How might turbulence affect animal flight in a changing world?

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Abstract

The influence of wind on animal flight costs and flight decisions is well established. Far less is known about the effects of turbulence. Here, I briefly assess naturally occurring and anthropogenic drivers of turbulence, before considering how turbulence affects the metabolic costs of flight and how animals might respond in the wild. Turbulence has a measurable effect on flight costs when eddy diameter is similar to the wingspan. The few metabolic data on this show that turbulence can cause a 25-100% increase in flight costs, similar to that caused by moderate to strong headwinds. The ability to meet the costs of flying in turbulence should decrease with increasing body mass, following the reduction in available power (which also limits the range of possible flight speeds). More data are therefore needed on the metabolic costs of flight in relation to eddy characteristics (e.g. length scale and velocity), flight speed and morphology. This is pertinent since turbulence is ubiquitous in the natural environment and could influence the energy expended across flying animals. Anthropogenic activity is changing the nature, strength and distribution of turbulence, with the built environment and wind farms both typified by high turbulence intensities. In fact, the marked and consistent avoidance of offshore wind farms by large birds is consistent with an avoidance of turbulence, and analysis of flight trajectories in relation to the development of the far-wake region could provide new insight into the proximate and/ or ultimate drivers of avoidance.

Summary statement: Turbulence is ubiquitous yet we know little about how it affects animal flight costs and decisions. This matters as anthropogenic activity is changing its distribution and magnitude.

Keywords: boundary layer, aeroecology, gusts, wind farm, offshore wind, metabolic rate.

Introduction

“Turbulent motion is the natural state of most fluids” (Davidson, 2015).

The aerial environment profoundly impacts the energy required to fly and the speed at which animals cover ground (i.e. the groundspeed) (Tucker, 1966, Furness and Bryant, 1996, Chapman et al., 2011). Animals adjust their behaviour accordingly, modifying their flight routes, timings, speed, and potentially their flight mode (e.g. flapping or gliding) in relation to airflows (Sapir et al., 2014, Sapir et al., 2011, Bohrer et al., 2011). Flying animal responses to wind and updrafts are relatively well understood (e.g. Thorne et al., 2023, Pennycuick, 2008). Far less is known about the effect of turbulence on animal flight (Ortega-Jimenez et al., 2016, Combes and Dudley, 2009). This is an important knowledge gap, as human activities are introducing turbulence at multiple scales e.g. through habitat modification, infrastructure projects, such as wind farms, which can cover several thousand square kilometres, and large-scale atmospheric changes (see section 1). Human activity is therefore affecting where turbulence occurs, the characteristics of turbulence, such as the length scale of the turbulent eddies, and the extent to which it is predictable. There is therefore a need to understand how these factors are likely to affect animals in flight. In this commentary I will (1) assess naturally occurring and anthropogenic drivers of turbulence and the implications for spatial and temporal patterns in turbulence, (2) summarize what is known about how turbulence affects the metabolic costs of flight and (3) examine behavioural responses to turbulence, focusing on responses to sustained turbulence, rather than discrete gusts (Reynolds et al., 2014). The focus will be on birds, which have been studied in laboratory and field settings, but many of the points will apply to other flying animals. Overall, the aim is to highlight the importance of turbulence, identify some specific knowledge gaps and make some preliminary predictions assuming that responses to turbulence are related to flight capacity.

(1) Turbulence in the field: how does it vary in space and time?

Turbulence evades a simple definition, but can be taken as the random, chaotic component of motion (Davidson, 2015). Various measures are used to summarise the magnitude and characteristics of turbulent flow. The simplest is the magnitude of the variation around the mean flow. The instantaneous fluctuations around the mean can be calculated for any of the 3-dimensional components of the flow, or as the root mean square of all three. The "turbulence intensity" (TI) gives the magnitude of these variations, either as the r.m.s or the standard deviation, as a function of the mean wind velocity. This provides an intuitive metric that can be compared across wind speeds. However, it may not be the most biologically relevant parameter, as flight responses are affected by the size, or "length scale" of the turbulent eddies (see below). The length scale will vary from centimetres to kilometres, depending on the turbulence source, and animals flying through turbulence will experience eddies across a range of scales as energy is transferred through eddies of decreasing size, before being finally dissipated through heat at very small scales.

