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Introduction



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Coevolving advances in animal flight and aerial robotics

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Our understanding of animal flight has inspired the design of new aerial robots with more effective flight capacities through the process of biomimetics and bioinspiration. The aerodynamic origin of the elevated performance of flying animals remains, however, poorly understood. In this themed issue, animal flight research and aerial robot development coalesce to offer a broader perspective on the current advances and future directions in these coevolving fields of research. Together, four reviews summarize and 14 reports contribute to our understanding of low Reynolds number flight. This area of applied aerodynamics research is challenging to dissect due to the complicated flow phenomena that include laminarturbulent flow transition, laminar separation bubbles, delayed stall and nonlinear vortex dynamics. Our mechanistic understanding of low Reynolds number flight has perhaps been advanced most by the development of dynamically scaled robot models and new specialized wind tunnel facilities: in particular, the tiltable Lund flight tunnel for animal migration research and the recently developed AFAR hypobaric wind tunnel for high-altitude animal flight studies. These world-class facilities are now complemented with a specialized low Reynolds number wind tunnel for studying the effect of turbulence on animal and robot flight in much greater detail than previously possible. This is particular timely, because the study of flight in extremely laminar versus turbulent flow opens a new frontier in our understanding of animal flight. Advancing this new area will offer inspiration for developing more efficient high-altitude aerial robots and removes roadblocks for aerial robots operating in turbulent urban environments.

1. New reviews of aerial robotics and animal flight

Animal flight offers diverse and surprising solutions for extending aerial robot mission times [1,2]. This ranges from energy-efficient perching behaviours and silent flight to allocating computational resources more effectively during exceptionally long missions inspired by how birds sleep on the wing. Conversely, mechanical concepts and measurement techniques that have shaped the development of first airplanes and now aerial robots have been essential to underpin our understanding of animal flight mechanistically (figure 1).

For engaging in flight, takeoff and landing are critical behaviours to transition from the terrestrial to the aerial environment [3]. The short flight times of current small flying robots make perching, as animals do when they switch between terrestrial and aerial locomotion, especially valuable to achieve versatility. The review by Roderick et al. [3] not only presents state-of-the-art perching performance of aerial robots, but also provides a unique overview of the broad range of underused solutions that animals demonstrate for perching on natural and engineered surfaces in the environment. In addition to perching, Karydis et al. [6] discuss how careful component selection, energy-aware flight planners and controllers, and multimodal locomotion in general can greatly extend mission utility. The same concepts can be used to generate new hypotheses for interpreting animal flight behaviour. The behaviour of animals is often enabled through unique morphological specializations. Wagner et al. [4] review how the integument specialization of owls, unique silent feathers, are perhaps one of the most inspiring solutions available for making aerial robots quieter. Finally, a

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Figure 1. Knowledge transfer between the coevolving fields of animal flight and aerial robotics. (*a*) Biologists study animal flight using mechanical concepts such as force, energy, efficiency and advanced measurement methods from engineering, while engineers develop aerial robots inspired by key biological principles that enable animals to fly reliably and robustly in variable environments (image credit, William R. Roderick; [3]). (*b*) Example of how biologists collaborate with engineers using laser-based particle image velocimetry techniques to determine how the feather morphology of owls enables them to fly extremely silently (image credit, Andrea Winzer; [4]). (*c*) Example of how engineers can benefit from new biological discoveries. The poorly understood capacity of some birds, such as the great frigatebird, to sleep on the wing (image credit, Damond Kyllo; [5]) might inspire future aerial robots to budget their situational awareness and signal processing more effectively during extremely long missions.

mostly overlooked specialization in animal flight is that birds can sleep on the wing. Rattenborg [5] offers a critical introduction in this poorly understood aerial behaviour and shows how great frigatebirds sleep in unexpected ways and for remarkably small amounts of time. This ability offers new inspiration for managing situational awareness and information processing in flying robots.

