The Role of Wind-Tunnel Studies in Integrative Research on Migration Biology

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Synopsis Wind tunnels allow researchers to investigate animals’ flight under controlled conditions, and provide easy access to the animals during flight. These increasingly popular devices can benefit integrative migration biology by allowing us to explore the links between aerodynamic theory and migration as well as the links between flight behavior and physiology. Currently, wind tunnels are being used to investigate many different migratory phenomena, including the relationship between metabolic power and flight speed and carry-over effects between different seasons. Although biotelemetry is also becoming increasingly common, it is unlikely that it will be able to completely supplant wind tunnels because of the difficulty of measuring or varying parameters such as flight speed or temperature in the wild. Wind tunnels and swim tunnels will therefore continue to be important tools we can use for studying integrative migration biology.

Introduction

Animals’ flight has long fascinated researchers and has been studied both for its own sake and as a model for man-made flying machines. Leonardo da Vinci’s early sketches of flying machines, helicopters, and gliders were inspired by observations of birds and bats, as was Otto Lilienthal’s early book on aviation (1889), which stands at the beginning of an astounding progression from early gliders to modern airplanes. While qualitative arguments about the implications of animals’ form and function as adaptations for flight have existed at least since the beginnings of aviation (Headley 1912; Averill 1920; Savile 1957), quantitative mathematical models of birds’ and bats’ flight are relatively recent, with the notable exception of early work by Walker (Walker 1925, 1927).

Wind tunnels have been an important source of information about the biomechanics and physiology of animals’ flight, because they allow for detailed observations of flight in the controlled environment of a laboratory. Based on studies in wind tunnels, Pennycuick (1968a, 1975, 1989) and Greenewalt (1975) each developed mathematical models that described the flapping flight of birds; a separate, purely theoretical model (Rayner 1979) was created in response to these. These models have contributed enormously to our understanding, not only of animals’ flight, but also of ecological phenomena, such as migration and foraging, that require trading off costs of activity with some other “currency”.

The most important ecological “currencies” that animals have to trade-off during migration in order to maximize fitness are arguably time, energy, and safety (Alerstam and Lindström 1990). The conceptual frameworks of optimal migration theory and optimal foraging theory (Norberg 1981; Alerstam and Lindström 1990; Hedenström and Alerstam 1995; Weber et al. 1998) make predictions about animals’ optimal behavior, based on the dependence of energetic costs of flight on body mass and on flight speed, while considering competing physiological and behavioral necessities. These frameworks highlight the inter-connection of physics, physiology, and behavior. To make predictions about how animals “should” behave, we need knowledge about
their physiological and behavioral capabilities, and we need a detailed understanding of the underlying aerodynamic principles of flight. An impressive body of publications on flight of vertebrates has emerged in the past couple of decades. The goal of this article is to give an overview of how wind tunnels have contributed to our understanding of various aspects of animal flight, ranging from biomechanics to energetics and thermoregulation, and to bring these lines of research together in an integrative view of a highly complex phenomenon: animal migration. While wind tunnels are equally suitable for the study of the flight of birds, bats, or insects, and the conceptual framework may be applicable to swimming migrants in flow tanks, we are most familiar with the avian literature and therefore restrict our discussion largely to birds.

**Wind tunnels**

It is not easy to obtain physiological or kinematic data from a flying animal, and the approaches to this problem are continuously changing as technology improves (Robinson et al. 2010). One of the earliest estimates of metabolic rates during flight was derived from the mass lost during a long flight in the wild and the assumption that fat constituted most of this loss (Nisbet et al. 1963). Later, doubly-labeled water was used to measure the energetic cost of flight, sometimes in combination with time–energy budgets (LeFebvre 1964). With the development of biotelemetry, satellite transmitters, and data loggers, it became possible to obtain physiological, behavioral, and atmospheric measurements during free flight (Bowlin and Wikelski 2008; Cochran et al. 2008). Provided the transmitters or loggers are small compared to the animals’ body size, one can obtain data from animals in their natural environment during their normal activities. Such data are hard to obtain otherwise. Despite these advantages, such studies face considerable technical challenges and suffer from the fact that most such devices measure only one or a few parameters; as a result many aspects of the animal’s behavior and the conditions during flight are not known. Furthermore, it is not possible to experimentally control some parameters, like ambient temperature or flight speed.

