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# Inspiration for wing design: how forelimb specialization enables active flight in modern vertebrates

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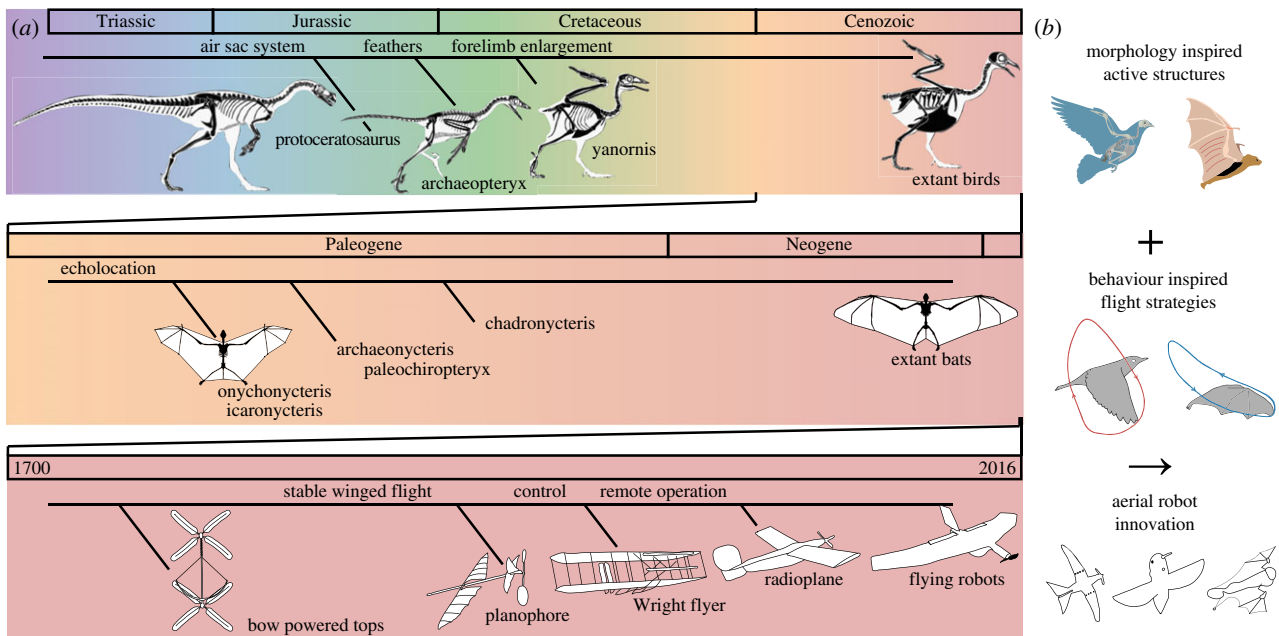
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Harnessing flight strategies refined by millions of years of evolution can help expedite the design of more efficient, manoeuvrable and robust flying robots. This review synthesizes recent advances and highlights remaining gaps in our understanding of how bird and bat wing adaptations enable effective flight. Included in this discussion is an evaluation of how current robotic analogues measure up to their biological sources of inspiration. Studies of vertebrate wings have revealed skeletal systems well suited for enduring the loads required during flight, but the mechanisms that drive coordinated motions between bones and connected integuments remain ill-described. Similarly, vertebrate flight muscles have adapted to sustain increased wing loading, but a lack of *in vivo* studies limits our understanding of specific muscular functions. Forelimb adaptations diverge at the integument level, but both bird feathers and bat membranes yield aerodynamic surfaces with a level of robustness unparalleled by engineered wings. These morphological adaptations enable a diverse range of kinematics tuned for different flight speeds and manoeuvres. By integrating vertebrate flight specializations—particularly those that enable greater robustness and adaptability—into the design and control of robotic wings, engineers can begin narrowing the wide margin that currently exists between flying robots and vertebrates. In turn, these robotic wings can help biologists create experiments that would be impossible *in vivo*.

## 1. Introduction

Millions of years of natural selection have shaped the wings of birds and bats, yielding versatile, robust and effective design solutions for flight. These vertebrates followed evolutionary pathways with different biomechanical constraints to succeed in ecological niches. Birds evolved from large, theropod dinosaurs from the Jurassic period [1,2], and gradually developed modern avian features such as air sac systems, feathers and enlarged forelimbs [2]. By contrast, bats evolved much later from small, quadrupedal mammals [3–6], eventually developing membranous wings, but the exact evolutionary path has yet to be elucidated. Both birds and bats went through intermediate evolutionary steps and transitional forms, most of which became extinct. This evolutionary vetting of body design resulted in two distinct classes of vertebrates with aerodynamically shaped forelimbs that enable active flight. Vertebrate wings can now adapt to variable atmospheric conditions [7] and facilitate feats ranging from non-stop transoceanic migrations [8] to complex manoeuvres for capturing prey [9]. Observations of animal flight first sparked the invention of flying machines, and continue to inspire and challenge engineers to develop aerial robots that can emulate these flight capabilities (figure 1). Currently, about 90% of bio-inspired aerial robots draw inspiration from insect flight (from 1984 to 2014 [16]). However, insect-inspired robots cannot fly as long, far or high, and have limited payload capacities due to scaling limitations



**Figure 1.** Birds, bats and man-made machines successfully took to the air through a long process with intermediate designs that became extinct and culminated in tried-and-tested solutions for flight. (a) Birds originated from dinosaurs [2] as theropod subgroups gradually evolved appropriate breathing systems, followed by feathers and enlarged forelimbs that eventually formed a wing capable of active flight. The origins of bat flight are less clear, but bats are likely to have evolved from a small, shrew-like mammal [4–6] which eventually developed enlarged hands to support a membrane wing [6]. This independent pathway occurred much more recently during a time in which birds had already established their current body plans. By contrast, the first man-made flying toys, hand spun helicopters, were only invented around 400 BC. Stable winged flight supported by a propeller was developed in the 1870s [10–12]. Since then, gradual steps (not shown) have resulted in the first radio-controlled model airplanes, and recently autonomous aerial robots guided by a satellite-based global positioning system. (b) Future aerial robot innovation will benefit from harnessing the morphological and behavioural solutions that enabled vertebrates to conquer the skies. Avatars adapted from [2,6,10,13–15], photograph from Guy Ackermans and open source photographs.

associated with their small size [17]. By contrast, scaling effects are much more favourable for realizing hand-sized aerial robots with high performance and payloads. Consequently, there exists an opportunity to improve the design of aerial robots inspired by how birds and bats fly. These improved designs could reach a level of robustness and adaptability that opens the door for widespread use of aerial robots in applications such as package delivery, search and rescue, and cinematography.

In contrast with the millions of years of evolution that shaped bird and bat flight, flying machines arose only when humans began developing more advanced tools. The first known flying machine was the ‘Chinese top’ developed around 400 BC—a rotor made out of feathers attached to a stick that was spun and released by hand [10]. Toy fliers and hypothetical designs persisted, but stable winged flight was not successfully implemented until the 1870s, with the development of planophores with propellers and ornithopters with flapping wings [11]. These early inventions led to the development of the Wright flyer as well as smaller, radio controlled planes, ultimately resulting in today’s flying robots, or drones. Given the comparatively brief natural history of human design in the realm of flight, and the similarities between the process of engineering design and natural selection, it is compelling to study bird and bat biomechanics to find new ideas for designing flying robots. However, morphological and behavioural adaptations exhibited by these animals serve other purposes as well, such as terrestrial locomotion, protection against harsh climates or the attraction of potential mates. Therefore, not all adaptations are well suited for flight, so discretion is necessary when selecting biological features to inspire engineering design.

In this review, we focus on the forelimb adaptations in birds and bats that are relevant to enabling effective flight. We begin by comparing and contrasting wing morphology specialization in birds and bats that accomplish the complex task of flapping flight. Throughout this comparison, we highlight which biomechanical and physiological functions remain to be understood. We examine the morphological differences on a skeletal and muscular level in order to identify the role that each plays in controlling the wing surface. This leads to a discussion of integument specialization, in which we discuss how bird feathers and bat membranes help enable robust and efficient flight. We conclude this section by comparing properties of vertebrate wing morphology with structures and actuators currently used in flying robots. Next, we describe behavioural adaptations exhibited by birds and bats, both in terms of their flight kinematics and control strategies used for manoeuvring. Together, morphological and behavioural adaptations govern the aerodynamic performance envelope of birds and bats, just as the structure and actuation of robotic wings governs their performance. This enables us to discuss the functional consequences of differences among birds, bats and robots in terms of their flight performance, manoeuvrability and robustness. Finally, we address current progress and future challenges in designing bioinspired aerial robots, as well as opportunities to use these robots as mechanical models to better understand biological flight.

## 2. Morphology as active structures

Flying animals and robots require structures to span the aerodynamic lifting surfaces and hold together the actuators that

move and change the shape of the wing. In robots, structures and actuators are typically distinct subsystems. In flying vertebrates, these functions are integrated in the musculoskeletal system that shapes the wing and generates its motion. The skeletal system forms a rigid structure that connects the wing to the body and defines its general shape. Muscles actuate this internal structure, and the integument furnishes the external layers, refining the aerodynamic outer surface that generates lift.

