

METABOLIC CONSTRAINTS ON LONG-DISTANCE MIGRATION IN BIRDS

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Summary

The flight range of migrating birds depends crucially on the amount of fuel stored by the bird prior to migration or taken up *en route* at stop-over sites. However, an increase in body mass is associated with an increase in energetic costs, counteracting the benefit of fuel stores. Water imbalance, occurring when water loss exceeds metabolic water production, may constitute another less well recognised problem limiting flight range. The main route of water loss during flight is *via* the lungs; the rate of loss depends on ambient temperature, relative humidity and ventilatory flow and increases with altitude. Metabolite production results in an increased plasma osmolality, also endangering the proper functioning of the organism during flight. Energetic constraints and water-balance problems may interact in determining several aspects of flight behaviour, such as altitude of flight, mode of flight, lap distance and stop-over duration. To circumvent energetic

and water-balance problems, a bird could migrate in short hops instead of long leaps if crossing of large ecological barriers can be avoided. However, although necessitating larger fuel stores and being more expensive, migration by long leaps may sometimes be faster than by short hops. Time constraints are also an important factor in explaining why soaring, which conserves energy and water, occurs exclusively in very large species: small birds can soar at low speeds only. Good navigational skills involving accurate orientation and assessment of altitude and air and ground speed assist in avoiding physiological stress during migration.

Key words: migration, energetics, water balance, fuel stores, time minimization, allometric relationships, flight altitude, navigation, birds.

Introduction

‘What intensity and gladness of life was in it, what a wonderful inherited knowledge in its brain, and what an inexhaustible vigour in its slender frame to enable it to perform that annual double journey of upwards of ten thousand miles!’ Not only Hudson (1939; here expressing his excitement about the migratory ability of the upland sandpiper *Bartramia longicauda*) but many other ornithologists have realized for years that birds need brains as well as muscles to conduct a long-distance migratory journey successfully. In this review, I focus on the latter and discuss a few physiological characteristics that probably greatly determine and constrain the behaviour of migrating birds. Finally, I discuss the impact of our knowledge of navigation on ecophysiological studies of bird migration in the conviction that good navigational skills will alleviate the impact of physiological constraints for migrants.

Necessity of fuel stores

Migratory birds often have to cross large areas, such as deserts and oceans, without a suitable habitat for fuelling. Before such inhospitable areas can be passed, body stores have to be built up to fuel the energetically costly flight (e.g. Pennycuik, 1975, 1989; Masman and Klaassen, 1987). In

long-distance migrants, body mass may more than double prior to migration. However, apart from ecological barriers, time constraints can also explain the accumulation of fuel stores for migration. Ultimately, the total amount of fuel stores is probably a trade-off between the effects of fuel stores on the energetics, duration and risks of migration.

Time constraints act simply because seasons are of limited duration. Moreover, early arrival may be rewarded with a higher competitiveness for limiting resources (von Haartman, 1968). But why does this make it so important for a time-minimising migrant to build up fuel stores? For a number of possible reasons (Hansson and Petterson, 1989; Klaassen and Biebach, 1994) the rate of refuelling is initially low upon arrival at a stop-over site. During the first few days, the migrant may even lose some weight. These problems during settling reduce the speed of migration and favour a reduction of the number of stop-overs. Consequently, fuel stores are increased. Variability in the quality of refuelling sites also influences the size of stores. When a bird happens to find a relatively good refuelling site, it uses the opportunity to build up larger fuel stores than on average sites. Moreover, as a bird cannot foresee the situation on the staging sites to come, it builds up some extra fuel to reduce the risk of starvation. Thus, variation in site quality also determines the amount of fuel stored.

However, with an increase in fuel stores, flight costs in energy per unit distance increase rapidly (Pennycuick, 1975, 1989). Besides the increased energetic costs with increasing fuel load, other types of costs might also exist that migrants may take into account in determining their optimal fuel load. These other costs could include increases in the risks of injury, illness and predation and a decrease in foraging efficiency (for a review, see Witter and Cuthill, 1993). These considerations suggest that fuel stores must be kept at the lowest possible level and that the migratory journey must be undertaken in short hops rather than long leaps. On the basis of these arguments, several theoretical models have been developed to explain the size of fuel stores in migrants (Alerstam and Lindström, 1990; Gudmundsson *et al.* 1991; Lindström and Alerstam, 1992; Weber *et al.* 1994, 1995; Klaassen and Lindström, 1996). These models have emphasized the need for more empirical data on the costs and benefits of fuel stores.

Allometric considerations in relation to fuel loads

Size-dependent physiological problems may occur in relation to migration. For instance, when large migratory birds (are forced to) use flapping flight, they face larger energetic problems than smaller birds. Fuel loads are limited by the morphological capabilities of birds; above a certain threshold, birds will not be able to take off (Hedenström and Alerstam, 1992). Maximum fuel-carrying capacity (the ratio of total body mass to lean body mass, h_{\max}) decreases with body mass (Hedenström and Alerstam, 1992; Fig. 1A). Because flight range increases almost linearly with fuel load (Fig. 1B), maximum flight range will also decrease with body mass. Thus, when covering a certain distance between the summer and winter areas with maximum fuel load, large birds will have to refuel more frequently than small birds. As mentioned earlier, each stop-over normally involves some time loss because the rate of refuelling is initially low. At the staging site, large birds face another energetic problem that limits their speed of migration: their maximum rate of fuel deposition is relatively low. This is the result of a more or less universal maximum limit to the daily metabolizable energy intake (Kirkwood, 1983). On theoretical grounds, maximum fuel deposition rate is expected to scale to body mass with an exponent of -0.27 , a value that is largely supported by empirical data (Lindström, 1991; Fig. 2).