Therefore, researchers have long taken advantage of the idea of having animals fly in a restricted space under controlled conditions—e.g., in a wind tunnel. The function of a wind tunnel is to create a stable, and ideally, laminar air flow. The flying animal moves relative to this air stream but remains stationary in space, which allows for detailed observation, videography, or the attachment of measuring equipment such as respiration masks. Furthermore, the wake that a flying animal leaves behind, very much like a “footprint” in the air, can be visualized using digital particle image velocimetry or similar systems that track small particles in the air. The first attempts to have a bird fly in a wind tunnel were probably those of Greenewalt (1961), who put a feeder for hummingbirds directly downstream of an electric fan. The flight speed of the bird could be controlled by adjusting the speed of the fan. Since the 1960s, a number of wind tunnels have been constructed in various laboratories to study the aerodynamics and physiology of animals’ flight; perhaps as a result, the number of studies using wind tunnels has increased continuously since then (Fig. 1). Early studies involving wind tunnels used open-circuit tunnels that consisted of a fan that accelerated air through a contraction chamber into a test section where the animal was placed. Depending on whether the fan was located upstream or downstream of the contraction chamber, the wind tunnel could be classified as a “suction” type or a “blower” type. The design of this type of wind tunnel is simple and the costs of building one are low (Mehta and Bradshaw 1979), but the resulting flow of air is non-uniform (i.e., it is turbulent). A closed-circuit design, in which the air constantly re-circulates, can create a more uniform flow than suction or blower tunnels; for example, the closed-circuit wind tunnel at Lund University has an average turbulence level of ~0.04–0.06% (Pennycuick et al. 1997), three different open-circuit wind tunnels have turbulence levels

![Fig. 1 Frequency histogram of papers published on the flight of birds and bats in wind tunnels (N = 252). Histogram is based on a search of the ISI Web of Science database, using the keywords “wind tunnel” and “flight” and either “avian”, “bird*”, or “bat*”. Results which were only conference abstracts (N = 25) were manually excluded from the search.](image-url)
of approximately 0.3–0.5%, 1.10%, 15 and 2.3%, respectively [Saarland University wind tunnel, data from Rothe and Nachtgall (1987), turbulence factor converted into approximate turbulence level using Barlow et al. (1999); Harvard University wind tunnel, Hedrick et al. (2002); Duke University wind tunnel, data from Tucker and Parrott (1970), turbulence factor similarly converted]. No systematic study has been carried out on the effects of turbulence on the results of wind-tunnel experiments on birds, but turbulence may increase the energy expenditure of flying birds (Bowlin and Wikelski 2008) and turbulence represents a source of error in flow-visualization studies. However, closed-circuit wind tunnels are also much more space-intensive and cost-intensive than open-circuit tunnels, and much thought is needed to design a tunnel with good flow characteristics (Pennycuick et al. 1997). These requirements are often prohibitive, and to date only a handful of closed-circuit wind tunnels have been designed specifically to study animals’ flight. However, these tunnels have advanced our understanding enormously due to the stable air flow inside.

It is also possible to construct wind tunnels that can be tilted (Pennycuick et al. 1997), thereby allowing researchers to study climbing and/or descending flight. Bruderer et al. (2001), for example, used such a tilting mechanism to study the behavior and kinematics of barn swallows as they climbed, descended, and made level flights in a wind tunnel. Tilted tunnels have also been used to study the lift-to-drag ratios of gliding birds (Pennycuick 1968b; Tucker and Heine 1990; Tucker and Parrot 1970; Rosén and Hedenström 2001), which determine performance in cross-country soaring migration. Finally, we can use tilted wind tunnels to estimate the partial efficiency of flight (Tucker 1972; Bernstein et al. 1973). These measurements are the origin of the universal use of 0.23 as a value for the conversion efficiency of energy during birds’ flight (Pennycuick 1975).

**Linking physics and physiology**

In steady flight, the average lift and thrust forces are in equilibrium with weight and drag (because there is no acceleration). To generate these forces, the animal must flap its wings. Throughout the wing-beat cycle the aerodynamic forces vary, but the mean forces (lift = vertical force, and thrust = horizontal force) taken over an entire wing beat are constant in steady flight. A reduction of negative thrust (drag) from the upstroke is achieved by an asymmetry between the downstroke and the upstroke, either by flexing the wing to reduce the span during the upstroke or by adjusting the angle of attack to control the production of lift. The mechanics of bird flight were described during the 1960s (Pennycuick 1968a; Tucker 1968), with two fundamental results that especially pertain to animal migration. These are the so-called “power curve” and the “range-curve”, respectively.