## 2.1. Skeletal adaptation

Flying vertebrates move their forelimbs in different patterns than terrestrial vertebrates. However, their skeletal structure is homologous. The proximal arm-wing is formed by the humerus and the distal arm-wing by the radius and ulna. These connect via a wrist to the hand wing, which is spanned by digits. The hand and arm bones support the wing's lift generating surfaces. The forces generated during flight cause unique loading patterns that require different adaptations from terrestrial vertebrates. While the net reaction force is about two to four times body weight in flapping flight [18,19], which is similar to reaction forces in running [20], the loading pattern is different. In addition to high compressive and tensile loads, both bird and bat wings must also resist high torsional loads [21–24] (figure 2*a,b*), due to the wing's flapping motion and lift generation. Compared with similarly sized land animals, bird forelimb bones are subjected to higher shear forces [30] and lower bending forces [30]. Accordingly, bird wing bones are capable of withstanding significantly more force in shear than in bending [30].

The wing bones support flight loads in two primary ways—physical and structural properties. Physically, the skeletal mass of birds, bats and terrestrial mammals makes up a similar proportion of body weight [31], and the humerus density is similar [26] (figure 2*c*). However, the bone structure varies at both the macro- and the micro-level. At the macro-level, both bird and bat wings differ in shape from terrestrial mammals [22]. In birds, bones are typically larger in diameter and have thinner cortical walls [22] (figure 2*d*). This structure enables a larger resistance to both bending and torsion per unit weight than found in other vertebrates [32]. Bats only have this thin-walled, large diameter bone structure in their humerus and radius [22], and not nearly to the same degree as in birds. By contrast, bats have large diameter bones closer to the body and small diameter bones more distally, which gives the wing a lower moment of inertia and reduces power requirements [24]. At the micro-level, laminar bones enable better torsional resistance [33]. Bird wing bones are frequently highly laminar with circular canals [28,34] (figure 2*c*), whereas bat wing bones lack this laminarity [35].

Beyond the structural design of individual bones, the skeletal layout determines how well loads are supported. In birds, the radius and ulna lie parallel with an offset between them (figure 2*a*), which increases their combined resistance to bending in the wing plane [23]. Each bone is adapted to its primary load; the radius experiences primarily tensile forces, while the ulna experiences primarily compressive forces [28]. This arrangement also allows coupled elbow and wrist motion, minimizing the need for bulky actuators (muscles) in the distal portions of the wing [23,36]. This elbow–wrist coupling is not present in bats, because their

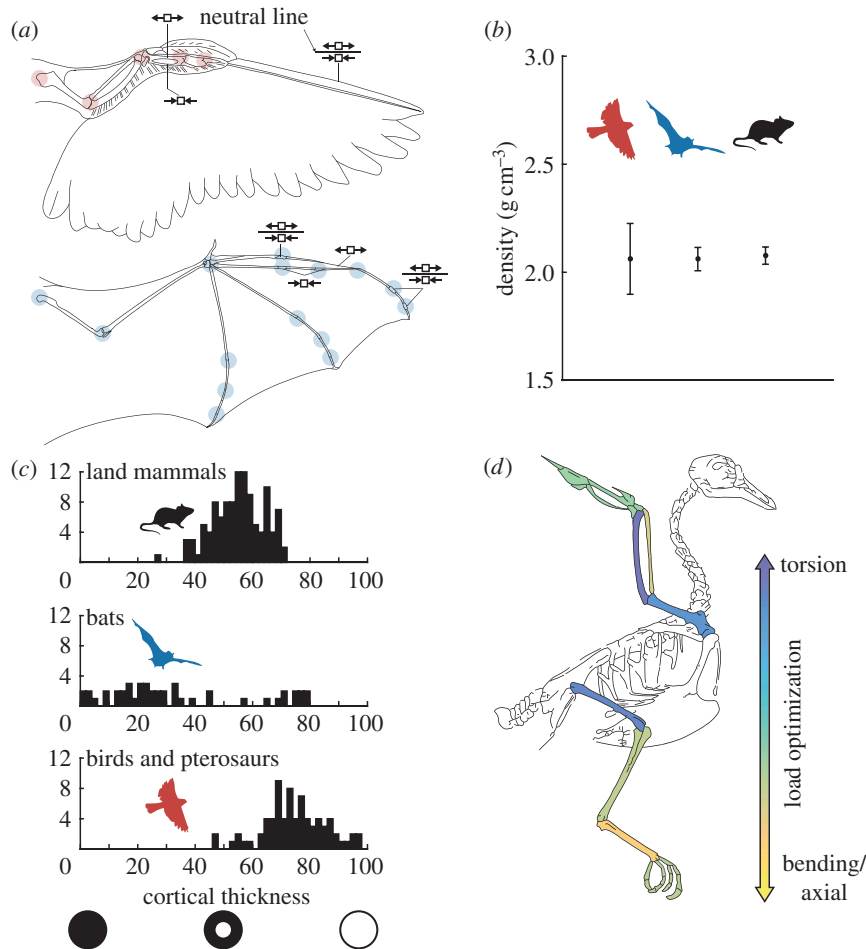
ulna is degenerate and does not extend all the way to the wrist [37]. The wrist bones of birds lock in the loading direction to resist dislocation from high forces present during the downstroke [36,38]. By contrast, bat wing bones are more flexible and deflect under flight loads in ways that presumably improve flight performance [39]. The actual musculoskeletal mechanisms coordinating the motion between vertebrate wing bones and their connected integuments are not well understood. Better understanding of these mechanisms can inspire new load-bearing structures for dynamically morphing robot wings.

## 2.2. Muscular function

Like other vertebrates, avian and bat forelimbs are driven by a complex network of muscles and tendons responsible for tasks varying from propulsion to minute adjustments in wing shape. However, the specific groups of muscles that produce each motion are currently postulated from either anatomical analysis alone or a few studies of muscle activation and shortening in a select number of muscles [40,41]. During anatomical studies, muscle function is often categorized by tensioning the muscle and observing the motion produced across one or multiple joints, such as those portrayed in figure 3*a* [45] for birds and for several bat species [46–48]. This provides insight into what a muscle could be responsible for, but not necessarily its *in vivo* function. This is particularly relevant for muscles that act over two separate joints, such as the extensor carpi radialis (figure 3*a*). Based on anatomic studies alone, one might conclude that the muscle flexes the elbow while extending the hand [45]. However, *in vivo* the elbow and hand extend together, because the aforementioned skeletal system within the wing automatically couples extension and flexion of the wing joints [36]. This bird-specific adaptation simplifies feathered wing morphing [36]. Muscle function that works in opposition to this skeletally coupled motion would not produce efficient motion and demonstrates the need to record *in vivo* muscle activity.

Supplementing anatomic studies with knowledge of muscle activity can help determine whether the muscle is working to extend or flex the wing. Muscle activation is measured using electromyography (EMG), which records the electrical signal sent from motor neurons innervating the target muscle. Correlating the activation of a muscle with wing kinematics allows researchers to narrow the range of possible muscle functions. The most detailed EMG study in birds so far (figure 3*b*, [40]) shows activation of various wing muscles throughout the wingbeat cycle, which helps elucidate some of the functions in question [40]. In the case of the extensor carpi radialis, EMG data show that it is only activated while the wing extends [40], while other more powerful muscles, including the humerotriceps, are activated to prevent flexion at the elbow [36,41]. This illustrates why the *in vivo* function of many groups of wing muscles needs to be recorded to determine their function in concert, without which the wing muscle function remains hypothesized (figure 3*d*).

The way muscles generate force and change length when they are activated determines if they generate net mechanical power, or alternatively, if they store or dissipate energy [49]. This function has been best studied for the primary flight muscles of birds and bats, the pectoralis and supracoracoideus.

