



Introduction

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Moving in a moving medium: new perspectives on flight

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One of the defining features of the aerial environment is its variability; air is almost never still. This has profound consequences for flying animals, affecting their flight stability, speed selection, energy expenditure and choice of flight path. All these factors have important implications for the ecology of flying animals, and the ecosystems they interact with, as well as providing bio-inspiration for the development of unmanned aerial vehicles. In this introduction, we touch on the factors that drive the variability in airflows, the scales of variability and the degree to which given airflows may be predictable. We then summarize how papers in this volume advance our understanding of the sensory, biomechanical, physiological and behavioural responses of animals to air flows. Overall, this provides insight into how flying animals can be so successful in this most fickle of environments.

This article is part of the themed issue 'Moving in a moving medium: new perspectives on flight'.

1. Introduction

Air is arguably the most dynamic medium: it is turbulent, it can move at high speeds (winds $\geq 10 \text{ m s}^{-1}$ are common at migration altitudes), and the strength and variability of air currents vary from sub-second to seasonal scales, as well as through evolutionary time [1]. This has profound consequences for animals that move within it [2,3]. To take one example, animals must fly faster than the flow if they are to orientate independently from it and approach their desired landing point in a controlled manner. Yet flight speeds in birds are only 0.7–1.6 times those of typical wind speeds [4,5]. This is equivalent to a Boeing 747 having to operate in winds of some 780 km h^{-1} . In fact, even though wind speeds are a much lower proportion of the flight speeds of commercial aircraft (the ratio of flight speed to flow speed is in the order of 9.7:1), wind speed is still a key determinant of fuel consumption, journey time and flight route.

The fact that air is almost never still provides animals with potential opportunities as well as challenges. Organisms from aphids to eagles time their flights in order to exploit particular flow vectors [6,7], enabling them to travel with very low energetic costs [8]. Movement timing is one of the simplest responses to airflows in the behavioural repertoire, although it is an interesting one, as periods of inactivity, as well as avoidance of particular airspace, may provide insight into the environmental factors that represent limits to flight performance. Animals also modulate their flight speed, route and mode (e.g. flapping versus soaring) in relation to airflows to reduce their costs of transport. One area of research advanced in this issue is how these responses may be modulated further by risk. In most ecological areas of research, risk is associated with predation or the ability to find food. While both these factors can exert powerful influences on flying animals [9,10], there are other types of risk, some of which are uniquely aerial, associated with flight mode and performance [11], the possibility of collision and drift (which is also relevant to aquatic movement).

This volume provides insight into how flying animals can be so successful in this most fickle of environments, by considering biomechanical, physiological,

behavioural and sensory responses of animals to air flows. In this introduction, we provide a brief synthesis of the variability of airflows, and summarize how the papers in this volume advance our understanding of how animals respond to the costs, risks and opportunities associated with them. We conclude by considering how biological solutions to the variable aerial environment could inform the flight planning and design of unmanned aerial vehicles (UAVs).

2. Airflow components and flight speed

Airflows are three-dimensional and so can be split into three components. Typically, in fluid dynamics, the horizontal components are referred to as u and v , with the vertical component being w . For simplicity, the axes are often chosen so that u is in the direction of the mean wind. Each component is considered to consist of two parts, the mean (or average) wind speed (denoted by an overbar) and the instantaneous fluctuations about this mean value (denoted by a prime). So for example, $u = \bar{u} + u'$. Turbulence (the flow variability or gustiness) is related to the fluctuations [12]. The convention of treating the three components separately serves the biological community well, as u and w are linked to the mechanical power requirements of flight, with vertical motion affecting induced power costs, and wind causing power use to vary in relation to distance. Sustained turbulence or gusts can also influence flight costs when the turbulent components are of similar scales to the animals themselves, as kinematic or aerodynamic adjustments may be required to maintain flight stability [13,14]. Yet despite the ubiquity of turbulent features, our understanding of how turbulence affects flight performance remains limited. Recent advances in this area are reviewed in this issue by Ortega-Jimenez *et al.* [15] particularly in relation to hummingbird flight. These authors also consider how the susceptibility to turbulent features and the ability to respond to them are likely to vary with flight speed and body size.