Thus, the larger the migratory bird, the larger the energetic problems it faces when using flapping flight. Soaring is energetically much cheaper and could be a good alternative to flapping flight if the bird is energy-constrained. Moreover, large birds have a relatively high soaring speed, making soaring a good alternative to flapping flight not only to conserve energy but also to save time (Pennycuick, 1989; Hedenström, 1993). It is not only their typically low soaring speed that makes soaring a poor alternative for time-constrained small migratory birds. Small birds will also be blown off course easily when soaring at low speeds (Hedenström, 1993). At temperate latitudes, thermal

convection is only available during part of the day. This results in a restricted daily period when migration by soaring flight is possible. Therefore, with an increase in latitude, large species increasingly use flapping instead of soaring flight (Hedenström, 1993).

Composition of fuel stores

To maximise flight range at the lowest possible costs, fat is the preferred fuel for flight. Fat is the most energy-dense metabolite and can be synthesised from any type of food that is digested. Indeed, body stores of migratory birds were long thought to consist almost entirely of fat (Connell *et al.* 1960; Odum *et al.* 1964, 1965), but evidence is continuously accumulating that the synthesis of protein is often also involved (Piersma, 1990). Studies on the composition of body stores for migration using carcass analyses may provide insight into the nature of these tissues. After having noted that many earlier studies were flawed as a result of methodological

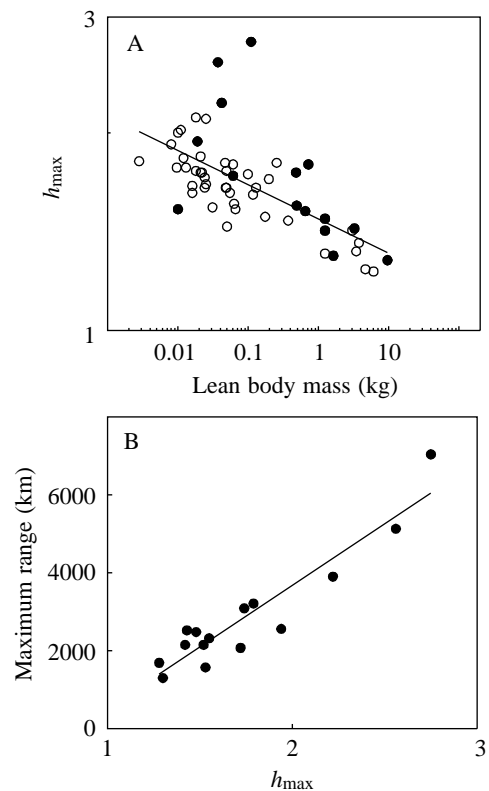


Fig. 1. (A) Calculated maximum fuel-carrying capacities (ratio of total body mass to lean body mass, h_{\max} ; filled symbols) for 15 species of birds with known aerodynamic characteristics as a function of lean body mass. In addition, maximum observed fuel-carrying capacities in 41 species of free-living birds (open symbols) in relation to lean body mass are presented. (B) Calculated maximum flight range according to Pennycuick (1989) as a function of calculated maximum fuel-carrying capacities for the 15 species of birds with known aerodynamic characteristics. Least-squares regression lines are drawn (A, $r^2=0.431$, $P<0.01$; B, $r^2=0.874$, $P<0.01$). Data from Hedenström and Alerstam (1992).

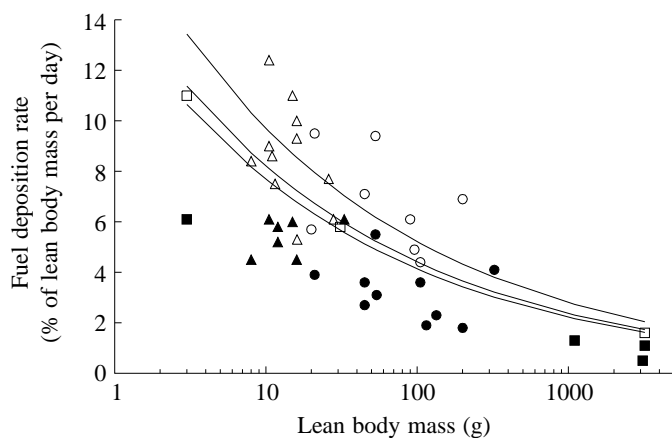


Fig. 2. Maximum fuel deposition rates (percentage of daily mass increase relative to lean body mass) in migrating birds of different sizes. From top to bottom the three lines depict the predicted maximum fuel deposition rate for non-passerines, shorebirds and passerines, respectively, based on allometric considerations. Observed maximum fuel deposition rates of populations (open symbols) and individuals in the field (filled symbols) are presented for passerines (triangles), non-passerines (squares) and shorebirds (circles). From Lindström (1991) (reprinted with permission).