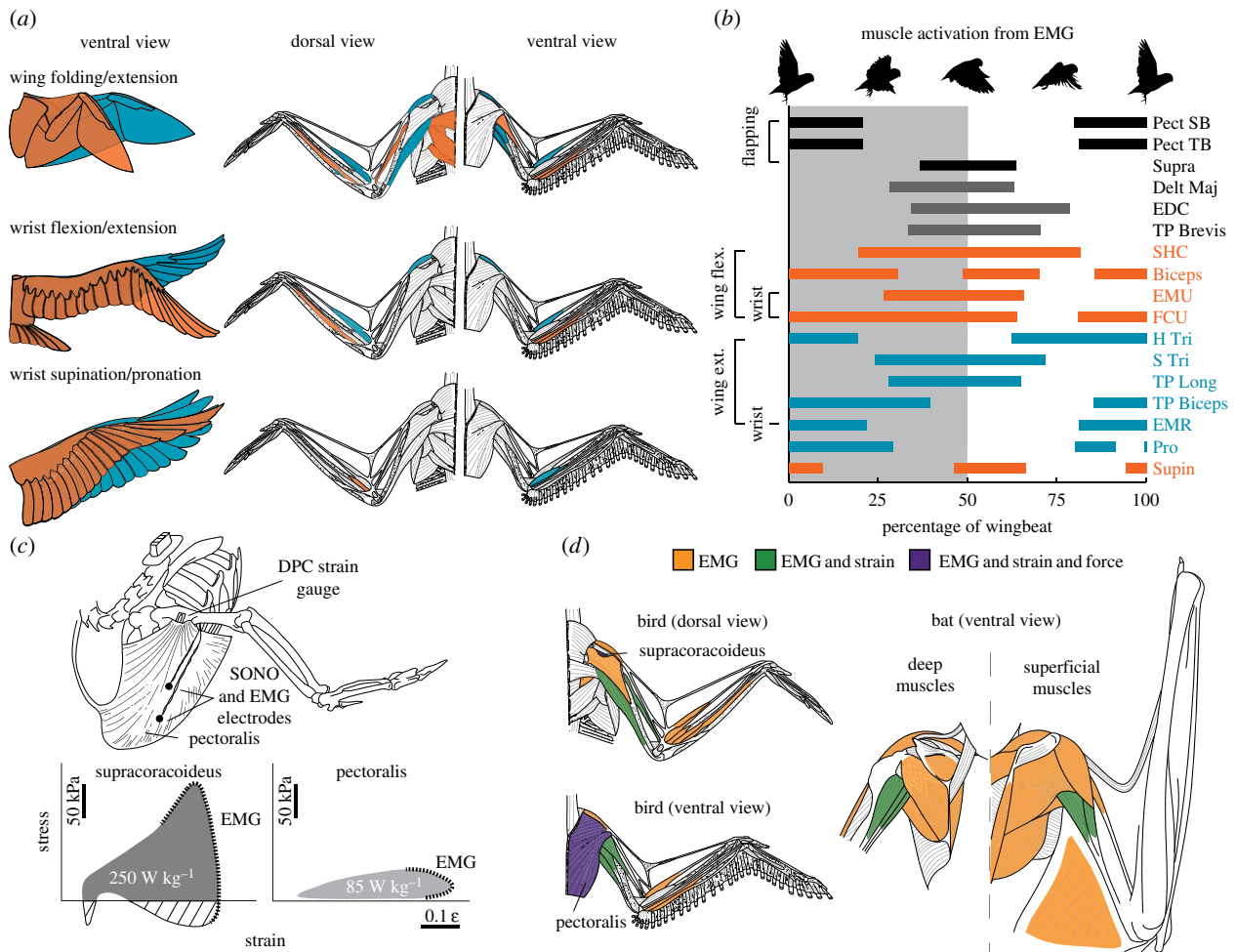


**Figure 2.** Wing bones differ between birds and bats, but both are capable of resisting flight loads effectively. (a) In both bird and bat wings, bones resist the integrated shear, bending and torsion loads due to aerodynamic and inertial force distribution [23]. In birds, the load-bearing chain of bones along the leading edge connect to articulated flight feathers that form the wing. Bats have a set of fingers that extend from the leading to the trailing edge to tension the skin membrane that forms the wing. These fingers, along with the hind legs, are thought to offer bats more skeletal degrees of freedom to change wing shape than birds ([25]; light blue versus red circles). (b) Despite the adaptation of bird and bat skeletons for active flight, their bones have the same density as land mammals [26], but have lower mineralization that slightly decreases weight [27]. (c) While bat wing skeletons are not particularly light, bird wing skeletons use thin-walled, large diameter bones, enabling higher strength and stiffness per unit mass [22]. However, bat wing bones have smaller diameters in the more distal segments [24,27], and larger diameter bones in the proximal segments, which decreases the moment of inertia during flapping. (d) Bone morphology varies in birds primarily in response to the need to resist bending versus torsional loading. As a result, wing bones possess more torsionally resistant cross-sectional shapes, while leg bone shapes offer greater axial strength and bending resistance [28]. Figures adapted from [22,26,29], bird skeleton avatar from open source image.

Simultaneous measurements of muscle activation, length change and force production define each muscle's work loop, which represents the net mechanical work produced throughout a wingbeat (figure 3c). Length change is typically measured using sonomicrometry, piezoelectric crystals implanted into the muscle fascicle that signal ultrasonically to each other to determine separation [42], which is used to calculate strain (figure 3c). A newer technique tracks radiopaque markers using fluoroscopes [50]. Force is calculated from strain measured at the insertion points where the flight muscles connect to the humerus (figure 3c) [42]. To calculate force from the strain, a correction factor is needed that is subject to inaccuracies from the required post-mortem calibration [42] and the highly simplified aerodynamic, inertial and internal wing force models [43]. Nevertheless, this approach has greatly advanced our understanding of the antagonistic function of the pectoralis and supracoracoideus. Despite the fact that the pectoralis primarily powers the downstroke and the supracoracoideus primarily powers the upstroke and supinates the wing, they appear to operate simultaneously during stroke reversal [42]. Although this is energetically costly, it provides

greater stability and control over the joint [51]. These measurements also suggest that the supracoracoideus produces a much higher mass-specific power than the pectoralis in flight (figure 3c). One possible explanation for this is elastic energy storage in the supracoracoideus tendon [42].

Tendons serve as a tough elastic attachment between muscles and bones that are stretched and relaxed due to muscular contractions or joint movement [52,53]. Since tendons are passive elements within the wing, they can be used as an energy saving measure for bats and birds [52,53]. For example, in pigeons (*Columba livia*), elastic energy storage in the supracoracoideus tendon could provide 28–60% of the network that the supracoracoideus performs during the downstroke, which is then released during the upstroke [42]. Although tendons can play a large role in muscle actuation and efficiency, flight tendon function has not been measured *in vivo* in any of the bird wing muscles and only in a few bat wing muscles. Tendon properties including size, stiffness and composition determine tendon stress due to limb motion and thus affect function [52–54]. Therefore, the extent of energy storage within the tendon is difficult to determine from



**Figure 3.** A complex set of interacting muscles allows birds and bats to flap and morph their wings, but current understanding of individual muscle function *in vivo* is limited. (a) Bird wing folding and extension, wrist supination and pronation, and wrist flexion and extension require different groups of muscles to be activated to generate the suite of stress–strain combinations required for wing morphing (left). The muscles that have been associated with each movement are highlighted using the corresponding wing motion colour (right). (b) Electromyography (EMG) studies show which muscles are active during which portions of a wingbeat cycle (grey area, downstroke). Muscles are grouped and coloured by associated motion from (a), flapping flight power muscles (black), and other (dark grey). Muscle names are abbreviated as pectoralis major pars thoracicus sternobranchialis (Pect SB) and thoracobrachialis (Pect TB); supracoracoideus (Supra); deltoideus major (Delt Maj); scapulohumeralis pars caudalis (SHC); tensor propatagialis pars longus (TP Long); pars brevis (TP Brevis) and pars biceps (TP Biceps); biceps brachii (Biceps); humerotriceps (H Tri); scapulotriceps (S Tri); extensor metacarpi radialis (EMR) and ulnaris (EMU); extensor digitorum carpi (EDC); flexor carpi ulnaris (FCU); pronator superficialis (Pro); and supinator (Supin). (c) The deltopectoral crest (DPC) on the humerus of some birds allow for *in vivo* pectoral and supracoracoideus muscle force measurements in concert with muscle contraction (SONO, sonomicrometry) and activation (EMG, electromyography) measurements. The force and contraction can be recalculated as muscle stress and strain, which define the muscle work loop. Pigeon flight muscle work loops reveal that the supracoracoideus generates a much higher mass-specific power than the pectoralis, potentially due to elastic storage in its tendon during the downstroke. (d) An overview of the muscles that have been studied quantitatively in birds (left) and bats (right), coloured by measurement method: EMG, contraction measurement to calculate strain, and strain measurement to calculate force. Figures adapted from [15,37,42–44] with data based on [36,40,45].

anatomic analysis alone. *In vivo* characterization of the phase lag between the associated muscle contraction and joint movement provides insight into a tendon's potential to store energy. Such analysis in the bat triceps suggests that energy stored during the end of downstroke is released to aid elbow extension in late upstroke [50]. A similar phase lag is apparent in the humerotriceps of pigeons [41].

Many of the flight muscles for both bats and birds have not undergone any of the aforementioned techniques for determining *in vivo* function. The most widely used technique for analysing muscles within both the bird and bat wing is EMG. An EMG study performed in birds included 17 of the flight muscles of the wing (figure 3d) [40]. A similar EMG study in bats included 18 flight muscles (figure 3d), predominantly for the proximal flight muscles in the back and shoulder [55]. Despite the fact that both of these EMG

studies are exceptionally inclusive, activation is unknown for a similar number of remaining muscles. For example, Videler [56] estimates that there are 45 muscles in a bird wing, although there is no consensus on the total number of muscles in bird and bat wings. This uncertainty over a seemingly simple concept underscores the open challenge to decipher muscular function by expanding *in vivo* measurements of the remaining wing muscles (figure 3d). Whereas the primary flight muscles are relatively well understood, the function of the wing muscles in both birds and bats is primarily hypothesized from anatomic studies and limited EMG studies for just a few flight behaviours [40,55,57,58].

### 2.3. Integument specialization

Although the musculoskeletal structures of birds and bats are similar, the integument specializations of their wings provide

different solutions to forming effective aerodynamic structures. Bird wings are composed of feathers, individual keratin elements that work together to form a wing. Bat wings, alternatively, comprise a thin membrane spanning between the body and the bones of the arm and hand. Feathered wings and membrane wings have vastly different architectures, but both are adapted for efficient flight [59].