Most animal flight occurs within the atmospheric boundary layer (ABL), but there is increasing evidence that waders and passerines migrate above the ABL at flight heights of 4-7 km above ground (Sjöberg et al., 2023, Sjöberg et al., 2021). Here, wind speeds tend to be stronger and more uniform due to a decrease in surface effects. Several studies have hypothesized that birds operating at these heights could benefit from lower turbulence generally found at these altitudes (Kerlinger and Moore, 1989, Schmaljohann et al., 2007, Bowlin and Wikelski, 2008). Nonetheless, birds may still encounter turbulence in storm clouds as well as clear air turbulence (CAT)), which is caused by strong wind shear associated with jet streams and frontal turbulence at the boundaries of different air masses that vary in temperature or density. This can introduce turbulence with length scales from metres to kilometres and low, moderate or TI values (classed < 5%, 5-15% or > 15% of the mean wind speed respectively by the aviation industry). Models of clear air turbulence show pronounced regional variation that could also be relevant for migrants, including those moving between northern Europe and sub-Saharan Africa. Patches of CAT can have large horizontal extents (80-500 km in the direction of the wind), but layers tend to be thin in comparison (reported as 500-1000 m in general, but ≤ 4500 m near mountains (Pandharinath, 2014)), potentially enabling migrants to avoid them through selection of appropriate flight altitudes.

Turbulence dominates within the ABL due to the effects of surface friction and heat flux on the mean flow. This influences typically extends to 1 km above ground, extending to ~ 3 km over deserts, dry fields and boreal forests. Characteristic turbulence intensities may be ~ 5-20 % of the mean wind speed, with most of the turbulent kinetic energy being associated with eddies from metres to ~ 1 km, with the length scale of eddies increasing with height (LeMone et al., 2019). All animals will therefore experience turbulence with eddies that vary in length scale and velocity, whether they operate over flat, open landscapes or near topography and/ or obstacles that perturb the flow. Nonetheless, there will be spatial and temporal patterns in the likelihood, magnitude and the nature of turbulence depending on the surface characteristics and regional atmospheric conditions i.e. wind speed and solar heat flux.

Areas with strong solar heating will experience convective turbulence, or thermal turbulence, driven by the uneven heating of the substrate. This can cause perturbations over scales from millimetres to kilometres (cf. Ortga Jimenez 2018 living in a trash can). In unstable atmospheric conditions, air heated by warmer areas of the substrate rises, drawing in cooler air at the base. This creates convective "cells" that expand with altitude and can span the depth of the boundary layer. Thermals can also cover a large proportion of the ground surface area, for instance, thermals with a minimum diameter of 40 m covered 40-50 % of a survey area in Colorado, with other studies reporting similar fractional area coverages (Young, 1988). Turbulence occurs at the boundaries of thermals, due to local changes in air density and temperature and, in cases with extreme surface heating, the flow within the convective cells can also become turbulent (Chillà and Schumacher, 2012).

Wind also generates turbulence in the ABL through "mechanical forcing", where surface friction slows the flow close to the substrate, producing wind shear and turbulent eddies, with the turbulence intensity increasing with the wind speed (all other factors being equal). Turbulence is also generated by topography, forming in the lee of hills, and by obstacles in the flow including buildings and trees. In fact, there are strong similarities between the flow over cities and over plant canopies (Roth, 2000). A shear layer develops near the top of the canopy, where the canopy converts the mean flow to turbulent flow and reduces the wind speed. Individual elements, whether buildings or trees, also generate turbulent wakes, with the size of the eddies being related to the size of the obstacle. In the case of forests, wind also generates smaller eddies with length scales linked to the leaves, twigs and branches that produced them (Poggi et al., 2004). In the case of cities, wind-driven turbulence interacts with the urban heat island effect, which increases atmospheric instability near the surface and generates further mixing, amplifying the turbulent eddies (Roth, 2000). The net effect of the many sources of turbulence in the urban environment is that the rate of turbulence production and the turbulence intensity is up to twice as much as in flat, rural environments (Roth, 2000).