2. Animal flight advances

Robust locomotion in cluttered and turbulent natural environments is showcased every moment of the day by animals flying in their aerial habitats. In particular, the wings of insects are known to become severely damaged over time due to interactions with plant surfaces and predators. Insects also have to fly in the turbulent wakes of plants, trees and the atmospheric boundary layer in general. Many birds, on the other hand, need to deal with annual moulting feathers on the wing, generate lift through unsteady aerodynamics and traverse at high speed through trees and forests. Seven reports offer new mechanistic insight into the biological solutions for all these and other challenges that may inspire engineers to develop new solutions to improve aerial robots (figure 2).

A key question for robots in general is what do you do if you fall from a building or out of a tree without being in flight orientation? To land on one's feet, aerial righting can make a difference. Zeng *et al.* [7] show how 2 cm wingless stick insect nymphs perform controlled mid-air righting with rapid rotations followed by a sudden deceleration within a mere one-third of a second by controlling leg motion. This study shows how legs do not only enable robots to locomote on surfaces, but may also improve their aerial agility and robustness. In contrast to robots, when flying insects suffer wing damage, they quickly adjust their wingbeat pattern and continue to fly [8]. Muijres et al. [8] show that flies can continue flying even with half their wing removed, and that they achieve this using a sophisticated control system. Based on these findings, they derived a general damage control algorithm for flapping flight that can be particularly insightful for roboticists. An unexpected function of the wings of insects with a pair of active wings is that they can vary the degree of overlap in gliding flight. Ortega et al. [9] show how such wing assembly changes affect the ability of the wing to generate leading-edge vortices and determine efficiency and stall behaviour in gliding flight. Limiting the effect of wing stall might be particularly important in turbulent air. Crall et al. [10] used a wind tunnel to study how perturbations in environmental turbulence experienced by foraging bumblebee workers affect their flight performance. The bees respond by shifting wing movement patterns, revealing strategies that could be emulated by insect-scale aerial robots.

To design flying robots that flap their wings like birds, we need to better understand how birds use unsteady

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Figure 2. New animal flight studies reveal strategies for robust locomotion ranging from aerial righting behaviours that commence after falling and flying with moulting or damaged wings to flying in atmospheric turbulence. (*a*) Aerial righting behaviour in stick insects (image credit, Anand Varma; [7]). (*b*) Fruit flies can fly fine with extreme wing damage (image credit, Florian Muijres; [8]). (*c*) Simulated wing overlap in butterflies shows how this affects the generation of leading-edge vortices in gliding flight (image credit, Rob Wood and Mirko Kovač; [9]). (*d*) Bumblebees adapt their wing movement patterns to negate turbulent flow (image credit, Callin Switzer; [10]). (*e*) The sandpiper is one of three species who all make use of similar unsteady aerodynamics to generate lift (image credit, Roi Gurka; [11]). (*f*) A study with a Jackdaw flying in a wind tunnel revealed how moult gaps in the middle of the wing, as opposed to more proximal or distal gaps, are most detrimental to efficiency (image credit, Aron Hejdström; [12]).

aerodynamics to generate lift. By reconstructing the air-flow patterns in the wakes of three species of wild birds, Gurka et al. [11] discovered unsteady aerodynamic effects may play a common role in their lift generation during forward flight. One key challenge these and other birds face is that they need to fly despite moulting wings. KleinHeerenbrink & Hedenström [12] quantified the consequences of moulting for the aerodynamic performance in vivo. They found that a gliding Jackdaw experienced maximal reduced aerodynamic efficiency for moult gaps in the middle of the wing. Inspired by this finding, they suggest that knowing which kind of wing damage may affect aerial robot performance most could inspire more robust robot designs. Finally, Ros et al. [13] contrast the challenge of flying through vertically oriented versus horizontally oriented clutter, by studying how pigeons fly through artificial forests. They found that, in comparison with flight past vertical obstacles, pigeons manoeuvred past horizontal obstacles faster and with less effort by selecting gaps most in line with their flight direction. The pigeons exhibited a remarkable kinesthetic sense of body position, adjusting wing stroke patterns to reduce risk of obstacle contact. Surprisingly, the pigeons moved their heads back-and-forth only in obstacle flights, possibly to augment depth-perception [13].