### 2.3.1. Feathered wings

In a bird wing, the main flight feathers, the primary, secondary and tertiary remiges, collectively form an aerofoil [60]. Their unique integumentary structures have hierarchical features ranging from the macro-scale to the micro-scale, which improves flight performance. In each flight feather, softer vanes frame the stiff central rachis. The vanes are comprised of parallel barbs which have a central shaft, the ramus, with branching barbules [60]. The micro-scale barbules hook the barbs together, forming the air-resistant vanes (figure 4a) [62]. This hierarchical geometry of feathers enables strong, compliant, and lightweight structures [62]. Feathers are tailored for their function in flight; vanes are more resistant to upward aerodynamic forces, which feathers experience more typically compared with downward ones [62]. Modern primary feathers have evolved specialized asymmetric vanes, with shorter barbs leading and longer barbs trailing the rachis [67]. Asymmetry in feathers has been thought to improve aerodynamic function; moving the rachis towards the leading edge gives each feather a more aerofoil-like cross-section [68,69]. Asymmetry also serves to prevent undesired aeroelastic flutter during flight, increasing the air velocity threshold by modifying feather stiffness and geometry [70,71]. In special cases, aeroelastic flutter can be desired; birds use the phenomenon to produce sound. Male hummingbirds dive at high speeds in a mating display, spreading their tail feathers at the correct moment to produce a chirp-like sound due to tail feather flutter [72]. Feather mechanical properties depend on the vane, formed from barbs with independently variable lengths and attachment angles [67]. The middle and tip of each flight feather can resist larger out-of-plane forces compared with the base, which is protected by smaller covert feathers [62]. Leading edges of the outermost primaries comprise barbs with small attachment angles, which increases stiffness to resist high forces, in contrast to the more compliant trailing edge vanes [67]. Beyond driving stiffness properties, the hooking barbule geometry also enables vanes to be reversibly 'unzipped' when exposed to high external loading. This Velcro-like coupling function protects the feather from permanent damage; barbs are subsequently connected again through preening [73].

The arrangement of feathers in the wing fulfils specialized aerodynamic functions that are thought to be analogous to high-lift devices found on fixed-wing aircraft. These ideas stem from aeronautical concepts used to interpret morphology. The feathered thumb of a bird wing, the alula, prevents stall at low speed flight [63]. Early studies hypothesized that the alula functions similarly to a leading edge slat in aircraft wings (figure 4c, top), delaying stall at high angles of attacks [74]. More recent work provides evidence that the function of the alula is more akin to a vortex generator [63], delaying flow separation like an aircraft's strake, which facilitates unsteady manoeuvres [75]. Covert feathers

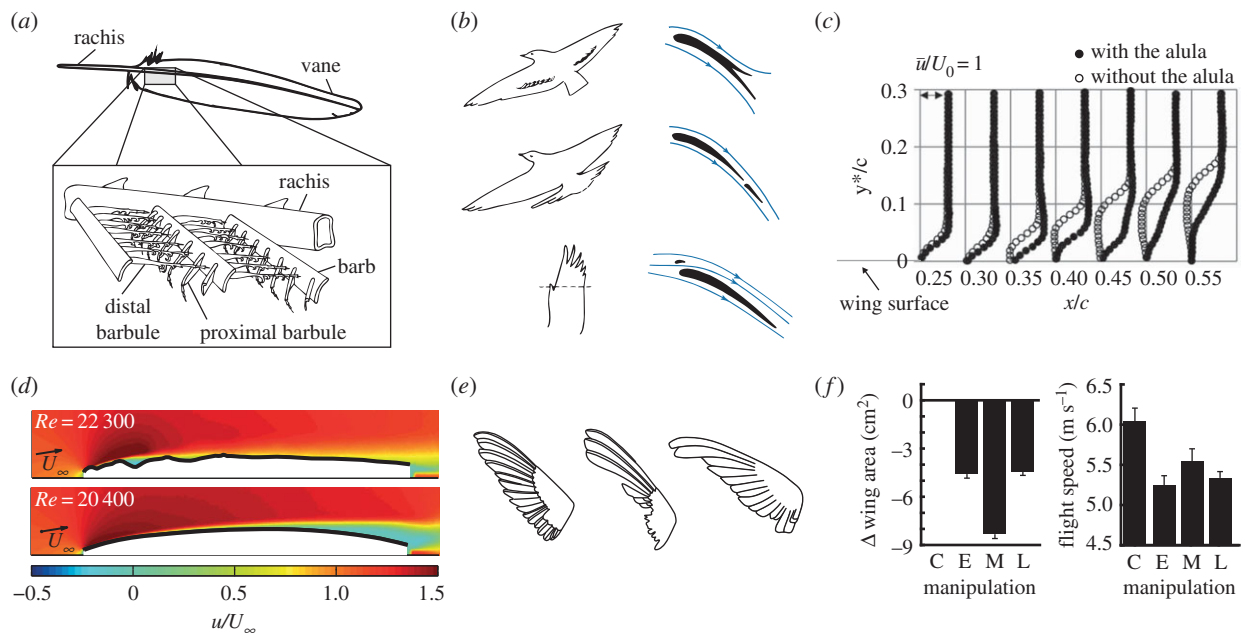
further improve aerodynamic performance of the wing at high angles of attacks. These feathers on the upper surface passively deflect upwards near stall (figure 4d, middle), which prevents backflow of separated airflow analogously to split flaps [29]. Additionally, long forked tails of certain bird species can be spread close to the leading edge of the wing (figure 4d, bottom). This is thought to extend the lifting surface area and to keep flow attached further along the trailing edge like a Fowler flap on an aircraft [29]. Lastly, the emarginated outer primary feathers found in soaring birds enable them to create slotted wing tips. Individual feathers separate, forming tip sails consisting of individual aerofoils that parallel the winglet structures found on aircraft [76]. These wing tip slots reduce induced drag due to upwash from the tip vortices [77].

At the wing surface level, feather morphology affects flow separation, and specialized feathers can help detect it. The overlapping feather vanes form valleys and the thick rachis form bumps that together create as much as 1–2% surface roughness with respect to the chord length in small birds (figure 4d). This roughness prevents flow separation at lower Reynolds numbers by making the boundary layer turbulent at cruise angle of attacks [64]. Slender hair-like feathers, called filoplumes, protrude from the skin and transfer vibrations from adjacent feathers to mechanoreceptors in the skin [78]. Filoplumes are found on both the avian wings and body, originating within the follicle of a contour or flight feather. Studies of the discharge frequencies of the filoplume mechanoreceptors suggest that birds may be able to detect both flow speed and flow separation from feather vibration [79].

Although each feather contributes to shaping the wing, they are redundant; birds can fly with damaged feathers or with missing feathers while moulting. To compensate for the loss of wing area, birds can adapt their behaviour. For example, starlings prefer to spend more time perching, fly slower, and decrease body mass when undergoing moult (figure 4f) [66]. Likewise, hummingbirds hover less and also reduce body mass during moulting, which reduces the vertical lift force required to hover [65]. Lowering body mass reduces the loading of the 'actuator disc' swept out by the wing, and thus increases hover efficiency. The loss of secondary feathers impacts flight performance less than loss of primary feathers, highlighting the role the primary feathers have in flight (figure 4e) [65]. Much is still not known about the resiliency of birds to missing feathers and their coping strategies, but this robustness to damage can be a source of inspiration for developing more robust robot wings. While feathers are a unique integument specialization for bird wings, they are not the only solution for lifting surfaces.

### 2.3.2. Membrane wings

In contrast to feathered wings, membrane wings are continuous structures spanning from a bat's body to the digits of the hand (figure 5a). Membranes comprise skin lined with thin muscle and elastin fibre bundles, resulting in a highly anisotropic structure [82]. Elastin fibres give bat wings their wrinkled texture, allowing spanwise elongation parallel to the fibres. This enables bats to stretch their wings outwards along the unfolding axis, keeping the membrane taut [83,84]. This anisotropic structuring illustrates an example of bat skin specialization to meet the needs of flight. Bat skin has the greatest failure strain perpendicular to the



**Figure 4.** Bird wings have hierarchical features ranging from the macro-scale of specialized feathers to the micrometer-scale barbules, enabling aerodynamic properties for flight performance. (a) Microstructures create hierarchical geometry, which drives the aerodynamic properties of feathers [61]. The rachis has branching barbs that in turn have branching barbules that shape the feather vanes. Figure adapted from [61,62]. (b) Hypothesized functions of feathers for improving wing lift (adapted from [29]). (Top) Covert feathers as split flaps. (Middle) Tail feathers as Fowler flaps. (Bottom) Alula as leading edge slat. (c) More recent research demonstrates that the alula generates a tip vortex that induces a higher momentum to keep the flow attached across the wing. Figure adapted from [63]. (d) Velocity field over a rough surface representative of a feathered swift wing (top) and smooth surface typical for aerial robots (bottom). Surface roughness helps prevent flow separation at lower Reynolds numbers at cruise angle of attack [64]. (e) Ruby-throated hummingbird (*Archilochus colubris*) moulting patterns and feather manipulations with significant wing area loss still generate sufficient lift for flight. (Left) Fully intact wing. (Middle) Intact three outer primary feathers, with inner primaries growing and secondary feathers plucked. (Right) Intact outer two primary feathers with inner primary and secondary feathers growing [65]. (f) European starlings choose to fly slower when missing feathers due to moult. Plot of wing area per manipulation (left) and level flight speed per manipulation (right). C, control; E, early-stage moult; M, mid-stage moult; L, late-stage moult [66]. Figures adapted from [29,61–66].

wing bones, allowing the skin to withstand aerodynamic loads without tearing [83]. Skin stiffness, on the other hand, is greater parallel to the bones. The reduced stiffness perpendicular to the bones enables the wing shape changes needed for flexion and extension of the wing [83]. These properties, skin toughness and stiffness, enable a thinner, more lightweight membrane capable of bearing flight loads. Besides the passive material properties, bat skin also has active elements. Embedded in the membrane are muscle arrays called the plagiopatagiales proprii that, when activated, change the stiffness of the membrane, potentially allowing bats to control wing deflection [80]. EMG data of the plagiopatagiales muscles track activation primarily during the downstroke (figure 5b), supporting the hypothesis that they aid in aerodynamic force production [80].