inconsistencies, Lindström and Piersma (1993) re-evaluated the available data and found strong indications that birds generally, but not always, deposit protein before take-off. Recalculating data for bar-tailed godwit *Limosa lapponica* (Piersma and Jukema, 1990), Lindström and Piersma (1993) estimated that migratory fuel stores consist of 35% non-fat components (probably protein with associated water). By accurately measuring the energy balance of individual birds and relating the difference between metabolizable energy intake and energy expenditure to changes in body mass, the energy density of fuel stores, and hence their composition, can be determined. Such a method, although it can unfortunately only be used in birds kept under laboratory conditions, does not suffer from the methodological problems outlined by Lindström and Piersma (1993) for carcass analyses. In three migratory bird species, this method has been used to evaluate the composition of fuel stores during the migratory period, yielding values for fat content in the range 71–82% (Klaassen *et al.* 1990; Klaassen and Biebach, 1994; M. Klaassen, Å. Lindström and R. Zijlstra, in preparation). Again, more support for body stores containing a mixture of protein and fat comes from nitrogen balance studies in both migratory (M. Klaassen, Å. Lindström and R. Zijlstra, in preparation) and non-migratory birds (Lindgård *et al.* 1992, and studies cited therein). These nitrogen balance studies revealed that the fat content of fuel stores ranged between 62 and 81%. Finally, Jenni-Eiermann and Jenni (1991) found elevated levels of uric acid in the blood of actively migrating passerines at a high mountain pass in the Swiss Alps, which is an unambiguous indication that protein, as well as fat, is catabolized during migration.

Studies of muscle mass in relation to the accumulation of body fat for migration show adaptive increases in muscle size, while composition and function are similar on a mass-specific basis (Kendall *et al.* 1973; McLandress and Raveling, 1981; Marsh, 1983, 1984). These increases in flight muscle mass for migration are generally thought to be necessary to carry the extra weight of body stores (Pennycuick, 1975; Marsh and Storer, 1981; Dawson *et al.* 1983). It is possible that it is this extra muscle mass in migratory birds that is reflected in the 18–38% wet protein (i.e. protein plus associated water, which normally occur in the ratio 3:7) in the body stores. It is also possible that the proteins are stored in active tissue other than muscles to support the higher metabolic demands of a bird with a high fuel load. Alternatively, or additionally, it might be impossible for an animal to function normally without some protein utilisation or turnover.

Whatever the reason for storing a mixture of fat and protein, rather than just fat, the important consequence of this for a migratory bird is its impact on maximum flight range. 1 g of tissue containing, for example, 75% fat and 25% wet protein yields 22% less energy than 1 g of pure fat. The distance a migratory bird can cover with the fat/protein mixture is thus also 22% shorter than it could cover if it had been catabolizing fat exclusively.

Problems of water

The necessity for migratory birds to balance their energy budget is obvious. However, we should not oversimplify the matter. Apart from fat and protein, there are further body resources that are burdened under the extreme effort of long-distance migration. Water imbalance may also limit a bird's flight range (Carmi *et al.* 1992). I will discuss (1) the routes of water gain and loss, which are very different from those of energy, and (2) evidence that problems of water balance participate in governing migratory behaviour.

When crossing seas and deserts, a bird's water budget must be carefully balanced because no fresh water is available for rehydration. However, when crossing less inhospitable areas, intermittent stop-overs to rest, drink or eat should also be avoided because they are costly events, especially when cruising at high altitude. Reaching these high air layers is energetically expensive (Hedenström and Ålerstam, 1992). When heat-stressed, birds use water for evaporative cooling. Under such circumstances, a bird may rapidly dehydrate. Even under thermoneutral conditions or when cold-stressed, dehydration may easily follow from passive water loss. Most water is lost *via* the lungs. Inhaled ambient air is brought to body temperature and saturated with water. During exhalation, the air is cooled down, causing condensation of water vapour and recovery of water that was added to the air upon inhalation. However, the exhaled air temperature is still well above the inhaled air temperature (Berger *et al.* 1971) and the inhaled air is rarely saturated with water, in contrast to the exhaled air, resulting in a net loss of water.

During flight, both fat and proteins are catabolized as

discussed above. The consequent increase in levels of uric acid and other plasma metabolites, possibly in concert with some dehydration, will result in an increased blood plasma osmolality, endangering the proper functioning of the organism.

With an increase in flight altitude, partial oxygen pressure drops, leading to an increase in the ventilatory flow through the lungs and a concomitant increase in water loss. Water loss may be balanced by water production. For example, catabolism of fat alone yields $27 \mu\text{l H}_2\text{O kJ}^{-1}$. When catabolizing a mixture of 70% fat and 30% wet protein, the water yield is somewhat more favourable at $34 \mu\text{l H}_2\text{O kJ}^{-1}$.