In comparison, the effects of sustained horizontal and vertical flows on flight performance are relatively well understood. Indeed, in the case of wind, the U-shaped curve of power against speed allows energetically optimal flight speeds to be predicted, as well as how they vary with the head/tail wind component, and the ecological context for the flight e.g. food searching or not [16,17]. In this volume, Hedenström & Åkesson [18] examine how a range of internal and external factors combine to affect airspeed selection in a range of tern species during flapping flight. They show that the ecological objective, wing morphology, wind strength and direction, and number of flock mates are the dominant factors affecting airspeed, highlighting the complexity of this apparently simple behavioural response. Indeed, the number of factors that need to be controlled for may explain in part why results from some previous studies have not aligned with theoretical predictions.

Predictions for optimal speeds of gliding flight are based on the glide polar. Recognizing that these optima vary with both the headwind and updraught speed, which are unlikely to vary in isolation, Taylor and co-workers [19] derive the glide speeds that correspond to the aerodynamic cost of transport minima, in relation to simultaneously varying u and w values. They then test this framework using airspeeds measured on-board a gliding steppe eagle (*Aquila nipalensis*). The results are consistent with a strategy to reduce the aerodynamic costs of

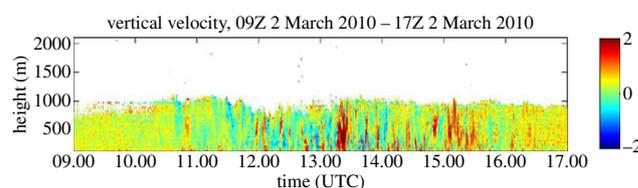


Figure 1. Remote sensing can now provide vertical velocity profiles through the boundary layer. LiDAR measurements of vertical velocity (sampled every minute) are shown in colour in relation to height and time. It is clear that there are much weaker vertical motions at night and early morning, and stronger, more coherent updraughts and downdraughts later in the day driven by thermal heating. The nature of the variability in relation to altitude and time give an idea of the structures that can be seen in a daytime convective boundary layer. Measurements were made above a valley top, in conditions of low winds and clear skies, nonetheless, thermal heating was limited as data were collected in March 2010 and daytime temperatures reached up to about 7°C (adapted from the COLPEX project, see Price *et al.* [27]).

transport in relation to headwinds. Flight speeds were also among the parameters quantified by Harel *et al.* [20] in rich, long-term and high-resolution movement datasets from Eurasian griffon vultures (*Gyps fulvus*). These authors compared three proxies of time, energy and risk minimization across three spatio-temporal scales, ranging from seconds and metres, to months and thousands of kilometres. They show that birds minimized time (by minimizing thermal climbing time in relation to the distance gained during subsequent glides) and energy (by flapping less) but were more risk prone (steeper inter-thermal glide angle), when flying to a known destination compared to flights with an uncertain destination. These performance metrics also vary with environmental conditions and individual age.

3. Flow selection

(a) Detecting wind direction

Animals modulate their flight trajectories at a range of scales, and in both the horizontal and vertical dimensions, in order to benefit from flow assistance and reduce wind drift. Of course, animals have to be able to detect flows in order to respond to them, which is not necessarily straightforward given that air is both invisible and highly dynamic. But here too, it seems that the variability itself may have its benefits, being a potential source of information. For instance, insects use fine-scale anisotropic turbulence to detect the wind direction when flying hundreds of metres above ground. This enables them to reduce wind drift from seasonally optimal directions and maximize their travel distance [21]. In this volume, Reynolds *et al.* [22] review the different cues that insects may use to detect wind direction, and present a new mechanism for sensory detection based on the ‘jerks’ that insects experience in flight. While visual cues may or may not be important for high-flying insects, they are certainly used by insects in other scenarios [23] as well as birds, which can use the apparent ground movement to correct for wind drift [4,18,24].

(b) Airflows and route selection

All other things being equal, animals are predicted to avoid factors that increase their power use and opt to fly in regions