The power curve describes the relationship between the mechanical power ($P_{mech}$) required to fly and the flight speed relative to the air (airspeed, $U$), and is calculated as the sum of the main three drag coefficients and airspeed as

$$P_{mech} = U(D_{ind} + D_{par} + D_{pro}),$$

where $D_{ind}$ is the induced drag, $D_{par}$ is parasite drag, and $D_{pro}$ is profile drag. For a recent treatment of the derivation of the different drag components, see Pennycuick (2008). Induced drag results from the generation of lift, i.e., the creation of an induced downwash and wing tip vortices, parasite drag is the drag of the body, and profile drag is the drag from the flapping wings. Each component of drag varies in relation to speed, but in different ways, where $D_{ind}$ is proportional to $U^{-1}$, $D_{par}$ is proportional to $U^2$, and $D_{pro}$ remains relatively constant in the region of typical flight speeds. The resulting relationship between $P_{mech}$ and $U$ is U-shaped. A U-shaped power curve is a cornerstone of optimality models that predict, for example, the behavior of migrating animals (Norberg 1981; Alerstam and Lindström 1990; Hedenström and Alerstam 1995). While aerodynamic models predict mechanical-power requirements, living organisms expend and trade off metabolic energy, of which only a small fraction can actually be converted to mechanical power by the flight muscles. It is not yet clear how metabolic costs relate to mechanical costs. Often, a fixed conversion efficiency $\eta$ that relates the whole animal’s metabolic rate ($P_{met}$) and the power it requires for flight as $P_{mech} = \eta P_{net}$ is assumed to be in the range of 18–23% (Norberg 1996; Ward et al. 2001). Aerodynamic models are thus extended to predict metabolic flight costs instead of mechanical power requirements.

Metabolic flight costs varying with speed in a U-shaped manner imply several ecologically significant flight speeds, most importantly the minimum power speed $U_{mp}$, which minimizes the power per unit flight time, and the maximum range speed $U_{mr}$, which minimizes power per unit distance travelled (Fig. 2). Birds are predicted to choose one or the
other of these speeds depending on their task (Norberg 1981; Pennycuick 1978; Hedenström and Alerstam 1995; Hedenström 2002). This body of theory has inspired many studies, both in the field and in the laboratory, and while some field measurements of flight speeds in various life-history contexts have supported predictions based on aerodynamic models, at least qualitatively (Hedenström and Alerstam 1995; Bruderer and Boldt 2001), others have offered only partial support (Henningsson et al. 2009). Several hypotheses may explain the mismatch between predictions and empirical field measurements: false theoretical prediction of metabolic flight costs, a shallow power curve, or that birds are weighing time and energy costs differently than assumed. Only an experimental determination of the power curve for each species, which must be done in a wind tunnel, can distinguish between these hypotheses.

A number of efforts have been made to measure the power-versus-speed relationship of birds in wind tunnels (Table 1) and to test whether the empirical measurements of power reflect the expected U-shape of the relationship (Equation 1) or not. Although the number of species studied is low, they represent a sizeable fraction of the avian phylogenetic spectrum. The studies can be divided into three categories: (1) measurements of mechanical power or muscle power using the work-loop approach (Tobalske 2007), (2) measurements of metabolic rate using a respirometry mask, and (3) measurements of metabolic rate of unrestrained birds using respirometry (where the whole wind tunnel is sealed and used as a respirometry chamber) or doubly labeled water. The studies in which muscle power was measured in relation to speed show U-shaped relationships (Table 1) with one possible exception (Dial et al. 1997), and one study about mechanical-power output only found an increase in power with speed (Pennycuick et al. 2000). The latter may be a result of the limited range of speeds investigated, which would have excluded the lower part (<U_{mp}) of the curve. Taken together, the predicted U-shaped relationship between power and speed does appear in those studies measuring a quantity closely related to mechanical-power output, which is strictly the topic about which the theory makes predictions (Equation 1).

In some situations, including migratory flight, however, natural selection is more concerned with metabolic power than with mechanical power, and at first glance the metabolic relationships seem more equivocal (Table 1). This has led some to argue that there is no U-shaped metabolic power curve, at least for migratory birds (Chernetsov 2010). However, this is not the case. Of the 15 investigations of the relationship between metabolic power and flight speed (Table 1), five showed a clear U-shaped curve, and six showed an increase at higher speeds. Four are truly flat. The most likely explanation for the different results is the range of flight speeds investigated. The range of speeds at which animals will fly in a wind tunnel appears limited compared to free flight, especially in the upper range (Liechti and Bruderer 2002; Henningsson et al. 2009). Speeds during flights in wind tunnels may therefore represent only the shallow, middle part of a power curve, and are truncated at both the lower and upper ends. Supporting this idea, the average range of speeds in the studies that found a U-shaped curve (Table 1) was 9.1 ms^{-1}, while those showing an increase had an average range of 6.4 ms^{-1}. Three of the four studies showing flat curves examined a range of speeds of 5 ms^{-1} or less, although one did investigate a range of 10 ms^{-1} and still found no increases in power with speed (Torre-Bueno and Larochelle 1978). We encourage future researchers to investigate as wide of a range as possible; only then will we know if the curves that have been described as flat are truly so. Regardless, the existing data cannot be used to refute the existence of a U-shaped metabolic power-speed relationship in bird flight since the majority of studies show a U-shaped curve or an increase in power with speed, and we can conclude that the mechanical theory of bird flight remains a useful concept. Why animals refuse to fly at slower or faster speeds in wind tunnels is still unclear. It has been suggested that this truncation may come about through
metabolic limitations, such that birds are already flying at their maximum metabolic rate at intermediate speeds. However, several studies have reported relatively low metabolic costs of flight in wind tunnels: flight costs of budgerigars measured by Bundle et al. (2007) and Tucker (1968) were lower than those measured previously under highly turbulent conditions (Tucker 1966), suggesting that their range of speeds in the later studies was not set by aerobic limits. Similarly, Epting (1980) reported dramatically increased metabolic rates for hovering hummingbirds that had lost wing feathers due to molt compared to similar flights in which their plumage was intact. The absence of a consistent relationship between limitation of performance in a wind tunnel and otherwise measured, or predicted, maximum metabolic rates suggests that nonmetabolic factors are involved in setting the limits of accepted speeds during flights in wind tunnels.