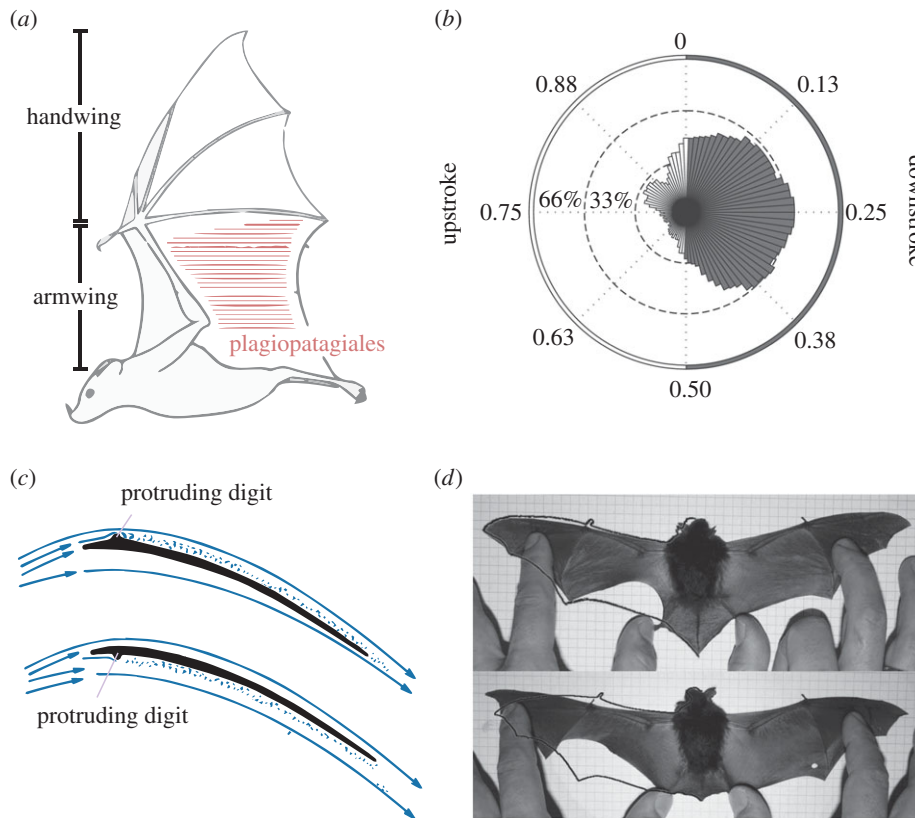
Aerodynamic loads cause the membrane of a bat wing to deflect and passively change shape, resulting in highly cambered wings that generate more lift, which aids in manoeuvrability by allowing a wider range of flight speeds [85]. Unlike birds, bats can actively control the camber in their wings by flexing the phalanges of the fifth digit or by lowering their hind limbs. This lowers the trailing edge, creating a structure similar to an aircraft (plain) flap [86]. Beyond camber, the wing inner area is actively adjusted to keep the outer wing taut and to avoid drag from membrane flutter [87]. Together, protruding arm bones and digits from the thin membrane act as turbulence generators, keeping the flow attached at higher angles of attack during slow flight (figure 5c). Similar to feather features in birds, skin wrinkles and hairs in bats create roughness that further reduce flow

separation [29]. The hairs on the wing are also thought to sense airflow, acting like filoplumes in birds. Depending on their length and geometry, the hairs respond to the boundary layer flow. The resulting motion is detected by mechanoreceptors at their base [88]. Behavioural studies suggest that the arrays of short thin hairs found on the trailing edge of the wing membrane help with manoeuvrability and stall avoidance [89].

Delicate membrane wings can suffer damage due to predators, injury or exposure to fungus, like the one responsible for bat white-nose syndrome [81]. While membranes can be regenerated over time, bats must continue to fly and forage for food with damaged wings to survive [90]. Captured bats with asymmetrically damaged membranes (figure 5d) have lower body mass and avoid complex flight manoeuvres compared with those with intact wings [81]. Similar to findings in hummingbirds, lowering body mass may lower the cost of lift generation, but may also be a consequence of reduced foraging ability [81]. Further studies across more species could shed light on how bats of different sizes adapt with different levels of wing damage, which can guide safe design of active membranes for robot wings. Despite the lack of a more redundant solution like the multitude of feathers in a bird wing, the bat membrane wing forms a robust and effective solution for flight.

## 2.4. Robotic structures and actuators

The majority of morphological flight specializations found in birds and bats have yet to be implemented in flying robots.



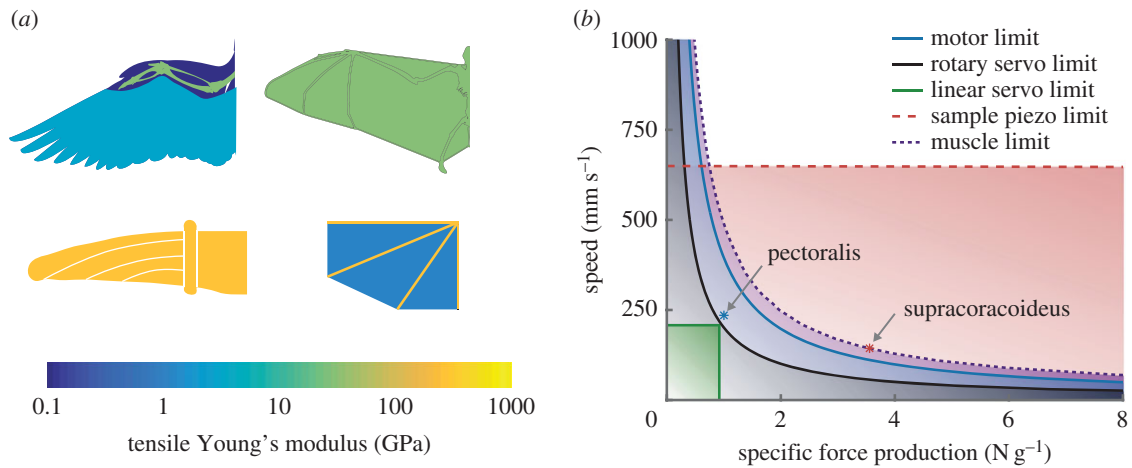
**Figure 5.** Active and passive membrane elements build the aerodynamic lifting surface of a bat wing, creating highly cambered wings that achieve high manoeuvrability within a wide range of flight speeds. (a) Bat membrane wings span from the body to the digits of the hand and comprise skin lined with elastin fibre bundles and thin muscles called the plagiopatagiales [80]. (b) Plagiopatagiales activation (EMG) during flight at  $5.5 \text{ m s}^{-1}$  during the wingbeat cycle. Radial column height represents percentage of wingbeats with muscle activity [80]. (c) Protruding digits may act as turbulence generators to help prevent flow separation in slow flight. Figure adapted from [29]. (d) Bats found with membrane damage in *Myotis albescens* (top) and *Myotis nigricans* (bottom) compared with intact wing outline still fly in the wild [81]. Figures adapted from [29,80,81].

Flying vertebrates have lightweight, flexible and streamlined wing structures. The analogous structures created from engineering materials share similar characteristics, but have limitations. A broad comparison of material stiffness, as measured by Young's modulus (figure 6a), reveals that engineering materials share similar or better stiffness properties, but are still unable to match the performance of biological architecture with its unique multi-level organization. For example, a recently developed silicone-based membrane closely matches the area density and tensile modulus of bat skin, but still cannot capture the full complexity of bat skin, which includes anisotropic elastin fibre bundles and muscle arrays that actively tension the membrane [84]. Biological materials harness hierarchical layers of organization and complexity, using molecular building blocks to form cells that in turn build the skeleton, muscles, organs and other structures that shape the entire organism. Bio-inspired engineering materials still need further development to capture the hierarchical complexity of biological structures, but emerging technologies such as three-dimensional printing with micrometer-level resolution hold promise for additional levels of features [97]. Besides mimicking passive material properties, smart structures have been developed to mimic active traits. For example, a bird-inspired airplane wing design can tune its wing shape by using deformable modular robotic elements [98]. Additionally, shape memory alloy actuators made out of nickel–titanium have been used to morph aircraft wings to change aerofoil parameters such as camber [99]. Although this specific form of wing morphing

has yet to be recorded in birds *in vivo*, it captures the active morphing that animals such as bats [100] perform to enhance flight control. Active sensory feedback combined with smart structures is another area ripe for bio-inspired advances. Animals integrate effective flow sensing networks like the filoplumes on birds and hairs on bat wings in their flight control [79,88]. Bio-inspired hair-like flow sensors have been previously developed [101], and seamlessly integrating such sensors with actively deformable structures would further advance bio-inspired flight control.