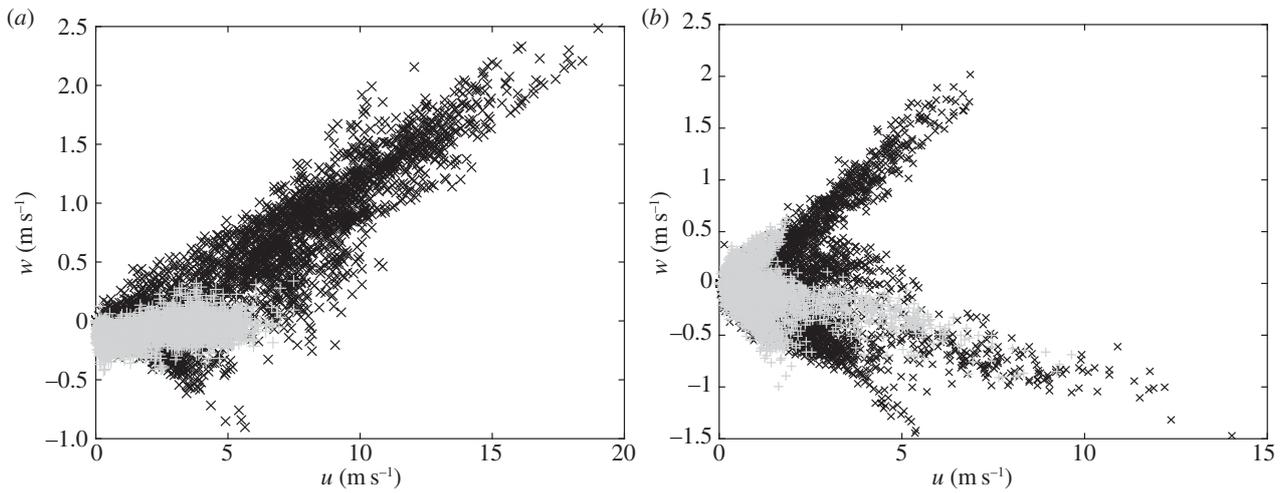


Figure 2. The spatial predictability in wind driven flows (including the vertical flow component) is demonstrated by site-specific measurements of vertical wind speed (w) against horizontal wind speed (u). Data are from tri-axial sonic anemometers measuring at two different heights (black, top of tower; grey, bottom of tower) on two different towers (a, b), on a complex hilly, forested site [33]. Wind speeds are 15 min averages from measurements made at 10 Hz. In all cases, there is a strong correlation between u and w , with sharp edges to the data suggesting that the wind is following preferred streamlines (either along the slope, or over the forest). On the left, the site was on a small plateau on the slope of hill. The lowest measurements (2.96 m) are dominated by the proximity to the surface of this plateau, which produces little vertical motion. The top measurements (15.65 m) are more influenced by the larger scale slope of the hill and also, possibly, the proximity to the forest edge. Site 2 was near the summit of the ridge, and hence air will be forced up or down, depending on the direction of the wind.

that offer power savings relative to still air. Organisms can achieve this in a variety of ways. Many alter their flight direction relative to the wind vector, in order to seek out beneficial tailwinds and reduce the costs of self-powered flight. This involves variation in altitude as well as variation in the horizontal path, and is seen among migrants from noctuid moths to oceanic seabirds and large raptors [4,21,25,26]. Power requirements are also reduced when flying through updraughts. In contrast to tailwind assistance, animals may be able to use updraughts to cease flapping altogether. Nonetheless, sustained static soaring requires detours to integrate spatial and temporal variability in rising air (this variability is illustrated in figure 1), and is therefore only profitable for larger fliers due to their relatively low mass-specific metabolic rates and high flight speeds [28].

Clearly, varying flight direction can only result in energy savings when there are regions with beneficial flow characteristics. The extent to which these opportunities exist depends on how heat and wind interact with the substrate. Heat-driven flows will generally be favoured in conditions of clear skies and light winds [1] but they are obviously strongly dependent on the time of day, with peak heating and thermal strength around midday/early afternoon (figure 1). In this issue, Shamoun-Baranes *et al.* [29] model the environmental envelope of modes of soaring *versus* flapping flight in breeding black-backed gulls (*Larus fuscus*) (i.e. the conditions under which each flight mode is observed). Their results demonstrate how the probability of soaring flight tracks diurnal changes in convective conditions. The flight costs of a range of flying animals may show some diurnal variation even for those that do not switch from flapping to soaring flight.