One reason we do not always find clear, U-shaped metabolic power curves may be that metabolic power curves are not necessarily a fixed multiple of mechanical power curves (Rayner 1999). It is possible that the efficiency ($\eta$) at which metabolic power is converted into mechanical power is not constant; $\eta$ is one of the least understood parameters of animal flight, and is not easily measured. Estimates for $\eta$ in birds range from 3% to 33% (Videler 2005). Based on measured $P_{\text{met}}$ and theoretically predicted $P_{\text{mech}}$ at zero and medium flight speed, Norberg et al. (1993) estimated values for $\eta$ of 11–15% for bats.

Within an individual bird, efficiency may increase with body mass (Kvist et al. 2001; Alexander 2005; Schmidt-Wellenburg et al. 2008a), and it may change with flight speed as well (Hudson and Bernstein 1983; Ward et al. 2001; Bundle et al. 2007), which could explain observed discrepancies between predicted $P_{\text{mech}}$ and measured $P_{\text{met}}$. A physiological mechanism responsible for modulating $\eta$, however, is still elusive, and it is not clear why animals should prefer to fly at intermediate speeds in wind tunnels if these are indeed the speeds of least efficiency.

### Table 1 Summary of studies examining the relationship between power and speed in birds

<table>
<thead>
<tr>
<th>Species</th>
<th>Method</th>
<th>Actual range (ms$^{-1}$) (Absolute range)</th>
<th>$U_{\text{mp}}$</th>
<th>Shape</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Branta leucopsis</td>
<td>Rm</td>
<td>15–17 (2)</td>
<td>–</td>
<td>/</td>
<td>Ward et al. (2002)</td>
</tr>
<tr>
<td>Anser indicus</td>
<td>Rm</td>
<td>18–21 (3)</td>
<td>–</td>
<td>—</td>
<td>Ward et al. (2002)</td>
</tr>
<tr>
<td>Colibri coruscans</td>
<td>Rm</td>
<td>0–11 (11)</td>
<td>7</td>
<td>—, /</td>
<td>Berger (1985)</td>
</tr>
<tr>
<td>Colibri thallasinus</td>
<td>Rm</td>
<td>3–11 (8)</td>
<td>3–7</td>
<td>—, /</td>
<td>Berger (1985)</td>
</tr>
<tr>
<td>Calypte anna</td>
<td>Rm</td>
<td>0–14 (14)</td>
<td>5.7</td>
<td>U</td>
<td>Clark and Dudley (2009)</td>
</tr>
<tr>
<td>Melopsittacus undulatus</td>
<td>Rm</td>
<td>5–14 (9)</td>
<td>9.7</td>
<td>U</td>
<td>Bundle et al. (2007)</td>
</tr>
<tr>
<td>Nymphicus hollandicus</td>
<td>Rm</td>
<td>5–15 (10)</td>
<td>9.8</td>
<td>U</td>
<td>Bundle et al. (2007)</td>
</tr>
<tr>
<td>Anser indicus</td>
<td>M</td>
<td>1–14 (13)</td>
<td>5</td>
<td>U</td>
<td>Tobalske et al. (2003)</td>
</tr>
<tr>
<td>Columbo livia</td>
<td>Rm</td>
<td>8–14 (6)</td>
<td>10.6</td>
<td>U</td>
<td>Rothe et al. (1987)</td>
</tr>
<tr>
<td>Streptopelia risoria</td>
<td>M</td>
<td>1–17 (16)</td>
<td>7</td>
<td>U</td>
<td>Tobalske et al. (2003)</td>
</tr>
<tr>
<td>Larus atricilla</td>
<td>Rm</td>
<td>6–12.5 (6.5)</td>
<td>–</td>
<td>/</td>
<td>Tucker (1972)</td>
</tr>
<tr>
<td>Sturnus vulgaris</td>
<td>R</td>
<td>8–18 (10)</td>
<td>–</td>
<td>—</td>
<td>Torre-Bueno and Larochele (1978)</td>
</tr>
<tr>
<td>Sturnus roseus</td>
<td>DLW</td>
<td>9–14 (5)</td>
<td>–</td>
<td>—</td>
<td>Engel et al. (2006)</td>
</tr>
<tr>
<td>Corvus ossifragus</td>
<td>Rm</td>
<td>7.4–11 (3.6)</td>
<td>–</td>
<td>—</td>
<td>Bernstein et al. (1973)</td>
</tr>
<tr>
<td>Corvus cryptoleucus</td>
<td>Rm</td>
<td>8–11 (3)</td>
<td>–</td>
<td>/</td>
<td>Hudson and Bernstein (1983)</td>
</tr>
<tr>
<td>Pica pica</td>
<td>M</td>
<td>0–14 (14)</td>
<td>6</td>
<td>, — (U)</td>
<td>Dial et al. (1997)</td>
</tr>
<tr>
<td>Hirundo rustica</td>
<td>Mech</td>
<td>6–11 (5)</td>
<td>6</td>
<td>/</td>
<td>Pennycook et al. (2000)</td>
</tr>
<tr>
<td>Taenopygia guttata</td>
<td>M</td>
<td>4–16 (12)</td>
<td>9</td>
<td>U</td>
<td>Askew and Ellerby (2007)</td>
</tr>
</tbody>
</table>