3. Aerial robotics advances

Dynamically scaled robot models that mimic aspects of animal flight have critically advanced our mechanistic understanding of low Reynolds number aerodynamics [14]. In this theme issue, we learn about studies of how wing 'stalks' modify hover performance in insects through the use of an advanced 'flapperatus'. An insect-scale tethered aerial robot takes this one step further by also simulating free body dynamics while station keeping in a lateral airstream. Finally, a robot embodying aeroelastic flapping – morphing bat wings enables the study of how wing morphology versus motion affects performance. In contrast to these laboratory-based robots, two other aerial robot platforms demonstrate effective flight control on the one hand, and diving at high speed into water on the other, thanks to the use of effective morphing wings inspired by bird flight (figure 3).

A poorly understood morphological aspect of many insect species is the offset between the root of the wing and the body formed by a 'stalk'. Phillips et al. [15] address this void in our understanding of petiolation. Using a robotic insect-like flapping device, they found that petiolate wings could give an insect-like flying machine high lifting capabilities but with compromised efficiency. It thus represents a trade-off between clearance and aerodynamic effectiveness. To determine how effectively insect-inspired flapping wings might negate lateral wind, Chirarattananon et al. [16] developed a new flight controller with disturbance rejection schemes capable of estimating and stabilizing the robot's position with respect to the ground in 0.8 ms⁻¹ lateral wind. The effectiveness of such flapping wings can be improved by aeroelastic tailoring and morphing them throughout the wingbeat like a bat. Using an artificial robot bat wing, Schunk et al. [17] show how wing kinematics has a much more profound influence on force generation than the aspect ratio of a membrane wing. Compared to the



Figure 3. A smorgasbord of robots used for studying how animals fly and embodying animal flight performance. (*a*) A robot flapping wing helped show how 'stalks' between the body and the wing affect its lift generation and aerodynamic efficiency (image credit, Richard Bomphrey; [15]). (*b*) An insect-scale flapping robot demonstrated how wing kinematics may contribute to flight stability in lateral wind (image credit, Pakpong Chirarattananon, Kevin Ma and Nick Gravish; [16]). (*c*) A robotic bat wing study showed that, because bat wings have a rather narrow range of wing slenderness, wing kinematics drives aerodynamic force generation (image credit, Cosima Schunk; [17]). (*d*) A robot with feathered wingtips uses wing morphing for both roll control and improving high-speed flight performance (image credit, Jun Shintake, Stefano Mintchev; [18]). (*e*) A bird-inspired aerial robot capable of diving into water (image credit, Ben Porter; [19]).

membranous wings of bats, birds morph their wings to much greater extent, whereas previous aerial robots demonstrated the effect of bird-like wing morphing on flight performance, Di Luca *et al.* [18] now demonstrate flight control through asymmetric wing morphing. Based on theoretical and experimental data, they show that fully deployed feathered wings improve robot manoeuvrability, while partly folded wings are beneficial for speed maintenance in strong headwinds. These new feathered wings, which can fold and unfold very rapidly, can also be used controlling the roll angle to initiate and control turning, without additional control structures such as traditional ailerons [18]. Finally, an aquatic aerial robot by Siddall *et al.* [19] is capable of diving into the water by folding its wings backward like a bird. The so-called 'AquaMAV' transitions passively from the air through the water surface at high speeds. The authors also show how the submerged robot can be launched through the water surface using a powerful water jet to propel itself out of the water. Despite these wonderful demonstrations, many of the transitional and unsteady fluid mechanic mechanisms of both robotic and animal flight remain unresolved.

4. Aerodynamic challenges and solutions

Much of the aerodynamics of low Reynolds number flight remains to be studied in sufficient detail [20]. The development of special wind tunnels for studying animal flight has helped resolve this, in particular, the Lund tunnel [21], which was used by KleinHeerenbrink & Hedenström [12] to study the rsts.royalsocietypublishing.org

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Figure 4. (Caption opposite.)

wake of moulting Jackdaws and the AFAR tunnel, which was used by Gurka *et al.* [11] to study unsteady wake dynamics in three birds, both featured in this special issue. However, two aerodynamic studies of wing aerodynamics published in this special issue underscore that more work in specialized low Reynolds number wind tunnels is needed (figure 4).

