper, I will focus on the effects of the discrepancies between empirical and aerodynamic flight cost models on the outcomes of higher-order migration models. It appears that these discrepancies can sometimes be huge, indicating that flight cost models need to be selected extremely carefully, and that studies using them should be accompanied at least by sensitivity analyses.

Not only energy balance but also water balance is thought to limit migratory performance in birds (Carmiet al., 1992; Klaassen and Biebach, 2000; Klaassen et al., 1999; Liehti et al., 2000). These predictions are based on rather complicated physiological migration models with a large number of parameters. Some of the parameter values are based on scanty empirical data. For one of the most critical parameters — exhaled air temperature — new data have now surfaced, and I review their impact here on the extent to which water deficit may limit flight range.

2 Water balance

In a sensitivity analysis of their water-budget model, Klaassen et al. (1999) identified two parameters that largely determined outcomes from the model: exhaled air temperature and power requirements for flight. These parameters are also often poorly understood and surrounded by much uncertainty. Below I discuss power requirements for flight in more detail and here only focus on exhaled air temperature. When a bird inhales air, the temperature of the air increases to near body temperature, and in the lungs becomes saturated with water. As the volume of water that air can contain increases exponentially with temperature, a flying bird try-

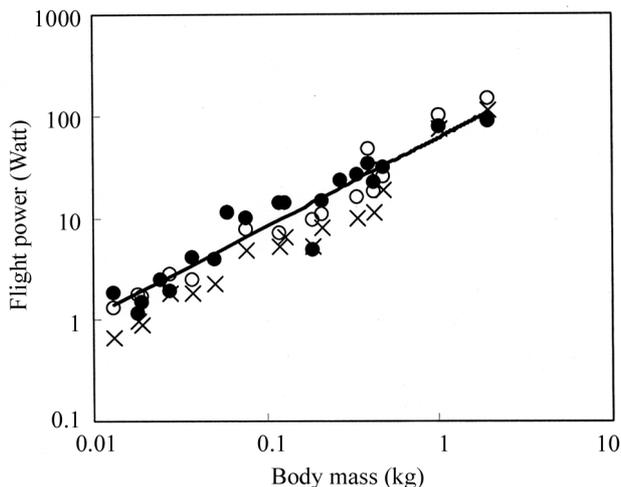


Fig. 1 Empirically estimated power requirements for flight for 20 species of birds in relation to body mass

Black dots — $Y = 10^{1.780 \pm 0.073} X^{0.868 \pm 0.065}$, $R^2 = 0.908$; error terms are standard errors. In the same graph are predicted power requirements according to Pennycuick (1989): circles — $Y = 10^{1.790 \pm 0.060} X^{0.914 \pm 0.055}$, $R^2 = 0.948$, $N = 17$; and Pennycuick (1996): crosses — $Y = 10^{1.644 \pm 0.060} X^{0.975 \pm 0.055}$, $R^2 = 0.954$, $N = 17$. Predictions from aerodynamic models were based on birds flying at sea level and with species-specific wing characteristics and flight speeds. Most empirical flight cost studies provided information for these parameters, but data on wing morphometrics were also obtained from Robbins et al. (1966), Masman and Klaassen (1987), Tobalske and Dial (1994), Pennycuick et al. (1996), Butler et al. (1998), Bruderer and Boldt (2001), and some internet sources. Additional flight speed data came from Bruderer and Boldt (2001). Taxa covered: *Anas rubripes* (Berger et al., 1970), *Branta leucopsis* (Butler et al., 2000), *Calidris canutus* (Kvist et al., 2001), *Columba livia* (Butler et al., 1977; Gessaman and Nagy, 1988; LeFebvre, 1964; Rothe et al., 1987), *Corvus cryptoleucus* (Hudson and Bernstein, 1983), *Delichon urbica* (Hails, 1979; Westerterp and Bryant, 1984), *Falco sparverius* (Gessaman, 1980), *Falco tinnunculus* (Masman and Klaassen, 1987), *Hirundo rustica* (Hails, 1979; Turner, 1982a, 1982b), *Larus atricilla* (Tucker, 1972), *Larus delawarensis* (Berger et al., 1970), *Luscinia luscinia* (Klaassen et al., 2000), *Melospittacus undulatus* (Tucker, 1966), *Progne subis* (Utter and Levebre, 1970), *Riparia riparia* (Turner, 1982a, 1982b; Westerterp and Bryant, 1984), *Sterna fuscata* (Flint and Nagy, 1984), *Sturnus vulgaris* (Torre-Bueno and LaRochelle, 1978; Ward et al., 2001; Westerterp and Drent, 1985). Only the least square fit through the empirical data points is depicted.