*Explanation of symbols: Rm, respirometry with mask attached to the bird; R, respirometry using the whole wind tunnel as chamber; M, work loop estimated from muscle work using either strain gauges and sonomicrometry or strain gauges and kinematics; Mech, mechanical power output calculated from muscle work as determined by stereo-videography of reference points on the bird’s body; DLW, doubly labeled water. Functional relationship between power required to fly and flight speed, where U is a U-shape, — is a flat relationship, / is an increasing relationship, \ is a decreasing relationship. Combinations of \, /, and — are used to describe composite relationships.*
A possible way to vary efficiency is through changes in kinematics. Some smaller species of bird, in particular, may reduce the mechanical power requirements of flight by flap-gliding at low speeds and by flap-bounding at high speeds (Ward-Smith 1984), which may allow the muscles to work near optimal contractile velocities. Starlings and budgerigars seem to use intermittent flight styles consistent with these predictions (Tobalske and Dial 1994; Tobalske 1995), a behavior that may potentially flatten their power curves. The metabolic flight costs of starlings are in fact almost constant over the range of speeds measured (Torre-Bueno and Larochelle 1978). Budgerigars, on the other hand, always display a U-shaped curve consistent with aerodynamic predictions (Tucker 1968; Bundle et al. 2007). However, all three metabolic studies on budgerigars used mask respirometry, which seemed to affect their flight style, because the animals rarely used intermittent flight while wearing a mask (Bundle et al. 2007). It remains unclear whether such mask-related kinematic responses alone can explain the apparent differences between U-shaped and flat power-to-speed relationships in birds.

While we understand aerodynamic principles, biomechanics, and energetics reasonably well on their own, less is known about how these aspects are functionally connected. Given the ecological significance of metabolic power curves, comparative attempts to quantitatively link the energetics and mechanics of flight will address considerable gaps in our understanding of the biology of avian flight. The most direct link between measurements of mechanical and metabolic power may be muscle strain, because it directly measures mechanical power output of the muscles moving the wing and imparting momentum to the air (Pennycuick 1989) and can be linked to metabolic power through muscle physiology. Wind-tunnel measurements of flight costs, in combination with muscle physiology (Askew and Ellerby 2007; Ellerby and Askew 2007), therefore seem to be a promising approach to bridge the gap between physics and the physiology of flight and should allow us to gain a better understanding of how metabolic power is converted into muscle power.