Mechanically driven processes also produce vertical motion, and these are more likely with stronger wind conditions. In these scenarios, regions of vertical air motion are either geographically fairly fixed e.g. airflow separation behind a hill [30,31] or forest edge [32] (figure 2), or propagating (e.g. mountain waves, sea breeze fronts [34]). What is interesting about the former, from the perspective of animal

flight paths, is that the distribution of vertical flows is relatively predictable, because given substrate features will always alter the mean wind condition, even though the precise regions where air is forced up or down will vary with the wind direction (figure 2). This leads to the question of whether visually orientating animals predict the distribution of beneficial or costly airflows *a priori*, according to wind direction (either from memory or reaction to current conditions), or whether they only establish where beneficial airflows are with respect to a landmark as they approach it. The latter strategy is potentially costly/risky given that rising air is spatially and temporally coupled with regions of sinking air.

Our understanding of static soaring flight and tailwind assistance owe much to the use of migratory (and wide-ranging) animals as models (e.g. [25,35,36]). Yet horizontal and vertical airflow components vary over fine scales—as indeed does turbulence. Far less attention has been paid to smaller-scale airflows in terms of whether and how they might affect flight decisions (although see [37] for an excellent consideration of the small-scale processes that have been associated with insect concentrations). Nonetheless, features as small as hedgerows, buildings and stands of trees generate updraughts and turbulence, and accelerate horizontal flow components in repeatable ways (figure 3). In this volume, Shepard and co-workers [38] demonstrate that gulls alter their flight trajectories in relation to wind conditions to exploit updraughts over features as small as a row of low-rise buildings (with their positioning at even finer scales potentially being beneficial for flight control in the face of gusts). Exploitation and/or avoidance of these and other small-scale features may lead to a much greater degree of predictability in the daily movement paths of flying animals than has generally been considered (see also [15]).

A final and exciting example of the exploitation of small-scale aerial heterogeneity is presented by Warrick *et al.* [39]. This study coupled high-speed video with measurements of near-ground wind speeds. The results demonstrate that barn

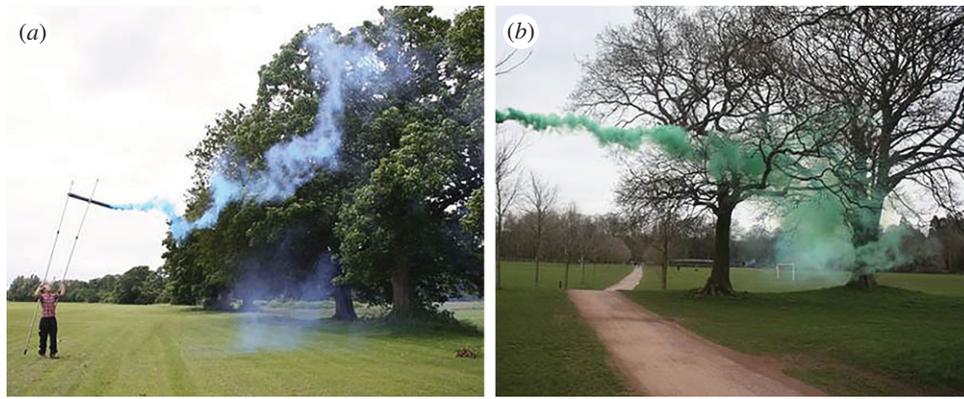


Figure 3. The use of coloured smoke ‘grenades’ demonstrate how a parallel wind field is altered by a tree, according to whether or not the tree is in leaf. Grenades were released into a section of piping that was held on poles at a height of 5 m, and parallel to the oncoming airflow, in order to direct a plume of smoke towards the target tree. Photographs taken in the summer and winter ((a,b), respectively) demonstrate how the oncoming airflow is directed over the tree when it is in leaf, producing vertical air motion, whereas the smoke passes through the tree in winter due to the lack of leaves. (Online version in colour.)

swallows (*Hirundo rustica*) use near-ground wind speed gradients to gain potential and kinetic energy in both flapping and gliding turns. This provides evidence that such exploitation of the shear layer is not solely the province of the Procellariiform seabirds. In fact, swallow flight is perhaps an ultimate example of aerial multi-tasking, as birds simultaneously harvest energy from the air, avoid obstacles (embedded in a solid substrate) and catch prey.

Overall, the vertical motion, wind gradients and gusts from which animals harvest energy, largely result from the interaction between the air and the substrate (whether solid or not). This leads to the interesting irony that while flying animals are celebrated for their ability to escape the apparent bonds of the ground, many of them exploit, and in some cases depend on [40], heterogeneity in the airspace that derives from the air’s interaction with the substrate, rendering them less ‘free’ than we might imagine them to be. In support of this, there is increasing evidence that the distribution of a range of highly aerial species is fundamentally linked to the properties of the aerial environment [41,42].