Wind farms also warrant particular consideration given the scale of their development (Drewitt and Langston, 2006). Wind farms have important impacts on the ABL, increasing turbulence and affecting the flow upstream and downstream of the turbines. The main upstream effect is a reduction in wind speed, due the blockage effect of turbines, but this may only amount to a 3% reduction in wind speed (Porté-Agel et al., 2020). The wind speed also decreases downstream, with this being much more marked in the near-wake region, which is 2-4 rotor diameters downwind of the turbine. This region is characterised by periodic helicoidal vortex structures, which are continuously shed from the tip and the root of the rotor blades (figure 1) with the shedding frequency increasing with the rotor speed. This whole region rotates in the opposite direction to the turbine blades. The helicoidal structures break down at the end of the near-wake region, 2-4 rotor diameters downstream from the turbine, where the near-wake region transitions to the far-wake (figure 1). Turbulence intensity peaks in this transition region, with the greatest turbulence near the upper edge of the wake. Nonetheless, turbulence remains high in the far-wake region: turbines introduce turbulence with scales of 1 – 10 m (Stevens and Meneveau, 2017) and turbulence intensities are some 10-30% above that in the incoming flow for offshore wind farms. These wakes can also extend up to 55 km downstream for offshore wind farms (Eecen et al., 2011). The length of the wake, and the dominant turbulent scales within it, are affected by the wind farm layout and atmospheric stability. Large turbulent eddies in unstable atmospheric conditions (100 m to kilometres in scale) break down the small-scale structures introduced by turbines. Wakes therefore persist for longer when the atmosphere is stable (Stevens and Meneveau, 2017), which explains why wakes are longer in offshore wind farms. Wind farms also introduce turbulence into the air above them, as a shear layer forms between the slower, wake-affected air and the faster-moving air above it, generating an internal boundary layer that can be a few metres thick or as deep as the ABL. A full internal boundary layer is more likely for offshore wind farms due to the influence of atmospheric stability on its formation (Porté-Agel et al., 2020).