Birds and bats actuate their wings with muscles, structural actuators that both aerodynamically shape the wing and power movement, which is notably different from current robotic actuation. Muscles lend compliance to the skeletal structure, allowing actuation and wing shape changes tailored to a wide range of different environments and situations. Currently, robotic actuators are typically separate from the load-bearing structure, unlike muscles that both handle loads and impart displacements. Incorporating the mechanical integration of muscles into effective robotic structures would reduce weight and enable direct structural shape changes. In contrast to current robot actuators, flying vertebrates have musculoskeletal systems that provide rapid high-force and high-torque actuation [102]. A force production versus speed plot (figure 6b) compares the performance envelopes and limits of muscles and robotic actuators. The power requirements for replicating vertebrate wing kinematics with a robot can exceed the abilities of existing actuators, which makes it difficult to attain





**Figure 6.** Engineered materials and actuators reach and even exceed the properties of biological structures and actuators, but animals still outperform robots in most flight scenarios. (a) In birds, a relatively stiff leading edge supports compliant feathers. In bats, the overall structure has similar stiffness in tension, but the membranes are compliant in compression while the bones are not. Bio-inspired robot wings (bottom row) mimic characteristics from birds and bats, but generally have more uniform material properties. Superior material properties in engineered vehicles do not necessarily produce better flight performance as higher level structures are comparatively rudimentary, less robust and cannot be morphed easily (properties from [22,26,83,91,92]). (b) Currently available servos and motors (green, purple and black curves) perform poorly relative to steady-state muscles (Hill type muscle model), operating slowly and generating lower forces for a given speed. More advanced materials such as piezoelectric [93,94] and nitinol shape memory alloys actuate quickly and with high forces, but lack the displacement capabilities of muscles. (Nitinol shape memory alloy actuators are not shown, because their force production per gram is much higher than  $8 \text{ N g}^{-1}$ ). Muscle limits (dashed purple curve) are calculated with Hill type muscle models [95] using cockatiel (*N. hollandicus*) pectoralis properties [96]. Sample values for the pectoralis and supracoracoideus are shown for a pigeon [42]. Servo and motor lines reflect best available gram-scale actuator options at the time of writing (Hitec HS-81MG rotary servo, Spektrum linear 2.9 g servo and Maxon EC 4 motor). A representative piezoelectric actuator line is shown for milligram scale actuators like those used in the RoboBee robots [93]. Cartoons adapted from [6,15].

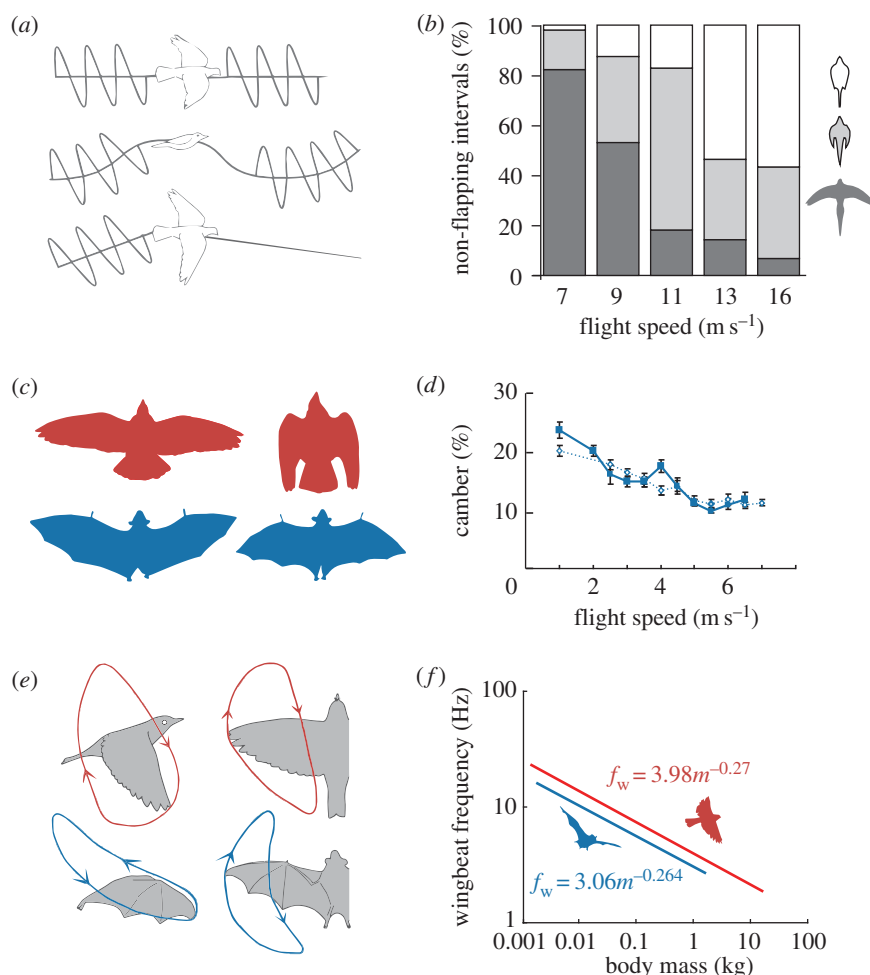
scale-appropriate flight dynamics. Piezoelectric actuators achieve the operating points that are currently unattainable by servos and motors, but have too small displacements with size-limited efficiency [93,94]. At the scale of a fruit fly, piezoelectric actuators efficiently power flight, but at a hummingbird size or larger, traditional motor actuators are better due to higher electromechanical efficiencies [17]. Electronically driven nickel–titanium alloy actuator wires contract quickly, operating well within the force-speed requirements of muscles, but their fast and high-force operation reverses slowly. These actuator wires require high currents, have a long cooling time to relax back to the original length, and risk rupturing under high force loads [103]. Integrated active structures with hierarchical complexity are a characteristic of biological materials, and important to understanding form and function in flight. Harnessing the characteristics of these structures in flying robots has the potential to create novel solutions and better performance for engineered flight. However, active structures and unique morphology comprise only part of the story; the success of vertebrate flight is also driven by how behaviour recruits the function of these unique structures.

### 3. Behavioural adaptations for flight

The wing morphologies and integument specializations of birds and bats enable them to sustain the aerodynamic forces needed for flapping flight. These morphological adaptations also shape a spectrum of behavioural adaptations exhibited during vertebrate flight, including wingbeat kinematics tuned for different flight speeds and various control strategies for manoeuvring.

#### 3.1. Wing kinematics

Birds flap their wings continuously or intermittently. Intermittent flight includes a range of behaviours from flap-bounding, when the wings are periodically flexed against the body, to flap-gliding, when the wings are periodically extended (figure 7a). During pauses in flapping, birds convert potential energy into kinetic energy, causing an undulating path. Flap-bounding is only used by small to medium-sized birds under 300 g [104], likely because required aerodynamic power increases with mass more rapidly than available flight muscle power; larger birds are thus unable to sustain the increased power output needed during these high-power flapping phases [104,107]. Bounds generally last less than 200 ms, during which the pectoralis remains inactive as the wings are flexed [104], but the body and tail still passively generate lift up to 20% of bodyweight [108]. Flap-bounding may provide energy savings at high speeds, when mechanical power is primarily allocated to overcoming pressure and skin-friction drag on the wings (profile power) and the body (parasite power). However, at low speeds, the power required for weight support (induced power) dominates, so the reduced lift during a bound becomes energetically prohibitive during the flap phase [104,109,110]. It is therefore unclear why flap-bounding is still sometimes used at lower speeds. According to the ‘fixed-gear’ hypothesis, it may be a way for birds with a limited range of useful strain rates in their flight muscles to vary their power output [105,109], but this hypothesis is unsupported by observations of zebra finches [111], budgerigars [105] and starlings [112]. Alternatively, a more recent ‘cost of muscle activation’ explanation describes how small birds use flap-bounding to reduce the mechanical power costs required for muscle activation during contraction; by



**Figure 7.** Birds and bats differ in their flight behaviours and wingbeat kinematics, but both adjust their wing shape based on flight speed. (a) Birds either flap continuously (top) or exhibit periodic non-flapping phases, which involves either folding the wings in against the body during flap-bounding (middle), or keeping the wings extended during flap-gliding (bottom). (b) Birds adjust flight behaviour according to speed: gliding decreases while bounding increases with speed. Glides, dark grey; partial bounds, grey; bounds, white. (c) While birds significantly vary wing span and area during intermittent flight or between down- and upstroke, bat wings do not exhibit the same range. (d) Instead, bats adjust wing camber according to flight speed, as shown for two individuals. (e) Birds and bats exhibit different kinematics within wingbeats. Side and top views of a typical wingbeat path are shown for a passerine bird and a bat. (f) Wingbeat frequency  $f_w$  scales similarly with body mass  $m$  for birds and bats, but is higher for birds than bats of the same mass, as shown by their least-squares regression lines. Figures adapted from [59,84,100,104–106].

bounding, the birds are able to extend the duration of their downstroke while still maintaining the necessary downstroke velocity to produce thrust [113].

Flap-gliding, on the other hand, reduces energetic costs across most speeds [104]. However, small birds with rounded, low-aspect ratio wings do not flap-glide, likely to be due to the combined effect of having relatively low inertia and a wing shape that increases drag [104]. Glides may last from less than a second to more than 10 s for larger birds. Birds with masses ranging from about 20 to 160 g and high-aspect ratio wings exhibit the greatest flexibility in flight behaviour [104]. Some of these intermediate-sized birds shift from flap-gliding to flap-bounding as flight speed increases (figure 7b), which is consistent with minimizing power output at any given speed [104]. Budgerigars (*Melopsittacus undulatus*), for instance, reduce their wing area over 50% from glides at low speeds to bounds at higher speeds [105]. According to the ‘cost of muscle activation’ hypothesis, flap-gliding reduces activation costs for work by enabling larger stroke amplitudes and downstrokes at efficient muscle contraction velocities. By gliding, birds are also able to avoid the high cost of performing slow, aerodynamically active upstrokes [113].