Ultimately, the extent to which animals vary their flight paths in relation to airflows will depend on the interplay between internal and external factors (cf. [43]). Internal factors include the driver for movement, the flight speed (in relation to flow speed), and the relative costs of assisted and unassisted flight. External factors include the spatial and temporal variability in flow conditions, temperature and other factors such as the availability of food. Åkesson and co-workers [44] demonstrate how intra-annual changes in ecological context lead to the use of different spring and autumn migration routes for common swifts (*Apus apus*) moving between northern Europe and Africa. In the autumn, animals cross the potential barrier of the Sahara on a broad front, using wind assistance, in a largely energy-selected migration. The more well-defined and conserved spring migration routes are driven by the need to exploit rich foraging grounds as well as favourable winds, in what are more time-selected movements.

4. Physiological and morphological factors

Flight is the most energetically demanding form of locomotion, per unit time [45]. The feats of exercise undertaken by birds in particular are at, or near, the extreme limits of organismal physiology. No taxon flies higher or migrates further than birds [46].

Birds occupy every continent on the planet and can fly in thin air at altitudes of over 7000 m while crossing the Himalayas [47], and can endure temperatures from -50°C – 45°C . They are also extreme endurance athletes, and are capable of travelling over 11 000 km non-stop during migrations comprising over 215 h of continuous powered flight [48]. The morphology and musculature that has evolved to provide the necessary functional units to allow such flight behaviour is unique to birds, and is discussed in detail in this volume by Tobalske [49]. The physiology that is required to power such endurance exercise is a detailed network linking primarily the cardiovascular and respiratory systems. The impressive fat stores that birds deposit, fuelling such long flights, are extensive, and key aspects of flight physiology are described by Butler [50].

During long-duration flights in particular, there is a great need for heat dissipation, due to the intense flight muscle activity generating heat (see [51] for a discussion of thermoregulation in insect flight). The dissipation of this heat is presumably hampered by the insulating fat and plumage layers, particularly in species that inhabit colder regions, and so may cause problems for birds during migrations. Indeed, migrations typically represent the largest sustained period of energy expenditure for birds over the annual cycle [52], and migrations are responsible for the highest cause of mortality in both juvenile and adult birds [53]. Increases in flight costs are likely to be exacerbated in species with a high wing loading [28]. One such species is the common eider (*Somateria mollissima*) and Guillemette *et al.* [54] provide evidence on how heat dissipation during migratory flights will contribute to shaping migration strategies, and flight duration. Changes in the airflow environment on a small scale will have substantial impacts on the flight costs of birds, and such impacts will be exacerbated during long migratory flights. Unfavourable or rapid changes in prevailing winds will all potentially contribute to higher flight costs, negatively affecting the energy balance of migrating individuals, having deleterious effects on their survival.

5. Modelling airflows

Our understanding of how animals interact with airflows has been greatly enhanced by meteorological models and measurements of airflows. These vary from relatively low resolution global forecasting and reanalysis models that incorporate heat and mechanically driven flows at regional scales, to

high-resolution models that predict complex airflows, such as those in urban environments and fragmented landscapes [55]. Atmospheric models can now be run with a resolution of down to 5 m horizontally and 3 m vertically [55]. Such resolutions allow the accurate representation of hills and mountains, and potentially urban areas, and are also capable of resolving the larger scales of turbulence in the atmosphere as well as the mean flow (e.g. [56]). These simulations provide new opportunities for understanding the world in which animals fly, incorporating not only the mean flow, but also the variability and predictability of that flow. Such high-resolution eddy-resolving simulations are computationally expensive and primarily research tools, however lower resolution simulations (of the order of a few kilometres resolution and Harel *et al.* [20] use RAMS with a spatial resolution of 1 km and temporal resolution of 5 minutes) are now run routinely both for general weather forecasting (e.g. the UK Met Office forecast model runs at 1.5 km resolution), and specifically for forecasting flight conditions for glider pilots (e.g. RASP). These simulations will not resolve the turbulence or small-scale thermals explicitly, but give a good general idea of where and when thermals might occur.