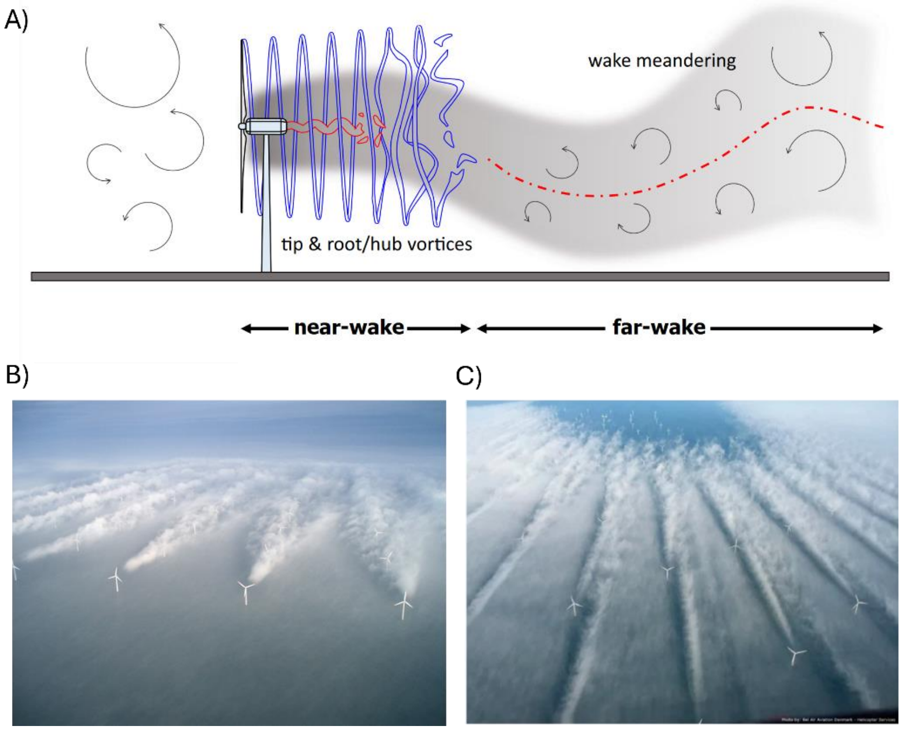

Figure 1. A). A schematic representation of the vortices generated by a wind turbine in the near-wake and far-wake regions (taken from Porté-Agel et al. (2020) in accordance with the Creative Commons Attribution (CC BY) license). B). Full-wake conditions when lateral wakes merge (Copyright Vattenfall) C). Partial-wake conditions where lateral wakes do not converge with (photo from Horns Rev 2 wind farm, taken from Hasager et al. (2017), in accordance with the Creative Commons Attribution (CC BY) license).

(2) The effects of turbulence on the metabolic costs of flight

Few data exist on how turbulence affects the metabolic costs of flight, but to give some context about the magnitude of these costs, I will first estimate how wind affects flight costs, considered per unit time (i.e. flight power). Wind affects flight power because head- and tailwinds change the speed that provides the minimum power per unit distance travelled i.e. the maximum range speed, U_{mr} (Hedenstrom and Alerstam, 1995). The change in costs can be estimated using the AFPT package (Klein Heerenbrink, 2020), which uses aeronautical theory to predict the form of the power curve from morphometric data, and then applies an optimality approach to predict the maximum range speed, and associated power, for a given head- or tailwind component. Not all species will be able to increase their airspeeds in the manner predicted, as the ability to increase speed, and the costs of doing so, vary with mass (figure 2). Indeed, Pennycuick *et al.* (2013) showed that only species with a mass < 1.1 kg migrated at speeds around their U_{mr}, whereas birds over 1.3 kg flew at speeds less than this. Species less than ~ 1 kg should therefore have the available power to increase their maximum range speeds when flying in headwinds. The increase in flight costs predicted for a 5 m s^{-1} headwind was therefore calculated for the 21 species in Pennycuick *et al.* (2013) with a mass < 1 kg and compared to flight costs at the maximum range speed in still air. The power increment for most species was 11-38% for flights with a headwind component of 5 m s^{-1} (increasing to 74 % for the pied wagtail, figure 2). A headwind of 5 m s^{-1} represents a condition that many animals will experience regularly, being classified as a gentle breeze on the Beaufort scale, although it represents some 75% of the predicted maximum flight speeds for species in figure 2 (Table S1).

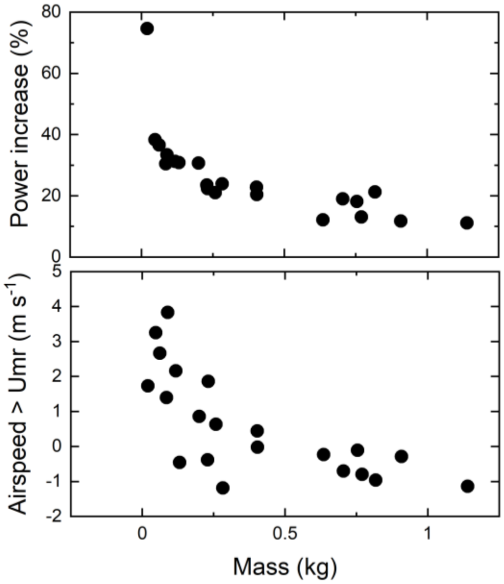

Figure 2. The predicted increase in aerodynamic power for 21 species flying at U_{mr} into a 5 m s^{-1} headwind compared to flight at U_{mr} in still air (upper panel). The lower panel shows the airspeed measured for each species on migration (taken from Pennycuick et al. (2013), table S1), less the airspeed predicted for U_{mr} in a 5 m s^{-1} headwind (lower panel). Positive values indicate that measured airspeeds exceeded those predicted for flight in a 5 m s^{-1} headwind.