ing to conserve water should attempt to cool down exhaled air as far as possible through heat exchange in the nasal passage. The extent to which a bird is successful in doing this largely determines its water loss.

Although this is a crucial determinant of water loss, only data from flights of seven American black ducks (*Anas rubripes*), which lasted no longer than 18 seconds anyway, were available for its estimation (Berger et al., 1971) — until recently. Over the past few years, the data set has expanded considerably (Fig. 2), with measurements from pigeons (*Columba livia*) flying from 1.5 up to 3 h (Michaeli and Pinshow, 2001) and Eurasian widgeon (*Anas penelope*) and teal (*Anas crecca*) flying from 4 up to 38 min. (R. Klaassen et al., unpubl). These new estimates, from advanced measuring techniques on different birds flying for much longer periods, appear to deviate only slightly from the black duck data. Thus, there still seems to be a strong case for earlier predictions that, under specific conditions, migratory flight may indeed be constrained by water budgets (Klaassen et al., 1999).

3 Estimating maximum flight range

Maximum coverable distance is an important parameter when migrating birds have to migrate across inhospitable oceans and deserts; and it is a paramount constraint on birds that use discontinuously distributed food resources and are bound to specific habitats on stopovers. The flight range of birds is generally considered to decrease with increasing bird size (Klaassen, 1996). That contention, however, is based solely on aerodynamic theory. Maximum flight range (m) can be derived by taking the maximum fuel load of an animal (J), dividing it by power requirements for flight (Watt or J/s) and multiplying that with its flight speed

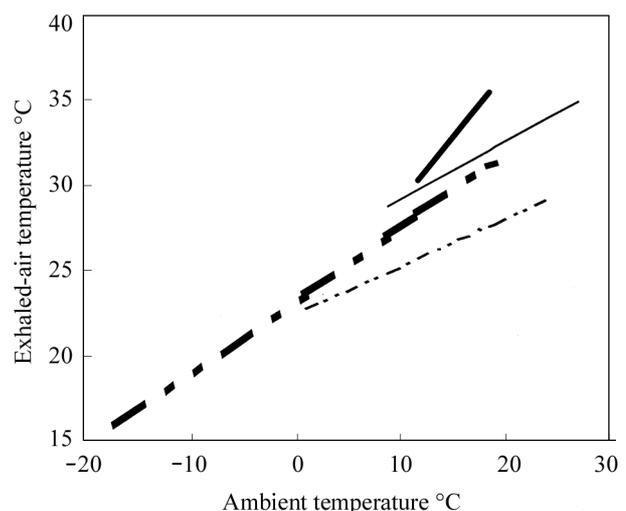


Fig. 2 Exhaled air temperature as a function of ambient air temperature in different birds

Heavy dashed line: American black duck (*Anas rubripes*); thin line: rock dove (*Columba livia*); thin dashed line: common teal (*Anas crecca*); heavy line: Eurasian widgeon (*Anas penelope*).

(m/s). Using Pennycuick's aerodynamic model, maximum flight range will decrease significantly with an increase in size. Using the empirical flight cost model of Masman and Klaassen (1987), however, will result in far smaller changes with size. According to it, changes will initially be positive and only slightly decrease at body masses of more than a kg (Klaassen, 2002).