**Use of fuel and the range equation**

The second fundamental relationship of optimal migration theory is the range equation, which is derived from the Breguet equation (Pennycuick 1975; Alerstam and Hedenström 1998), and gives the potential flight range given a specified amount of fuel. To fuel their long migratory journeys, birds predominantly use fat (Jenni and Jenni-Eiermann 1998; Jenni-Eiermann et al. 2002), and it is not uncommon for many bird species to double their body mass in preparation for long nonstop flights. Additional fuel not only increases a bird’s flight range, but also increases costs. A general format of the range equation is

\[
Y = c \ln(1 + f)
\]

where \(c\) is a constant including a number of physical and physiological parameters, and \(f\) is the fuel load relative to the lean body mass \(m_0\). Depending on whether added fuel increases the drag on the body or not, the potential flight range of an animal can be calculated from Equation 2 without added body drag or from an alternate equation with added body drag (Alerstam and Hedenström 1998), but the overall characteristic is a function of diminishing return (Fig. 3). The range equation implies that flight costs should decline over the course of a long flight as fuel mass is consumed and the bird becomes progressively lighter and lighter. The decrease in body weight throughout a flight depends not only on the consumption of energy, but also on the composition of fuel that was used to produce this energy. Although fat is the primary source of energy in flying birds, about 5–10% of the energy is derived from proteins (Klaassen et al. 2000; Jenni-Eiermann and Jenni 2003). Wet protein is about 10 times less energy dense than fat; therefore, the exact contribution of protein to the total production of energy during flight will have a relatively large effect on the loss of mass and the flight range.

![Fig. 3 Schematic graph of the relationship between flight range and fuel load (f) relative to lean body mass. Optimal fuel loads for migrating animals may be predicted on the basis of this range curve. Its shape depends on whether fuel load affects flight costs through increased body mass alone, or through additionally increasing drag (see text). Measurements of lift to drag ratios in wind tunnels may help distinguish between these two scenarios.](image)
that can be achieved by a given amount of fuel. The range curve is important for predicting migration strategies regarding, for example, duration of stopovers and fuel loads at departure. Migrants facing an ecological barrier likely base their decision of whether to accumulate fuel reserves for a crossing, or to carry fewer endogenous reserves and make a detour, on the marginal gain in range per additional unit fuel (Alerstam 1991). An example of how this framework can be applied to correctly predict the migration route of Nathusius's bats (Pipistrellus nathusii) around the Baltic Sea has been presented by Hedenström (2009).

The exact shape of the range curve depends on whether fuel load affects only the body mass of the animal (in which case it needs to produce greater lift to remain airborne) or the body mass and frontal area (in which case it needs to overcome higher drag forces as well). If only body mass is affected, the effective lift:to drag ratio (L:D) is constant and independent of fuel load and total body mass. If frontal area is affected, effective L:D should be proportional to \( m^{1/2} \) (Alerstam and Hedenström 1998). Although it is difficult to measure drag in a flying animal, especially during flapping flight, some studies in wind tunnels have succeeded in determining effective L:D for small birds (Hedenström et al. 2005; Tobalske et al. 2009; Henningsson et al. 2010). Whether, and how, effective L:D varies with body mass is not known.

Fat accumulated in preparation for migratory flights may affect migration in yet another way: there are indications that certain essential polyunsaturated fatty acids enhance exercise performance (Maillet and Weber 2007) and thus the distance that can be fueled by a given amount of fat. By choosing their diet with regard to fatty-acid composition and through metabolic routing, animals can influence the composition of endogenous fat reserves (Podlesak and McWilliams 2007). In a study on captive red-eyed vireos, Pierce (Pierce et al. 2005) showed that mass-specific peak metabolic rate during short, but very intense, exercise was higher in birds that had been fed relatively more monounsaturated fatty acids than in those on a diet with more polyunsaturated fat. Similarly, during prolonged flights in wind tunnels, rose-colored starlings that had accumulated body fat from a diet rich in monounsaturated fatty acids had higher energetic flight costs than did birds that were fed more polyunsaturated fat (McWilliams et al. 2008). We are only beginning to understand the physiological processes involved in the differential use of lipids, but the implications for migratory animals are potentially immense. Because wind tunnels provide easy access to animals during flight, they have the potential to be an invaluable tool in future studies of this nature.

The role of water in migration

Optimal migration theory suggests that three factors shape the physiology and behavior of actively migrating animals: time, energy, and safety (Alerstam and Lindström 1990). Predictions regarding migration strategy or duration of flight are therefore usually based on calculations trading off energy with some other currency (often time). Modeling approaches, however, have suggested that dehydration with its associated risks may be equally crucial under certain ambient conditions (Carmi et al. 1992; Klaassen 1995). Although a wind-tunnel study on red knots demonstrated that the experimental birds were in water balance even after prolonged flights (Jenni-Eiermann et al. 2002), measurements of water flux during the flight of pigeons (Columba livia) and rose-colored starlings (Sturnus roseus) suggest that dehydration may be a real risk for some species (Adams et al. 1997; Engel et al. 2006).