Bats also reduce their wing area during flapping flight at higher speeds [87,114–116], but area changes during gliding flight are limited compared to birds [100]. For example, a pigeon (*C. livia*) is able to reduce wing span to 37% of its maximum value and wing area to 62% when gliding [117], while a dog-faced bat (*Rousettus aegyptiacus*) can only reduce span to 83% of its maximum and area to 70% [100] (figure 7c). These differences stem from the different wing morphology of birds and bats. Birds benefit from independent, overlapping feathers that enable them to sweep their hand-wing backwards during upstrokes while their arm-wing remains partially extended. By varying their arm-wing extension, birds actively adjust their span ratio, the ratio between the horizontally projected wingspan during upstroke versus downstroke [84,117]. By contrast, the outer wing membrane panels and plagiopatagium of a bat are interdependent [100]; sweeping the hand-wing backwards would require collapsing the membrane, which increases drag and decreases lift. Instead, pteropodid bats bend their digits to retract their wings, and microchiropteran bats reduce their arm-wing span while keeping the hand-wing membrane relatively stretched [84,87,114,116,118,119]. While

birds and bats employ different mechanisms for adjusting wingspan, many exhibit a similar range of span ratios. Slow-flying passerine birds and pteropodid bats attain span ratios of around 0.2–0.4, while non-passerine birds and a microchiropteran bat (*Glossophaga soricina*) achieve ratios around 0.6–0.8. Hummingbirds are the exception with span ratios around 0.9–1, because they do not flex their wings as significantly during upstrokes [59,120,121].

Although their ability to vary wing span may be more limited, bats increase the camber of their wing more than any other extant flying taxa [114]. This is done by lowering the membranes between their digits and by deflecting the legs [59,84,87,114]. At low speeds, increasing camber helps with maintaining high lift coefficients at high angles of attack, during which it assists in the generation of a stable leading edge vortex [114,122,123]. At high speeds, lower lift coefficients are sufficient, so decreasing camber becomes more advantageous for decreasing profile drag. Accordingly, bats decrease their wing camber as flight speed increases [87,114] (figure 7d).

The kinematics of individual wingbeats also differ among birds and bats [124], primarily due to differences in how they flex their wings during upstrokes [59]. Whereas downstroke kinematics remain relatively consistent, upstroke kinematics vary among birds with flight speed and wing shape. At low speeds, birds with high-aspect ratio wings generally use a tip-reversal upstroke, in which the elbow and wrist flex while the hand-wing is supinated with the primary feathers spread [19,125–127]. More aerodynamically active swept-wing upstrokes, where the wing is kept partially extended, are used at intermediate to fast speeds [59,127]. Birds with low-aspect ratio wings typically use flexed-wing upstrokes across all flight speeds [125,128–130]. While tip-reversal upstrokes generate lift at low speeds [19], flexed-wing upstrokes likely do not [127,130]. Wingbeat kinematics further diverge between birds and bats; for birds, the path traced out by the wingtip during downstrokes is anterior to that of upstrokes, whereas the opposite holds true for bats (figure 7e). Bats adjust the camber and angle of attack of their wing membrane to generate weight support as they invert their hand-wing for the upstroke [84,114]. At low speeds, the rotation of the hand-wing manifests as a backward flick generating thrust and weight support [118,131,132], but at high speeds, the upstroke generates only weight support [84,132]. Bats may also generate thrust and negative lift at the end of their upstroke as the wing moves up with a negative angle of attack [115,126,132–134].

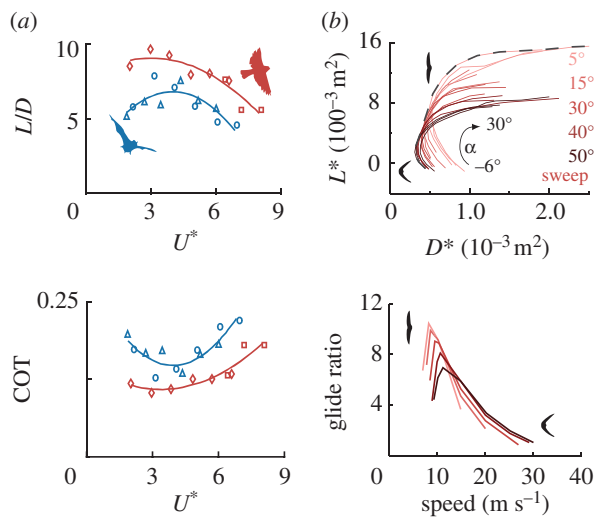
The frequency at which birds and bats beat their wings depends not only on body mass, but also on flight speed and species. How the wingbeat frequency depends on flight speed varies more among birds; the frequency is either constant [135], increases linearly [136] or in a parabolic (U-shaped) fashion with speed [137]. Wingbeat frequency among bats generally decreases with increasing flight speed until cruising speeds are reached, above which it remains relatively constant [84,114,138]. While frequency scales similarly with body mass for both birds and bats, birds have a higher wingbeat frequency than bats of the same mass (figure 7f), and they also have proportionally more flight muscle mass [106]. As the maximum body mass of a flying animal is limited by the aerodynamic power that it can generate, this may explain why the largest extant flying birds are about 10 times the mass of the largest bats [106]. Regardless

of size, both birds and bats select specific wingbeat frequencies to match with their ratio of wingbeat amplitude and flight speed. This matching improves flight propulsion efficiency by maintaining the Strouhal number ( $St$ ), the ratio of their flapping velocity to their forward flight velocity ( $St = fA/U$ ;  $f$  is the wingbeat frequency,  $A$  the tip-to-tip vertical wingbeat amplitude and  $U$  the horizontal flight speed), between 0.2 and 0.4 when cruising [106,125,139]. Whereas birds and bats exhibit larger Strouhal numbers at lower flight speeds when their stroke planes are tilted more horizontally, their downstroke Strouhal numbers, defined as half the wing's mean vertical velocity divided by its mean horizontal velocity, remain in the 0.2–0.4 range [84,87,130].

### 3.2. Performance, manoeuvring and stability

The contrasting wing morphology and kinematics of birds and bats lead to differences in their flight performance. Birds generate lift more efficiently, due in part to a more aerodynamic body shape throughout the stroke cycle and the ability to generate body lift during inactive upstrokes [108,126,140]. Bats, on the other hand, are comparatively less aerodynamic due to a less well-shaped aerofoil and appendages needed for echolocation. In particular, the ears and nose leaf of bats disturb flow over the body, which increases parasite drag [114,126,140]. Whereas large ears may contribute some lift, it likely reduces their inner wing performance [133]. These morphological differences explain why birds have higher lift-to-drag ( $L/D$ ) ratios, and a lower cost of transport compared with bats flying at the same speed (figure 8a) [126]. Birds further enhance flight performance by morphing their wings to adjust loading area and shape-related aerodynamic force coefficients for different flight modes. For instance, extended wings increase lift coefficients at high angles of attack, which is advantageous for slow glides and turns. Swept wings decrease drag coefficients at low angles of attack and provide the load-bearing capabilities needed for fast glides and turns (figure 8b) [141]. These performance advantages may explain why birds fly faster and migrate farther and more frequently than bats [126]. Nevertheless, both birds and bats use flapping kinematics that are more energetically efficient for their typical  $L/D$  ranges; based on theoretical models of large-amplitude flapping wings, an upstroke that generates positive lift is best at the higher  $L/D$  of birds. At the lower  $L/D$  of bats, an upstroke that generates thrust with negative lift is more efficient [126,142].

Most birds hold the advantage for cruising flight performance at all speeds, but hummingbirds and bats have the upper hand when it comes to low-speed manoeuvring [59,114,143]. Hummingbirds are aided by their small mass, high wingbeat frequency and active upstrokes for performing these manoeuvres [104,143]. Bats are also thought to use active upstrokes [114,131,133,144], and further benefit from a combination of lower wing loading [114] and ability to actuate the numerous joints in their wings to adapt their shape [87,100,145]. Although lower mineralization reduces the weight of their wing bones [24], the combination of solid bones (figure 2c) and muscular membranes (figure 5a) makes bat wings proportionally heavier than those of all other extant flyers [145]. As a result, bats can rely on changing wing inertia to execute falling and landing manoeuvres



**Figure 8.** Birds generally outperform bats in terms of flight efficiency, which they further improve by morphing their wings. (a) Birds exhibit greater flight performance than bats, based on effective glide ratio ( $L/D$ ) and normalized mechanical cost of transport (COT). The bird trend line (red) corresponds to data from a pied flycatcher (diamonds) and blackcap (squares), and the bat trend line (blue) corresponds to data from Pallas' long-tongued bat (circles), and the lesser long-nosed bat (triangles). (b) Birds further enhance their flight performance by morphing their wings. (Top) Speed-specific lift  $L^*$  versus drag  $D^*$  polars ( $L^* = \text{lift coefficient} \times \text{wing area}$ ,  $D^* = \text{drag coefficient} \times \text{wing area}$ ) are shown for angles of attack,  $\alpha$ , ranging from  $-6^\circ$  to  $+30^\circ$ . By varying sweep angle, swift wings achieve a much greater range of lift and drag (as shown by black dashed enveloping polar) compared with using fixed sweep angles (thin coloured polars). (Bottom) Low sweep angles enable high glide ratios at low speeds, whereas greater sweep angles improve glide ratio at high speeds. Figures adapted from [126,141].