Using physiological models of energy expenditure and water loss (Fig. 3), it has become clear that problems of water balance may indeed occur during crossings of the Sahara desert (Carmi *et al.* 1992; Klaassen, 1995; M. Klaassen and H. Biebach, in preparation). However, a deficit in water balance may also occur at higher latitudes. This deficit will be most noticeable in large birds that migrate using flapping flight. For example, the mute swan *Cygnus olor* (approximately 10 kg) has an estimated flight cost of 70 times its basal metabolic rate (Pennycuick, 1989) and is thus expected to have a high pulmonary flow. However, although measured at rest only, the mute swan appears to have a very low breathing frequency, high oxygen extraction and large tidal volume (Bech and Johansen, 1980). These characteristics will help mute swans to avoid water balance deficits during flight. Nevertheless, field observations on similarly sized and closely related whooper swans *Cygnus cygnus* make it conceivable that swans may still encounter water balance problems during migratory flight. Using a satellite transmitter, Colin Pennycuick (personal communication) was able to follow the flight path of a whooper swan migrating in 1 day from Iceland to Scotland. The bird flew at very low altitude, practically skimming the tops of the waves (humid and oxygen-rich air!). Nevertheless, the first

thing that this individual was observed to do upon arrival in Scotland was to drink large amounts of water.

Interaction between energy and water constraints

Assuming that ambient temperatures at ground level are low enough to avoid heat stress, water balance problems normally increase with altitude; although ambient temperature decreases, along with exhaled air temperature (low water vapour pressure), this decrease normally cannot compensate for the increase in pulmonary flow with reduced partial pressure of oxygen. Energetic costs of flight change little with altitude. Drag decreases, but the mechanical output needed to generate lift makes flight a slightly more costly enterprise at high than at low altitude. Wind assistance is generally regarded as being of major importance during long-distance migration (e.g. Alerstam, 1990; Piersma and Jukema, 1990; Piersma and van de Sant, 1992; Gudmundsson, 1993; Bruderer *et al.* 1995). It may be that, at altitudes where favourable winds prevail, conditions for the maintenance of water balance may be poor.

During autumn migration over the western Sahara desert in Egypt, favourable conditions for both energy and water balance prevail at relatively low altitude between 250 and 750 m during the night (Biebach and Klaassen, 1994; M. Klaassen and H. Biebach, in preparation; Fig. 4). During spring migration, conditions are expected to be less favourable for the migrants from a water balance perspective. Although temperatures are somewhat lower, which is more favourable for water balance, good wind conditions are usually to be found only at high altitudes. M. Klaassen and H. Biebach (in preparation) did not conduct measurements during spring. However, assuming identical meteorological conditions during spring and autumn and only reversing migratory direction resulted in a predicted optimal flight altitude from an energetic point of view of 3000 m. Taking the water balance into

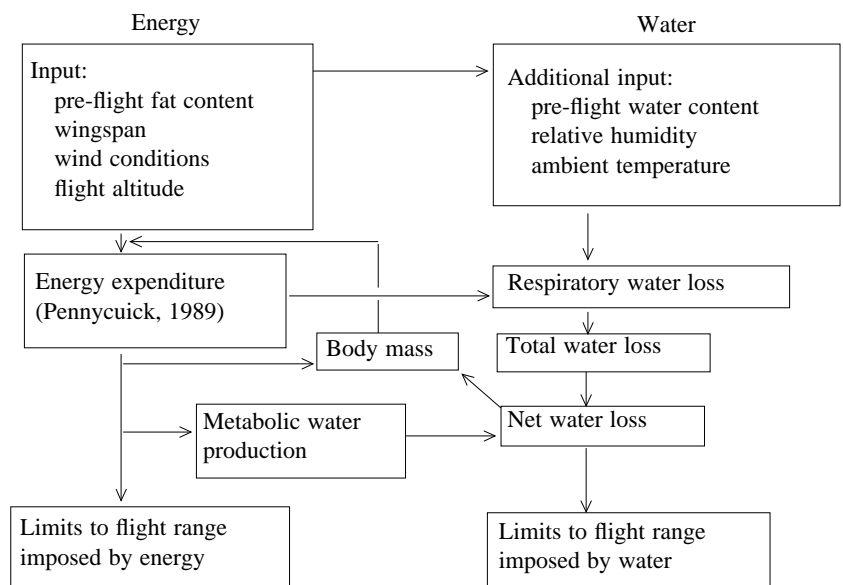


Fig. 3. Model used to estimate flight ranges of migratory birds. The model allows the calculation of flight range on the basis of limited fuel stores only, assuming that net water loss equals zero (i.e. the right-hand side of the model is not relevant). Alternatively, both alterations in energy and water budget can be considered simultaneously, requiring additional input of variables. For a detailed explanation see Carmi *et al.* (1992) and Klaassen (1995).

consideration, the optimal flight altitude was predicted to be only 1750 m (Fig. 4). Unlike the situation in autumn, we thus expect a conflict between optimisation of energy balance and water balance in spring.