Little is known about dehydration rates in the field. Availability of water at stopover sites seems to increase refueling rates (Tsurim et al. 2008), and passerines appeared to be dehydrated after a long non-stop flight over the Gulf of Mexico (Leberg et al. 1996). On the other hand, ambient conditions during even nocturnal trans-Sahara flights are often in a range that would invoke dangerously high dehydration rates for small passerines according to our current knowledge (Schmaljohann et al. 2008), but these birds routinely and successfully cross the desert.

Looking beyond the flight period

Much of the research on animals in wind tunnels has focused on flight itself. This research may have important implications for migrants, but often the connections are tenuous or unclear. The physiological studies discussed below, however, have directly impacted our understanding of migration. We encourage researchers focusing on animal flight to also consider their results in the context of migration.

The most obvious advantages of wind tunnels are the ability to control ambient conditions and the accessibility of the experimental animal. This has made wind tunnels indispensable tools for research into bird flight, and we owe much of our understanding regarding flight physiology or biomechanics to development of this technique. However, the
potential of wind-tunnel studies goes beyond the flight period and allows us to ask broader questions such as about the role of migration in an individual’s life, including carry-over effects (the effects of one life-history stage on another) of flight on other life-history stages. Breeding, molt, wintering, and flight are all integral parts of many migrants’ life-cycles, and animals may trade off success during one event with success during another. For example, does flight have fitness costs in terms of impaired immune function? How do birds fit the need to molt into their annual routine? How do long flights affect subsequent breeding success? These are all questions for which wind-tunnel studies have provided important insights.

For example, two studies have explored the effects of prolonged flight in wind tunnels on various aspects of the immune system (Hasselquist et al. 2007), and on corticosterone, the avian stress hormone (Jenni-Eiermann et al. 2009). Neither humoral immunity nor responses to phytohemagglutinin (which measures a combination of cell-mediated immunity and innate immunity; Martin et al. 2006a), differed between birds forced to fly long distances in the wind tunnel and birds that did not fly. However, eco-immunologists often obtain negative results when examining just a few immunological parameters, even if there is a trade-off between the immune system and the variable in question, simply because there are so many different aspects of the immune system and they can, and do, vary independently (Martin et al. 2006b). Thus, there may still be a relationship between long-distance flight and various aspects of immunity, but we will not know until further experiments are performed.

In an attempt to link stress hormones and long-distance flights Jenni-Eiermann et al. (2009) found no change in baseline concentrations of corticosterone (CORT) during or after long flights, but did find a decrease in stress-induced CORT following the flights. They argued that this decrease was adaptive, in that it would decrease proteolysis following flights, although it was not clear why circulating CORT would not then be higher in actively flying individuals than in controls, thereby encouraging proteolysis. Furthermore, a follow-up study (Falsone et al. 2009) on birds caught during natural migration failed to corroborate the results of Jenni-Eiermann et al. (2009). Further research may be able to identify the reason(s) for the discrepancies between the two studies. Another issue with both of the above wind-tunnel studies is that they were performed on a single species. Other species may trade-off the energetic costs of long-distance flight and immunity or adrenocortical responses differently.

Immunology and stress responses are not the only variables that may trade-off costs and benefits with long-distance flight. Birds periodically replace their feathers, because these structures become worn and damaged through contact with the environment (Weber et al. 2005). However, feathers make up most of the surface area of birds’ wings, suggesting a potential conflict between the benefits of having new feathers and the costs of flying with missing wing feathers while undergoing molt. Molting strategies—when to replace feathers, how many feathers to drop at one time, how quickly to re-grow feathers, the sequence in which wing feathers are molted, and how many and which feathers to replace during a particular molt—are almost as diverse as the avian clade itself (Jenni and Winkler, 1994). Many migratory birds, however, undergo molting of the wing feathers just prior to autumnal migration. Most of these species must maintain their ability to fly in order to forage, not only for self-maintenance and to replace the nutrients lost in their shed feathers but also to obtain fuel for migration. The demands of these two life-history events can therefore clash, and molting strategies can affect the evolution of migration strategies and vice-versa.