A clear mechanistic framework allows us to model how wind affects the costs of flight, according to wind support and bird morphology. Similar frameworks exists to predict how birds vary their airspeed in relation to updraft strength and availability (Pennycuick, 2008, Harel et al., 2016). The same is not true for turbulence. Even if we know the turbulence intensity, or even the length scale, we are currently unable to estimate how this will affect flight costs or predict whether these costs will vary with morphology. Nonetheless, the limited measurements that are available demonstrate that turbulence can increase flight costs substantially. Budgerigars (*Melopsittacus undulatus*) flying in highly turbulent air (43% r.m.s.) used oxygen at a rate that was double that for birds flying in smooth air (Tucker, 1966, Tucker, 1968). Ortega Jimenez *et al.* (2014) quantified the costs of flight in Anna's hummingbirds (*Calypte anna*) flying behind three different wake-generating cylinders with diameters equal to 38, 77 and 173% of the wing length and found that flight costs increased by 25% behind the largest cylinder when compared to control conditions. In the wild, the heart rates of migrating Swainson's thrushes (*Catharus ustulatus*) were also higher when flying in turbulent conditions (Bowlin and Wikelski, 2008).

Turbulence incurs a cost because animals make kinematic and postural adjustments to increase their flight stability and control. For instance, orchid bees (*Euglossa imperialis*) flying in front of an outdoor, turbulent jet of air became increasingly unstable about their roll axis as turbulence increased, eventually leading to them either crashing or being shot out of the jet i.e. a total loss of aerodynamic control (Combes and Dudley, 2009). Rolling instabilities have also been documented for bumble bees *Bombus impatiens* and *Bombus terrestris* flying in turbulence (Engels et al., 2016, Ravi et al., 2013). Orchid bees improved their roll stability by extending their hindlegs (a response also documented in hawkmoths, *Manduca sexta* (Ortega-Jimenez et al., 2016), but this increased drag and associated power requirements by 30% (Combes and Dudley, 2009). Hummingbirds also show increased instability in turbulent flow (Ravi et al., 2015) and varied the orientation and fan angle of their tails to increase passive stability. Similar to leg extension in insects, this also increased drag (Ravi et al., 2015).

Birds also increase their mean wingbeat frequency and/ or amplitude in relation to turbulence, both of which can enhance manoeuvrability and stability (Ravi et al., 2015, Ortega-Jimenez et al., 2014, Lempidakis et al., 2024). However, these changes are typically small compared to the magnitude of stroke-to-stroke changes in kinematics, including wingbeat amplitude, wingbeat frequency and stroke plane (Ravi et al., 2015, Ortega-Jimenez et al., 2013, Ortega-Jimenez et al., 2014). For instance, hummingbirds flying behind cylinders increased the standard deviation in their wingbeat amplitude and frequency by as much as 200% and 50%, respectively (Ortega-Jimenez et al., 2014). Similarly, pigeons (*Columba livia*) flown back to their lofts in a range of conditions showed a marked increase in the variability of their wingbeat frequency and amplitude when flying in strong turbulence (Lempidakis et al., 2024). Variable kinematics are thought to be more costly than a continuous flight style, due to the associated cycles of deceleration and acceleration. Indeed, this is likely to account for much of the 25% increase in flight costs for hummingbirds flying behind a large cylinder, given that their main kinematic response was an increase in the variability and bilateral asymmetry in wingbeat amplitude (Ortega-Jimenez et al., 2014). Nonetheless, there is no simple way of estimating the costs associated with variable kinematics, not least because part of the kinematic response could be passive. Separating the effects of active, behavioural control from aerodynamic effects of the flow on the wings requires is complex, as it requires direct quantification of neuromuscular activity (Liao et al., 2003). This highlights the need for more metabolic measurements, which can at least provide an estimate of the net cost of operating in turbulent flows.

Future priorities; moving towards a framework.