4 Size-dependent breeding strategy in arctic breeding birds

"Capital" and "income" breeding are two extreme strategies that lie on a continuous scale, the first relying exclusively on body stores and the second on local food sources for all nutritional requirements during breeding. Klaassen (2002) investigated size-dependency in the use of capital breeding strategy in arctic breeding migrants. Employing allometric equations, I evaluated migratory time and energy costs associated with carrying extra stores to the breeding grounds. It appeared that the outcome of this modeling depended critically on the power requirements for migratory flight.

As stressed earlier, maximum flight range predictions by the Pennycuick models and the empirical flight cost model vary greatly, being much shorter under the Pennycuick models. It can be expected that a capital breeder would want to take along extra reserves to the breeding grounds for egg production and incubation, and will thus need to be able trade distance for capital. According to the aerodynamic model, however, the scope for large birds to trade distance for extra reserves for investment in egg production upon

arrival on their breeding grounds is very small. In contrast, the empirical flight cost model predicts that the scope for capital breeding will only increase with size (Klaassen, 2002).

Striking differences between the two models appeared again in comparisons of estimated time required to acquire reserves for migratory flight or for egg synthesis and catabolism on the breeding grounds. Fuelling times for migratory flight predicted by aerodynamic theory were much longer than those based on the empirical flight cost model (Klaassen, 2002). Thus, if the Pennycuick predictions of power requirements are indicative for arctic breeding birds, a capital breeding strategy will be extremely difficult to realize for large birds given their short flight range and long refuelling times. If the empirical flight cost model is closer to the truth, capital breeding is probably less of a marginal life-style for large birds. Support for the empirical flight cost model comes from various sources that have found a capital breeding strategy in large but not small arctic breeding birds (Klaassen, 2002; Klaassen, Lindström, Meltofte and Piersma, 2001).

5 Departure fuel load

Conceivably, the flight costs for a bird on migration will decrease while fuel stores are being catabolized. Aerodynamic theory provides predictions for this. These predictions have now been challenged by a study by Kvist et al. (2001) on knots (*Calidris canutus*) flown in a wind tunnel. In Fig. 3, their findings are plotted against Pen89 and Pen96 predictions. The empirical data suggest that flight costs decrease at a much slower rate with a decrease in fuel load

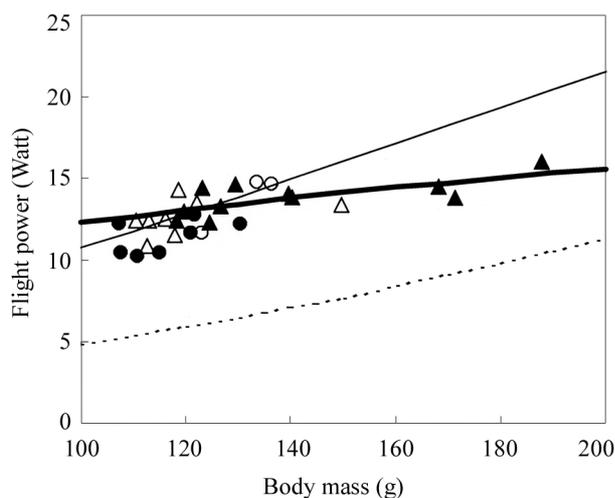


Fig. 3 Flight costs in relation to body mass for individual red knots (*Calidris canutus*)

Measurements according to Kvist et al. (2001), shown by original data points and the heavy line, and predictions by aerodynamic models (Pennycuick, 1989: thin line; Pennycuick, 1996: dashed line). For the aerodynamic models, the default settings of Pennycuick's (1989) program were used. For the model calculations, knots were assumed to have a lean mass of 100 g, a wing span of 0.512 m, an aspect ratio of 8.35, an energy density of fuel stores of 30 kJ/g, and to fly in air with a density of 1.25 g/L.