Bruderer *et al.* (1995) measured meteorological conditions and altitudinal distribution of migratory birds crossing the Negev desert in both spring and autumn. In accordance with M. Klaassen and H. Biebach's (in preparation) prediction of a conflict between energy balance and water balance considerations in spring, but not in autumn, Bruderer *et al.* (1995) found a clear peak in migratory altitude in autumn and a rather uniform distribution in spring. Unlike M. Klaassen and H. Biebach's (in preparation) use of a physiological model to integrate the impact of various meteorological parameters on flight range, Bruderer *et al.* (1995) linked the raw meteorological data and simple derivatives thereof to altitudinal distribution, neglecting the rather complicated interplay between the various variables. They found a high correlation between tail-wind velocity and altitudinal distribution in autumn. Interestingly, the fit with tail-wind

velocity was poorer in spring, and the significant effect of temperature indicated a certain preference of the birds to fly at low altitudes (oxygen-rich air; lower pulmonary flow).

Navigation and physiological constraints

Clearly, good navigational skills will alleviate the impact of physiological constraints for migrants and *vice versa* (Fig. 5). These navigational skills do not necessarily involve finding the shortest way to the destination. Sometimes physiological difficulties may be avoided by taking a roundabout way. In particular, many soaring birds avoid crossing long stretches of water because of the lack of thermal updraughts at these sites. White storks *Ciconia ciconia* show a migratory divide: those breeding west and east of 11° E migrate southwest and southeast, respectively (Cramp and Simmons, 1977). These two distinct innate migratory directions result in their crossing the Mediterranean over only narrow stretches of water in two unusually narrow fronts, across the Strait of Gibraltar and around the coasts of Levant. Another example is the blackcap