The framework for predicting how flight costs vary in relation to airspeed and wind speed is well-prescribed, with uncertainties relating to specific parameters such as drag coefficients (Klein Heerenbrink, 2020). The prospects of an analogous framework for turbulence seem slim, not least due to the variable characteristics of turbulence itself. Animals operating in turbulence will fly through eddies that vary in size and velocity, and in the extent that they produce horizontal and vertical variation in the flow. But experiments should be able to provide insight into the key determinants of the metabolic response. Animals only make marked kinematic adjustments when flying in turbulent eddies large enough to interact with both wings i.e. where the length scale is similar to, or greater than their wingspan. This result appears to hold for both insects and hummingbirds (e.g. Ortega-Jimenez et al., 2013, Ortega-Jimenez et al., 2014) and the threshold effect may explain why Tucker found no effects of small airspeed fluctuations (i.e. 0.88–1.44% RMS/mean values) on flight metabolism in the laughing gull (*Larus atricilla*) (Tucker, 1972). What remains unknown is how eddies with length scales greater than the wingspan affect flight costs. Is it that turbulence levies a constant cost once a threshold eddy size has been exceeded? It may not be that simple, for instance if birds vary the extent that they employ a passive response or active compensation depending on the length scale.

One of the challenges facing experimental biologists is how to simulate conditions that animals experience in the wild. The turbulence generated by grids is more akin to freestream turbulence than the regular and predictable eddies in von Kármán vortex streets (c.f. Ravi et al., 2015). Nonetheless, grids may not be good options for producing eddies with maximum length scales larger than wingspans within the confines of wind tunnel test sections. Gust generators are often mounted in wind tunnels to test how fixed wings respond to gusts and these could be usefully co-opted in studies of animal flight. For instance, wings mounted across the width of the test section can produce gusts that vary in length scale and magnitude (Balatti et al., 2022). This could be used to investigate the effects of gust velocity and length scale independently from flight speed (Ortega-Jimenez et al., 2013, Ortega-Jimenez et al., 2014) and therefore establish which elements are the most challenging for flight control and the most metabolically costly to respond to.

Finally, the few metabolic measurements made to date make it clear that turbulence can have a huge impact on flight costs, increasing energy expenditure by 25-100% (see above), but the kinematic and metabolic response may also vary with morphology. For instance, moths flying in vortex streets exhibited large variations in yaw but only moderate oscillations in roll, whereas bees showed increasing instability about their roll axis as flow variability increased (Ortega-Jimenez et al., 2013, Combes and Dudley, 2009). Birds also diverge in their manoeuvring style (Dakin et al., 2018) and it may be that this, or traits such as the range of motion (Baliga et al., 2019) affect their responses to gusts, with implications for the size and magnitude of gusts that birds can respond to and the associated energetic costs. The latter could be quantified using techniques such as the sodium bicarbonate method (Ward et al., 2001) to estimate the costs of flight over short timescales.

(3) Behavioural responses to turbulence

The general tendency for animals to reduce their maximal speeds in stronger turbulence provides further evidence that turbulence represents a cost for fliers. For instance, Anna's hummingbirds could fly at 14 m s^{-1} in unperturbed flow but were unable to fly at 12 m s^{-1} in the wake of a large cylinder (Ortega-Jimenez et al., 2014). Similarly, hawkmoths flew at 3 m s^{-1} in laminar flow but could only achieve 2 m s^{-1} when flying in large vortices (Ortega-Jimenez et al., 2013). Homing pigeons returning to their loft showed a different tendency, actually increasing their airspeed by 1 m s^{-1} in highly turbulent conditions relative to their speed in still air (Lempidakis et al., 2024). However, flight speed in wild birds could be affected by other currencies, such as the benefit of returning to the loft more rapidly when conditions favour soaring flight for raptors.

Is there any evidence that animals avoid turbulence, and the associated costs, in the wild? Flying animals have to be able to respond to conditions they encounter routinely, which will include low to moderate turbulence. Strong turbulence also occurs in the ABL and at high altitudes, and animals may therefore adjust their flight timing or route to reduce the probability of encountering it. It has long been theorised that this affects the timing of migration e.g. providing advantages to migrating at night and/ or at high altitudes as the flow is more laminar (Kerlinger and Moore, 1989). However, it is hard to distinguish the role of turbulence from other factors including temperature, and recent evidence suggests that heat balance plays a major role (Sjöberg et al., 2023).