Further insight into fine-scale variation in airflows, particularly relevant for many flying animals, is likely to come as researchers instrument UAVs with sensors usually carried by full-scale aircraft to inform model development. The development of UAVs offers exciting opportunities to observe the small-scale three-dimensional spatial structure of atmospheric flows over the lowest couple of 100 m of the atmosphere in a way that has hitherto not been possible with ground-based instruments or larger manned aircraft (e.g. [57,58]). Engineers also stand to gain from biological advances, and there is great interest in applying lessons from the way birds and insects fly in order to produce more efficient, stable and controllable UAVs (see [59] and papers in this special issue).

6. Unmanned aerial vehicles and bio-inspiration

The last decade has seen major technological advances in the development and use of UAVs. These are now being used for purposes as diverse as search and rescue efforts, military surveillance, habitat mapping and conservation efforts [60]. Nonetheless, key challenges remain in the performance of UAVs, including in their responses to both variable airflows and cluttered environments. The behavioural responses of animals to variable airflows, in terms of route and speed selection could potentially inform UAV flight path planning in this regard, particularly as their responses probably represent strategies that reconcile different currencies of risk and cost minimization (cf. [20,38]).

Liu *et al.* [61] review how robotics engineers have studied animal flight in general to understand how animals manoeuvre through the aerial environment, and regain flight control following a perturbation. This is an active area of research for both biologists and engineers, and one that is particularly pertinent for micro air vehicles (MAVs)—insect- and bird-sized drones, with maximal dimensions of 15 cm and speeds of around 10 m s^{-1} , which experience flight control challenges. Ortega-Jimenez *et al.* [15] suggest that flight research in hummingbirds presents opportunities for advancing our understanding of aerial manoeuvrability, as the flight performance of this group

far exceeds that of similar-sized MAVs. In fact, the kinematics of hovering in hummingbirds are strikingly similar to those seen in other hovering animals such as honeybees, hawkmoths and fruit flies, showing that similar solutions can operate over a range of scales (which may be the result of constraints in this case) [62]. The hovering performance of *Drosophila melanogaster* has been exceptionally well parametrized, and Dickenson & Muijres [62] review this here, as well as the aerodynamic, biomechanical and neurological underpinnings of the flight manoeuvrability of these tiny insects.

These advances are likely to be crucial for the further development of flapping-wing MAVs, an active research area, also reviewed by Liu *et al.* [61], which has biomimetics at its heart. Developments in biomimetic wing design are also important for flapping MAVs, and consequently there is much interest in the topography and geometry of insect wings. Bomphrey *et al.* [23] synthesize current understanding of wing morphology in Odonata and how this affects aerodynamics and force generation. They also present new data on a range of factors including the variation in flight speed, turn rate and acceleration for a variety of flight types, in a comprehensive treatment of aerodynamics and mechanics in this ancient and highly conserved group of fliers.

7. Conclusion

Recent advances in the ability to quantify animal movements and model airflows are opening up novel opportunities to investigate the many interactions between the aerial environment and the animals that move within it. Animal-attached tags are being routinely deployed, and are becoming ever smaller and more sophisticated, allowing researchers to quantify the biomechanical, physiological and behavioural responses of an increasing number of animals in flight, as well as the energetic implications of their decisions [63,64]. As most tags are still too big for all but the largest insects, a combination of remote sensing (e.g. through radar and LiDAR) and aerial sampling will remain key for investigating the movements of the smallest fliers. Ultimately, a greater understanding of how animals respond to airflows should allow researchers to predict flight paths, or aspects of them, over a range of scales, which has clear implications for conservation and management [65]. UAV engineers are also interested in animal responses to airflows, including the sensory mechanisms that underpin flow detection, as bio-inspiration lies at the heart of much UAV design and development [61]. Another fundamental driver of research into animal flight, which thankfully shows no signs of diminishing, is the sheer delight in watching animals move through a medium in ways that are largely inaccessible to us. Overall, these promise to be exciting times for flight research.

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Guest Editor profiles



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Steve Portugal is a Senior Lecturer in Animal Behaviour and Physiology at Royal Holloway University of London. His main research interests focus on collective flight and group living in animals. His work focuses on how animals adapt their behaviour and ecology to the challenges of their environment, within the constraints of their own physiological and anatomical limitations. Within this framework, other areas of research interest include avian vision, aggression in fish living in low oxygen environments, flight feather moult and eggshell gas exchange. Before starting at Royal Holloway in 2014, Steve worked at the University of Birmingham, and the Royal Veterinary College.

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