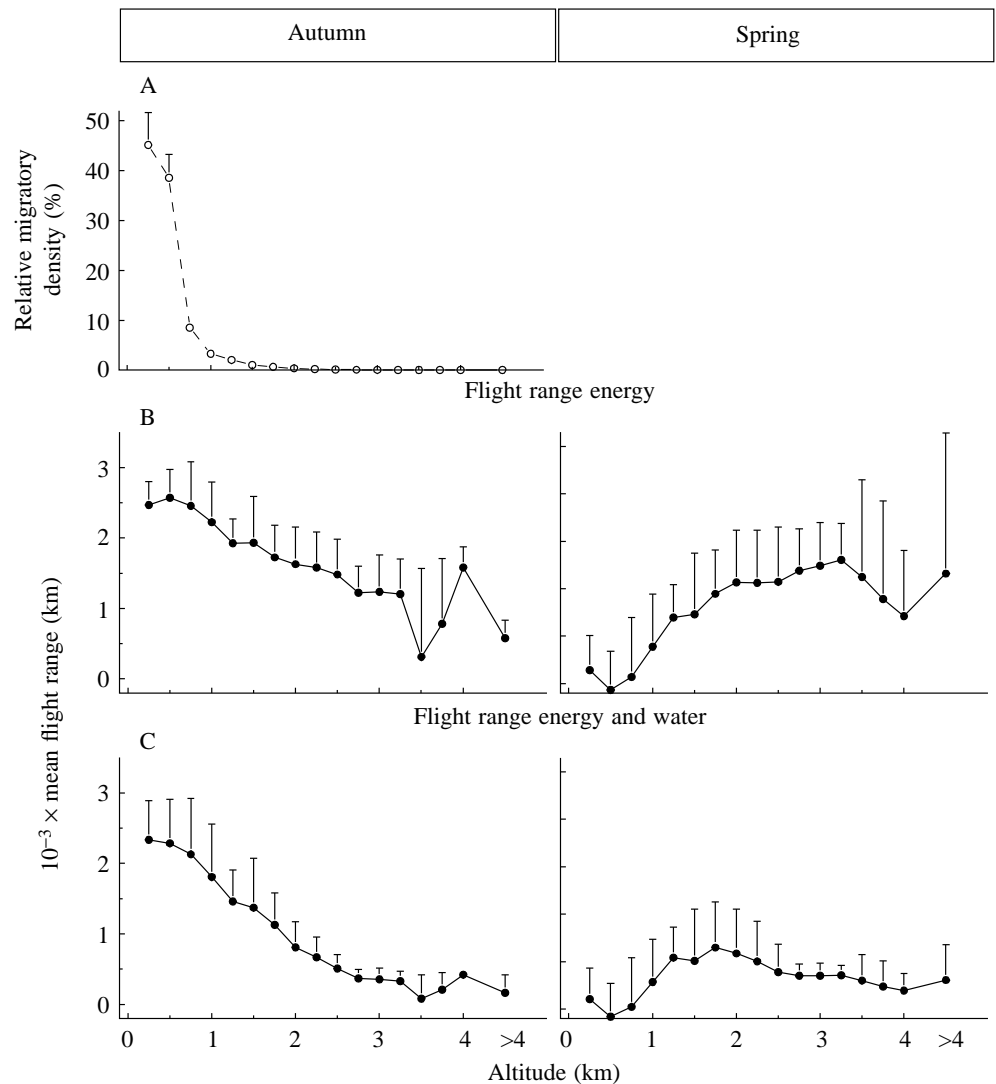


Fig. 4. Comparison of nocturnal migration over the western Sahara desert, Egypt, in autumn and spring. (A) Relative migratory density (mean + s.d., $N=133$) measured by radar in relation to altitude in autumn. Absolute migratory density was $7.45 \text{ birds m}^{-1} \text{ h}^{-1}$ on average. (B,C) Mean flight range (+ s.d., $N=14$) for willow warbler *Phylloscopus trochilus* in relation to altitude (in categories of 250 m) calculated from weather balloon measurements in autumn using both the energy model (B) and the energy-and-water model (C). The left-hand panels depict predictions for autumnal migration and the right-hand panels predictions for vernal migration. The vernal predictions were calculated on the basis of the meteorological conditions measured in autumn but assuming south-to-north instead of north-to-south migration. From M. Klaassen and H. Biebach (in preparation).

THIS WEEK?	TODAY?	TONIGHT?
<input type="checkbox"/> CORRECT SEASONAL TIMING <input type="checkbox"/> FUEL TANK FULL <input type="checkbox"/> WIND CONDITIONS	<input type="checkbox"/> LAST MINUTE TOPUP <input type="checkbox"/> WIND CONDITIONS <input checked="" type="checkbox"/> FLOCK-MATES AVAILABLE <input type="checkbox"/> CLOUD CONDITIONS <input type="checkbox"/> OVERALL VISIBILITY (DUST, FOG)	<input type="checkbox"/> WIND CONDITIONS <input checked="" type="checkbox"/> FLOCK-MATES AVAILABLE <input type="checkbox"/> VISIBILITY OF (SETTING) SUN <input type="checkbox"/> VISIBILITY OF STARS <input type="checkbox"/> SKYLIGHT POLARIZATION <input type="checkbox"/> MAGNETIC CUES <input type="checkbox"/> HEAT STRESS DURING FLIGHT <input type="checkbox"/> BREAKFAST AT DESTINATION

MIGRANT BIRD'S CHECKLIST

Fig. 5. Checklist of points of consideration a migrant bird has to consider successively before departing on a long-distance flight. Points indicated with an open circle refer to constraints of energy and water balance, those with squares to navigational considerations. A correct seasonal timing of departures (triangle) is an additional important prerequisite. From Piersma *et al.* (1990) (reprinted with permission).

Sylvia atricapilla. In this species, migratory behaviour varies from resident to long-distance migratory (Cramp, 1992). Like the situation in storks, long-distance migratory blackcaps breeding west of 12° E longitude migrate southwest and those breeding to the east migrate southeast. When reaching Africa, the southeast migrants continue to migrate towards the south and southwest. Orientation studies in blackcaps from eastern Austria have confirmed that the change in migratory direction is innate and coupled to a time programme. In September and October, these birds migrate southeast, and they change migratory direction towards the southwest in November (Helbig, 1991). Consequently, both storks and blackcaps, as well as many other bird species, not only avoid crossing the Mediterranean Sea, but also brush past the inhospitable centre of the Sahara desert.

I have emphasised that migrants locate air layers where both favourable winds and meteorological conditions that conserve water prevail. In addition, birds choose their flight speed depending on the amount of tail wind; with increasing tail wind, air speed is reduced so that available stores for migration are used optimally (Hedenström and Ålerstam, 1995). To reach the optimal altitude, to remain there and to fly at the energetically optimal speed, special navigational skills are required. As long as a bird can assess and integrate its air speed and its position with respect to the ground in all three dimensions, there is no problem. Visual cues can be used during the day, but what do birds use at night or when flying at high altitude? Proposed cues are the change in wind velocity and direction with height (Elkins, 1988), which could possibly be measured by airflow sensors in the wings (Brown and Fedde, 1993), barometric pressure, cloud formation, wind speed at low altitude or the echo of the bird's call *via* the

ground; alternatively, they may orientate with the help of changes in the position of (calling) conspecifics. There are many suggestions but few answers. To predict the optimal behaviour of a migrating bird with regard to its flight path is one thing, but we should of course also wonder with what mechanisms and with what accuracy it can achieve this. For instance, is the variation we observe in flight altitude (Bruderer *et al.* 1995; M. Klaassen and H. Biebach, in preparation) a result of the inability of migrants to find the optimal altitude for migration, or does it reflect inter- and intraspecific variations in optimal flight altitude?

Conclusions

Despite painstaking and highly praiseworthy work conducted by physiologists on flying birds (e.g. Tucker, 1966, 1968; Berger *et al.* 1971; Bernstein *et al.* 1973; Butler *et al.* 1977; Torre-Bueno 1978; Rothe *et al.* 1987), there is little information on how water, energy and protein balance vary with flight speed, altitude, humidity, ambient temperature and the bird's body mass. Much of what we use in models for predicting and explaining the behaviour of migrating birds is based on aerodynamic theory or extrapolated from measurements of birds at rest instead of flying. More empirical data are required and they should be assessed within a sound theoretical framework. The migratory journey not only entails flight but also stop-overs, where fuel loads are replenished. For a proper understanding of migratory behaviour, both migratory flight and refuelling should be integrated. In addition, in explaining the behaviour and physiological design of migrants, one should perhaps be more prudent in assuming that a bird's sensory ability is perfect during migratory flight; the

physiological safety margins of migrants are probably closely related to their navigational skills.