Very few studies have tested whether and how animals adapt their flight trajectories in relation to turbulence in the ABL, beyond the responses of soaring birds to rising air (e.g. Nourani et al., 2021, cf. Crall et al., 2017). Nonetheless, strong turbulence is associated with obstacles in the flow and particular substrate characteristics in windy and convective conditions, and it would be surprising if animals were not keyed into this. Some results are consistent with small-scale route changes to avoid turbulence, for instance homing pigeons took a different route when returning to the loft in strong turbulence (Lempidakis et al., 2022), and gulls adjusted their flight trajectories in strong winds, consistent with a strategy to reduce the risk of being displaced towards buildings by gusts (Shepard et al., 2016). However, estimating the time-varying turbulence along paths that birds opt to fly, and in areas they appear to avoid, remains challenging (Lempidakis et al., 2022).

Wind farms produce spatially-predictable patches of high turbulence, both within the footprint of the farms and in their wakes. These patches are particularly distinctive in the marine environment, as low levels of thermal convection mean the surrounding flow tends to be relatively laminar. We know from onboard loggers and radar tracking that certain taxa make striking detours around wind farms (Desholm and Kahlert, 2005, Plonczkier and Simms, 2012); a behaviour that has mainly been attributed to the perceived risk of collision from visual stimuli (May, 2015). Yet some of the main responses are also consistent with an inherent tendency to avoid strong turbulence. For instance, the increase in avoidance when turbines are active (Dierschke et al., 2016) and hence generating turbulence. Furthermore, the strongest, most consistent avoidance is found in heavy species, including waterfowl (mainly geese and common eiders, *Somateria mollissima*)(Desholm and Kahlert, 2005) and northern gannets (*Morus bassanus*) (Peschko et al., 2021), which have lower available power and hence less capacity to respond to an increase in flight costs.

Turbulence could also be a proximate driver of avoidance (along with visual cues (Martin, 2011), and/ or the sound of turbines operating etc.). Indeed, birds could respond to increased turbulence even if this was not the ultimate mechanism for avoidance. If birds are using turbulence as a cue, they should divert their path around wind farms at greater distances when approaching down-wind as they will encounter the far-wake before they reach the wind farm itself. The far-wake could therefore provide birds with information about wind farm activity over distances of many kilometres, although wind speed, atmospheric conditions and wind farm characteristics affect the wake development and length. It would be interesting to test whether the distance that birds approach offshore wind farms before diverting can be predicted by wind speed and bird approach angle, as birds are can divert around wind farms at tens to hundreds of metres or several kilometres (Drewitt and Langston, 2006).

Wake characteristics could also affect how birds move within wind farms, as the wakes behind individual turbines can converge, producing “full-wake” conditions and turbulent flow throughout the wind farm, or “partial wake" conditions, where corridors of lower turbulence remain between individual wakes, with the orientation of these corridors being determined by the wind direction (figure 1). To date, turbulence has been considered in how it may affect the ability of birds to manoeuvre away from moving parts, sometimes termed micro-avoidance, but it could play a role in predicting avoidance at the level of individual turbines and/ or whole wind farms (i.e. meso- and macro scales), all of which could influence collision risk. Onboard loggers provide a new prospect for investigating how birds adjust their flight paths in relation to changing levels of turbulence, as the signal from accelerometers and barometric pressure sensors varies with turbulence (Laurent et al., 2021, Lempidakis et al., 2022). Such information could usefully be combined with modelled flow characteristics to provide insight into the levels and characteristics of turbulence that different species can tolerate, as well as what they avoid.

In conclusion, turbulence is likely to levy a cost for all flapping fliers in the wild because it pervades all aerial habitats, including areas that might appear sheltered, such as underneath forest canopies. Nevertheless, we still know relatively little about the scale of the increase in metabolic costs, and how this will vary across habitats and atmospheric conditions. There is therefore a need to integrate turbulence into the ecology of flight, given that animals may adjust their flight decisions in relation to how airflows affect flight power and flight speed. The responses should also vary with the ability to meet additional costs (i.e. available power) and the consequences of a potential loss of flight control. The risks of the latter will be higher when birds are operating close to the ground or obstacles in the flow. While the effects of turbulence have been compared to that of wind, these factors covary, and animals will need to integrate the costs and risks of both in changing airscapes. A combination of field and laboratory approaches will be required to provide insight into how, when and why animals respond.

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