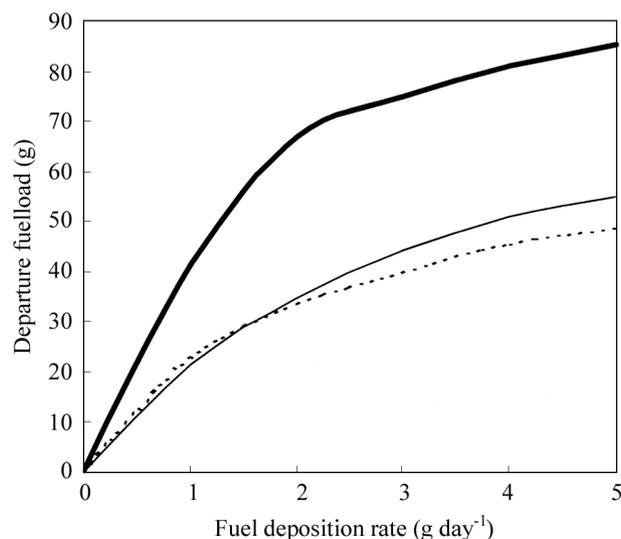


Fig. 4 Optimal departure fuel load in relation to fuel deposition rate (or site quality) for red knots (*Calidris canutus*) exhibiting the three different flight cost curves depicted in Fig. 2

Empirical flight cost model according to Kvist et al., 2001 (heavy line) and the Pennycuick 1989 (thin line) and 1996 (dashed line) aerodynamic flight cost models. Optimal departure fuel loads were calculated according to Alerstam and Lindström (1990), assuming a search/settling time of 2 days.

than indicated by the aerodynamic models. As for both airliners and refuelling birds at stopovers, the precise relationship between body mass and flight costs are of essential concern. Here the differences between empirical findings and aerodynamic models have an impact on maximum flight range.

Aerodynamic models have been used widely to predict stopover behavior (Alerstam and Lindström, 1990; Klaassen and Lindström, 1996; Weber and Houston, 1997; Weber et al., 1998), yielding, *inter alia*, estimates of optimal staging time, optimal range and optimal fuel load. It is of interest to see how such predictions change when one adopts alternative flight cost models. Using the optimal migration model advocated by Alerstam and Lindström (1990), for example, I calculated the departure fuel loads for knots in relation to fuel deposition rate (site quality; Fig. 4). Extrapolating the data of Kvist et al. (2001) to these optimal migration models yields much higher predictions of optimal departure fuel load than the Pennycuick models.

6 Conclusions

In principle, aerodynamic theory should be able to predict accurately the requirements of mechanical power for flight. However, in the transformation of mechanical power to chemical or total power, which is the parameter of concern to ecologists and physiologists, assumptions have to be made about overall muscle efficiency and power requirements for basal life functions, in addition to respiration and circulation during flight. On top of that, the values for some parameters in the calculation of mechanical power are in dispute, such as the coefficient of body drag (Hedenström and Liechti, 2001; Pennycuick et al., 1996). Such complications led Rayner (2001) to the conclusion that aerodynamic models cannot yet be extended reliably to predict total flight power. This notion is directly opposed to the views of Weber and Houston (1997) who advocate the use of aerodynamic rather than empirically derived models. They varied the parameter estimates of allometric flight cost equations within confidence limits and found considerable effects on departure fuel load and flight range. The lack of error terms in aerodynamic models, however, should not be taken to mean that the many parameters in those models are error free.

Models should be used primarily to put empirical findings into context and to guide empirical results. Clearly, measuring the actual flight costs of focal species under appropriate conditions is the most ideal alternative for any study relying on flight cost estimates. Yet, this is seldom feasible, forcing researchers to use empirical or theoretical models to generate predictions. The analyses presented by Weber and Houston (1997), Klaassen (2002) and here indicate that the choice of model may have a marked effect on the outcome and that sensitivity analyses of studies involving flight cost predictions should thus be standard procedure.

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