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References

- ALERSTAM, T. (1990). *Bird Migration*. Cambridge: Cambridge University Press.
- ALERSTAM, T. AND LINDSTRÖM, Å. (1990). Optimal bird migration: the relative importance of time, energy and safety. In *Bird Migration: Physiology and Ecophysiology* (ed. E. Gwinner), pp. 331–351. Berlin: Springer-Verlag.
- BECH, C. AND JOHANSEN, K. (1980). Ventilation and gas exchange in the mute swan, *Cygnus olor*. *Respir. Physiol.* **39**, 285–295.
- BERGER, M., HART, J. S. AND ROY, O. Z. (1971). Respiratory water and heat loss of the black duck during flight at different ambient temperatures. *Can. J. Zool.* **49**, 767–774.
- BERNSTEIN, M. H., THOMAS, S. P. AND SCHMIDT-NIELSEN, K. (1973). Power input during flight of the fish crow, *Corvus ossifragus*. *J. exp. Biol.* **58**, 401–410.
- BIEBACH, H. AND KLAASSEN, M. (1994). Is flight range limited by water or energy? *J. Orn.* **135**, 399.
- BROWN, R. E. AND FEDDE, M. R. (1993). Airflow sensors in the avian wing. *J. exp. Biol.* **179**, 13–30.
- BRUDERER, B., UNDERHILL, L. G. AND LIECHTI, F. (1995). Altitude choice by night migrants in a desert area predicted by meteorological factors. *Ibis* **137**, 44–55.
- BUTLER, P. J., WEST, N. H. AND JONES, D. R. (1977). Respiratory and cardiovascular responses of the pigeon to sustained level flight in a wind tunnel. *J. exp. Biol.* **71**, 7–26.
- CARMI, N., PINSHOW, B., PORTER, W. P. AND JAEGER, J. (1992). Water and energy limitations on flight duration in small migrating birds. *Auk* **109**, 268–276.
- CONNELL, C. E., ODUM, E. P. AND KALE, H. (1960). Fat-free weights of birds. *Auk* **77**, 1–9.
- CRAMP, S. (1992). (ed.) *The Birds of the Western Palearctic*, vol. VI. Oxford: Oxford University Press.
- CRAMP, S. AND SIMMONS, K. E. L. (1977). (eds) *The Birds of the Western Palearctic*, vol. I. Oxford: Oxford University Press.
- DAWSON, W. R., YACOE, M. E. AND MARSH, R. L. (1983). Metabolic adjustments of small birds for migration and cold. *Am. J. Physiol.* **245**, R755–R767.
- ELKINS, N. (1988). Can high-altitude migrants recognize optimum flight levels? *Ibis* **130**, 562–563.
- GUDMUNDSSON, G. A. (1993). The spring migration pattern of arctic birds in southwest Iceland, as recorded by radar. *Ibis* **135**, 166–176.
- GUDMUNDSSON, G. A., LINDSTRÖM, Å. AND ALERSTAM, T. (1991). Optimal fat loads and long-distance flights by migrating knots *Calidris canutus*, sanderlings *C. alba* and turnstones *Arenaria interpres*. *Ibis* **133**, 140–152.
- HANSSON, M. AND PETTERSON, J. (1989). Competition and fat deposition in goldcrests (*Regulus regulus*) at a migratory stop-over site. *Vogelwarte* **35**, 21–31.
- HEDENSTRÖM, A. (1993). Migration by soaring or flapping flight in birds: the relative importance of energy cost and speed. *Phil. Trans. R. Soc. Lond. B* **342**, 353–361.
- 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. (1995). Optimal flight speed of birds. *Phil. Trans. R. Soc. Lond. B* (in press).
- HELBIG, A. J. (1991). SE-migrating and SW-migrating blackcap (*Sylvia atricapilla*) populations in central Europe – orientation of birds in the contact zone. *J. Evol. Biol.* **4**, 657–670.
- HUDSON, W. H. (1939). *Far Away and Long Ago*. London: J. M. Dent and Sons Ltd.
- JENNI-EIERMANN, S. AND JENNI, L. (1991). Metabolic responses to flight and fasting in night-migrating passerines. *J. comp. Physiol. B* **161**, 465–474.
- KENDALL, M. D., WARD, P. AND BACCHUS, S. (1973). A protein reserve in the pectoralis major flight muscle of *Quelea quelea*. *Ibis* **115**, 600–601.
- KIRKWOOD, J. K. (1983). A limit to metabolizable energy intake in mammals and birds. *Comp. Biochem. Physiol.* **75A**, 1–3.
- KLAASSEN, M. (1995). Water and energy limitations on flight range in small migrating birds. *Auk* **112** (in press).
- KLAASSEN, M. AND BIEBACH, H. (1994). Energetics of fattening and starvation in the long-distance migratory garden warbler, *Sylvia borin*, during the migratory phase. *J. comp. Physiol. B* **164**, 362–371.
- KLAASSEN, M., KERSTEN, M. AND ENS, B. J. (1990). Energetic requirements for maintenance and premigratory body mass gain of waders wintering in Africa. *Ardea* **78**, 209–220.
- KLAASSEN, M. AND LINDSTRÖM, Å. (1996). Departure fuel loads in time-minimising migrating birds can be explained by the energy costs of being heavy. *J. theor. Biol.* (in press).
- LINDGÅRD, K., STOKKAN, K. A., LE MAHO, Y. AND GROSCOLAS, R. (1992). Protein utilization during starvation in fat and lean Svalbard ptarmigan (*Lagopus mutus hyperboreus*). *J. comp. Physiol. B* **162**, 607–613.
- LINDSTRÖM, Å. (1991). Maximum fat deposition rates in migrating birds. *Ornis Scand.* **22**, 12–19.
- LINDSTRÖM, Å. AND ALERSTAM, T. (1992). Optimal fat loads in migrating birds: a test of the time-minimization hypothesis. *Am. Nat.* **140**, 477–491.
- LINDSTRÖM, Å. AND PIERSMA, T. (1993). Mass changes in migrating birds: the evidence for fat and protein storage re-examined. *Ibis* **135**, 70–78.
- MARSH, R. L. (1983). Adaptations of the gray catbird *Dumetella carolinensis* to long-distance migration: energy stores and blood substrates. *Auk* **100**, 170–179.
- MARSH, R. L. (1984). Adaptations of the gray catbird *Dumetella carolinensis* to long distance migration: flight muscle hypertrophy associated with elevated body mass. *Physiol. Zool.* **57**, 105–117.
- MARSH, R. L. AND STORER, R. W. (1981). Correlations of flight-muscle size and body mass in Cooper's hawks: a natural analogue of power training. *J. exp. Biol.* **91**, 363–368.
- MASMAN, D. AND KLAASSEN, M. (1987). Energy expenditure during free flight in trained and free-living kestrels (*Falco tinnunculus*). *Auk* **104**, 603–616.
- MCLANDRESS, M. R. AND RAVELING, D. G. (1981). Changes in diet and body composition of Canada geese before spring migration. *Auk* **98**, 65–79.
- ODUM, E. P., MARSHALL, S. G. AND MARPLES, T. G. (1965). The caloric content of migrating birds. *Ecology* **46**, 901–904.
- ODUM, E. P., ROGERS, D. T. AND HICKS, D. L. (1964). Homeostasis of the nonfat components of migrating birds. *Science* **143**, 1037–1039.