Widmann & Tropea [22] found that the chord-based Reynolds number impacts the formation of leading-edge vortices on unsteady pitching flat plates, a canonical model of flapping flight. The influence of secondary flow structures on the shear layer feed into the leading-edge vortex and subsequent topological changes at the leading-edge result from viscous processes typical for this low Reynolds number regime. Through flow measurement, the team shows how the Reynolds number determines the transition mechanisms Figure 4. (Opposite.) The aerodynamics of the wings of flying animals and robots is remarkably complicated due to low Reynolds number effects; a new wind tunnel at Stanford University has been especially developed to address this. (a) At elevated angle of attack, the flow over a pitching flat plate separates, of which the extent is surprisingly dependent on Reynolds number (image credit, Alexander Widmann; [22]). (b) At low Reynolds number the lift generation of a standard NACA 0012 aerofoil breaks down (image credit, Joe Tank and Geoff Spedding; [23]). This low performance helps explain why animals have very different airfoils in their wings to generate lift more effectively. (c) A new interdisciplinary wind tunnel at Stanford University for studying the aerodynamics of flying animals and aerial robots throughout the low Reynolds number regime (image credit, Janina Kress and Lentink lab). The wind tunnel is capable of generating an airstream with either exceptionally low (less than 0.03%) or very high turbulence (less than 50%). The schematic of the wind tunnel shows its overall design with a fan to generate wind, silencers at both ends to attenuate acoustic noise, an air smoothing section with a honeycomb and five screens to reduce turbulence, and a removable turbulence generator upstream of the test section. (d) Actual wind tunnel in the laboratory with a removable test section (black section) behind which the acoustic wall can be seen that separates the test section from the fan. The test section can be replaced with collector flaps to operate the wind tunnel as an open jet for experiments that require more access (image credit, David Lentink). (e) The first bird flying in the wind tunnel with the guest editor in the background (image credit, Linda Cicero).

leading to LEV detachment from an aerofoil: in particular, because it determines the viscous response of the boundary layer in the vortex-wall interaction [22]. Although the full consequences of these flow phenomena on the aerodynamic force development have yet to be determined, the study by Tank et al. [23] in this theme issue underscores the challenges in predicting these forces at moderate Reynolds numbers. One would think that the increasing quantitative power of both experiment and flow simulation would result in significant advances in understanding the forces acting on a complex object, such as a flapping bird, a hovering insect or a robotic bat. It turns out, however, that there is a large class of problems that have not been solved, involving what some have called 'non-computable flows'. These are flows and geometries that may be simple, but just because of their particular small size and low speed, represent one of the hardest problems in fluid mechanics. At the low Reynolds numbers of animal flight, very small differences due to uncertainty in model geometries, ambient turbulence disturbances, surface imperfections and dust, and even acoustic perturbations in the form of noise, can have a strong influence on the average overall aerodynamic forces of a wing [23]. Tank et al. demonstrate these aerodynamic challenges using a simple fixed wing with a classic aerofoil, the NACA 0012 aerofoil, which is known to poorly perform at low Reynolds numbers. Regardless, the negative lift at small positive angles of attack, which contradicts every theoretical aeronautical model constructed, was an unexpected find. To better understand the physics of these sensitivities and to avoid confounding factors in low Reynolds number animal and robot flight studies, a new bird wind tunnel was constructed at Stanford University dedicated to this area of research. The new wind tunnel has exceptionally low turbulence and low noise flow in one mode of operation, but can also generate higher levels of turbulent flow tailored in closed loop (figure 4). The opening of this wind tunnel earlier this year was the main reason for editing this special issue, which shows both current state-of-the-art research and future directions in animal flight research and aerial robot innovation.

Competing Interests. I declare I have no competing interests.

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introduction integrates the popular media summaries written by the authors of all 18 papers and does not represent original work of D.L., who compiled and summarized these materials after conceiving the overall organization of the theme issue. Finally, D.L. wishes to express his appreciation to Tim Holt for the wonderful editorial collaboration and William R. T. Roderick for proofreading this introduction.

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