How these two life-history stages will affect one another depends on the relative costs and benefits of each; in particular, the effects of molt on the early stages of migration, when birds are trying to store fuel, will depend on the aerodynamic costs of molt. These metabolic and efficiency costs can be quite high in hummingbirds (Chai 1997; Chai and Dudley 1999), but the only other study to investigate the metabolic costs of flight to date, during real or simulated molt (Bridge 2003), found no effect of molt on metabolic costs. We are currently investigating the aerodynamic costs of molt using digital particle image velocimetry (DPIV), a method that visualizes the vortex wake left behind a flying animal, and which allows us to calculate the forces the animal exerts on the air (Spedding 2003). We are searching for any increased drag due to the presence of experimental and natural molt gaps; we can then use these measurements to estimate any increased energetic costs associated with flight during molt. So far, we have found that the presence of molt gaps does significantly increase drag, which will in turn increase the birds’ expenditure of energy (Bowlin et al., unpublished data). Although these results are not surprising, our data allow us to quantify these effects in a way that has not been possible before—and would not be possible at all with
free-flying birds. Using methods like these, we can begin to tease apart the consequences of variation in molting strategies and relate these consequences to the migratory strategies of avian species. Just as molt and migration may affect one another, with its high energy demands, can influence subsequent reproductive success through effects on body condition, including the extent of endogenous energy stores and differential organ reduction during prolonged flights (Biebach 1998; Battley et al. 2001). Birds arriving earlier on the breeding grounds often have a higher reproductive success than do late-arriving birds (Smith and Moore 2005), but so far, we know little about whether and how the flight workload during migration itself influences reproduction. The costs of migration in spring may negatively affect body condition or trade-off with preparations for breeding, such as the development of primary and secondary sexual traits. To our knowledge, only one study has experimentally approached carry-over effects of flight on subsequent breeding success, albeit with inconclusive results (Schmidt-Wellenburg et al. 2008b).

Thus, even though wind tunnels are specialized tools for studying avian flight, we can use them to understand migration in the context of the annual cycle, an important ‘grand challenge’ in migration biology (Bowlin et al. 2010). Using wind tunnels, we can vary the duration and speed of flights and determine what effects those flights have on the animals.

**Is flight in wind tunnels representative of free flight?**

We do not yet know how laboratory studies in wind tunnels (or, in the case of terrestrial animals and swimming animals, on treadmills and in swim tunnels, respectively) compare to natural conditions. The fact that animals in laboratory conditions have to move in a restricted space at a set velocity may affect their kinematics. They must also tolerate the noise of motors and move in an optically motionless and monotonous environment (although this can be fixed by projecting motion onto the walls and/or floor; Butler et al. 1977; Rothe and Nachtigall 1987). To what extent these factors affect the flight performance of birds in a wind tunnel is hard to quantify or even qualitatively judge, not only due to the difficulties of direct comparisons between free-flight and flight in a wind tunnel, but also due to variation in the design of the wind tunnels that have been used for studies of bird flight. One compilation of studies measuring metabolic flight costs of birds suggested that flight in wind tunnels is generally more energetically costly than free flight (Masman and Klaassen 1987), but early studies in wind tunnels were likely hampered by high levels of turbulence and often involved the birds carrying measuring equipment like respiratory masks. More recent studies have suggested that metabolic flight costs in wind tunnels (Bowlin, Meijer, and Wikelski, unpublished data) are similar to those during free flight (Wikelski et al. 2003).

One of the few direct comparisons of free flight to flight in wind tunnels showed that wing-beat frequencies (WBF) of swallows (Hirundo rustica) and house martins (Delichon urbica) in free flight are lower than they are during flight in wind tunnels (Liechti and Bruderer, 2002). The authors assumed that WBF relates directly to flight costs, in which case wind-tunnel flights are energetically more costly than free flight. Unfortunately, we still lack a clear understanding of how any kinematic measurement, including WBF, relates to metabolic power output (Park et al. 2001).

**Concluding remarks**

Wind tunnels, with their controllable ambient conditions such as speed, sink rate, climb rate, temperature and, in the case of one new wind-tunnel facility, even pressure (http://birds.uwo.ca), will probably remain the only practical tools for studies on the aerodynamics and biomechanics of animal flight in the near future; physiological research on animals in flight will also largely continue to rely on measurements in wind tunnels. Following the trend of the past few decades, we expect the number of wind tunnel studies to increase (Fig. 1). However, the interpretation of results from wind-tunnel studies within an ecological context is hampered by the fact that we know little about how wind tunnels change the behavior and performance of our experimental animals; we therefore encourage researchers to explore this topic.

With the constant refinement of field-deployable techniques such as accelerometry (Wilson et al. 2006), microphone transmitters (Cochran et al. 2008) and heart rate transmitters (Bowlin et al. 2005; Cochran and Wikelski 2005), direct comparisons with free flight in the wild have become possible and will probably become even easier in the future. Tools like data loggers, radio-transmitters, or satellite tracking are readily available nowadays, and in many cases small enough to be placed on small migrants. Never before have there been more opportunities to test the predictions from theoretical models or to compare natural migration with flight...
in wind tunnels. It is time to look beyond flights in wind tunnels as such and to study the interconnection of flight with other physiological processes and necessities, such as carry-over effects. Such studies will eventually help us integrate knowledge from a wide range of disciplines and to attain a more holistic view of animal migration as one life-history stage embedded in the life-cycle of a species.

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