- PENNYCUICK, C. J. (1975). Mechanics of flight. In *Avian Biology*, vol. 5 (ed. D. S. Farner and J. R. King), pp. 1–75. New York: Academic Press.
- PENNYCUICK, C. J. (1989). *Bird Flight Performance: a Practical Calculation Manual*. Oxford: Oxford University Press.
- PIERSMA, T. (1990). Pre-migratory “fattening” usually involves more than the deposition of fat alone. *Ringing & Migration* **11**, 113–115.
- PIERSMA, T. AND JUKEMA, J. (1990). Budgeting the flight of a long-distance migrant: changes in the nutrient reserve levels of bar-tailed godwits at successive spring staging sites. *Ardea* **78**, 315–337.
- PIERSMA, T. AND VAN DE SANT, S. (1992). Pattern and predictability of potential wind assistance for waders and geese migrating from West Africa and the Wadden Sea to Siberia. *Ornis Svecica* **2**, 55–66.
- PIERSMA, T., ZWARTS, L. AND BRUGGEMAN, J. H. (1990). Behavioural aspects of the departure of waders before long-distance flights: flocking, vocalizations, flight paths and diurnal timing. *Ardea* **78**, 157–184.
- ROTHE, H. J., BIESEL, W. AND NACHTIGALL, W. (1987). Pigeon flight in a windtunnel. II. Gas exchange and power requirements. *J. comp. Physiol. B* **157**, 99–109.
- TORRE-BUENO, J. R. (1978). Evaporative cooling and water balance during flight in birds. *J. exp. Biol.* **75**, 231–236.
- TUCKER, V. A. (1966). Oxygen consumption of a flying bird. *Science* **154**, 150–151.
- TUCKER, V. A. (1968). Respiratory exchange and evaporative water loss in the flying budgerigar. *J. exp. Biol.* **48**, 67–87.
- VON HAARTMAN, L. (1968). The evolution of resident *versus* migratory habitat in birds. Some considerations. *Ornis Fennica* **45**, 1–7.
- WEBER, T. P., ENS, B. J. AND HOUSTON, A. I. (1995). Optimal avian migration: a dynamic model of reserve gain and site use. *Evol. Ecol.* (in press).
- WEBER, T. P., HOUSTON, A. I. AND ENS, B. J. (1994). Optimal departure fat loads and site use in avian migration: an analytical model. *Proc. R. Soc. Lond. B* **258**, 29–34.
- WITTER, M. S. AND CUTHILL, I. C. (1993). The ecological costs of avian fat storage. *Phil. Trans. R. Soc. Lond. B* **340**, 73–92.