(figure 9a). Aerodynamic force modulation is probably also used [147], but it is not yet well understood to what extent [145]. By contrast, birds rely predominately on redirecting aerodynamic forces for low-speed manoeuvres, although they may also use inertial reorientation, particularly for small, within-wingbeat adjustments [57]. At higher speeds, birds may also change the shape of their wings or tail to adjust aerodynamic forces [19]. To redirect aerodynamic forces during low speed turns, pigeons (*C. livia*) use force vectoring, in which they reorient their body instead of the forces relative to their body (figure 9b) [19]. To initiate these body reorientations, birds generate a rolling torque by producing bilateral asymmetries in their wing velocities [148], wing trajectories [149], wingbeat amplitudes or feathering angles [150]. Cockatiels (*Nymphicus hollandicus*) [150] and hummingbirds (*Calypte anna*) [151] also reorient their bodies and stroke planes to carry out turns. Similar banking strategies are executed by aircraft, which generally increase their bank angle to make faster or tighter turns. Hummingbirds also adjust their body-dependent kinematics to make faster turns, but change their body-independent kinematics, such as wingbeat asymmetries, more significantly in response to different turning radii [151]. Force vectoring may also be used by birds to accelerate and brake, based on pitching movements that pigeons exhibit after takeoff and before landing [152]. However, further studies are needed to confirm if other birds also use the same force vectoring strategies as pigeons for these manoeuvres.

While the angular acceleration needed for turning requires active modulation of inertial or aerodynamic forces, yaw stabilization may be achieved passively by both birds and bats (figure 9c). When the body yaws during flapping flight, the velocity differential between the inner and outer wings produces a counter-torque that slows rotation, providing passive stabilization. Increasing wingbeat frequency amplifies both active and passive torque generation, which can increase manoeuvrability or stability by investing aerodynamic power [146]. Downstrokes also act as a stabilizing influence in the longitudinal direction. Active upstrokes, on the other hand, enhance manoeuvrability by reducing pitch stability [125,153]. Bats compensate for this reduced stability and enhanced pitch and yaw control by pitching their wings at the end of their upstroke [133].

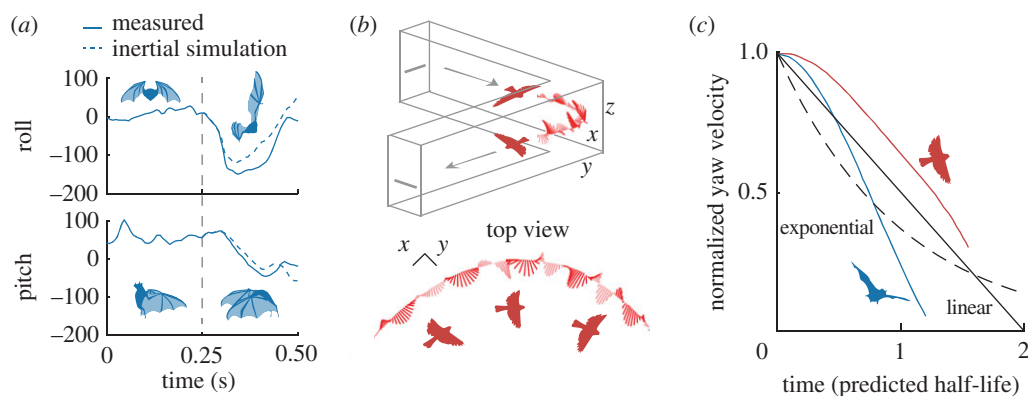
Animal wings also improve stability during gliding flight. Birds and bats enhance longitudinal stability by varying wing sweep to adjust the position of their centre of lift relative to their centre of mass [125,154,155]. Birds further improve longitudinal stability by rotating their sweptback handwing to create negative wing twist, which reduces the angle of attack of the wing tip. Although bats do not perform the same outer wing rotation, they deflect the trailing edge of their wing upwards to achieve a similar improvement in longitudinal stability [100]. Birds adjust roll stability by varying their wing twist, and lateral stability by generating a yaw moment with the sweep in their slotted wingtips [155,156].

While significant progress has been made in recent years, many gaps still exist in our understanding of vertebrate flight, especially with regard to manoeuvring flight and flight in different natural environments [124]. Additionally, many of the active control mechanisms identified for birds and bats have only been studied through the use of theoretical [153,154], computational [156] or robotic models [155]. Further quantitative, *in vivo* studies of manoeuvring flight in different settings will be critical to identifying the specific mechanisms that vertebrate flyers actually use to achieve their versatile performance. Nevertheless, bird and bat flight has already inspired several current and ongoing biomimetic and bio-inspired wing designs.

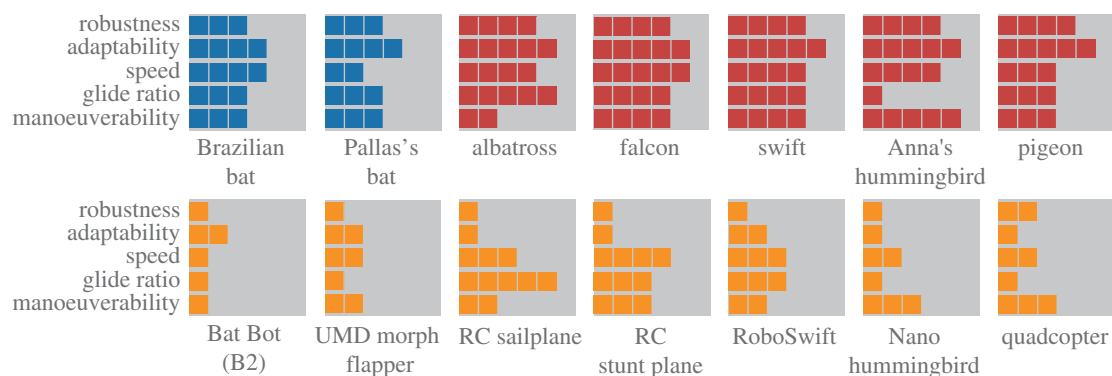
### 3.3. Robotic kinematics and performance

Flying robots now rival certain aspects of the flight capabilities of birds and bats. However, when rated by flight performance and manoeuvrability metrics (figure 10), vertebrate flyers have higher overall ratings and are more well-rounded flyers. Robots are less robust to wing damage, atmospheric turbulence and weather. Manoeuvrable robots such as quadcopters and the Nano-hummingbird [13] cannot glide significantly, achieve fast forward flight, or adapt their propellers or wing shapes to different flight conditions. In fact, the most adaptable of the robots (BatBot, B2) has limited manoeuvrability and efficiency, falling far short of the flight duration and range achieved by bats [164]. Closer modelling of vertebrate wing kinematics and selecting suitable control strategies could help close these gaps between the flight capabilities of robotic fliers and birds and bats.

The suite of vertebrate flight kinematics strategies offers a wide range of design solutions for flapping and morphing



**Figure 9.** Flapping wings enable bats and birds to use inertial and aerodynamic control strategies for stable, manoeuvrable flight. (a) Bats can effectively use inertial forces from their wings to reorient themselves during manoeuvres, shown for a bat's pitch-up manoeuvre before landing (simulations start at  $t = 0.25$  s). Simulated motions based on inertial effects of measured wing motion closely match measured body kinematics of a Seba's short-tailed bat (*Carollia perspicillata*). (b) Birds direct aerodynamic forces by reorienting their body to perform low-speed manoeuvres. Downstroke (red) and upstroke (light red) forces generated during a pigeon's  $90^\circ$  right turn down an L-shaped flight corridor. The forces are shown on corresponding centre of mass positions, vector lengths are normalized by bodyweight (axes lengths shown in the top view correspond to one bodyweight). (c) Birds and bats benefit from passive stabilization due to flapping counter-torque, based on how their yaw rate (normalized here by the initial rate) decays with time (normalized here by the predicted half-life for each animal). If flapping counter-torque is used, yaw rate should decay linearly (solid black line). If asymmetric flapping is used, yaw rate should exponentially decay (dashed black line). Figures adapted from [19,145,146].

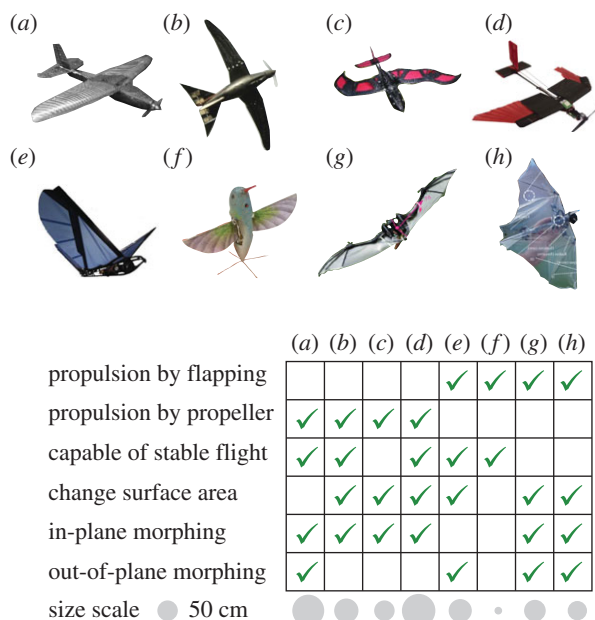


**Figure 10.** Birds and bats have a more balanced performance profile while robots excel in one area and perform poorly in others. Additionally, birds and bats greatly exceed robots in robustness to natural environmental conditions across the board. Adaptability in the form of wing morphing has been incorporated into a few recent robots, but these attempts are rudimentary in comparison to vertebrate wings, offering only 1–2 degrees of freedom in flying robots [141,157,158]. All fliers were rated on a five-point scale for their robustness to collisions, the adaptability of their wing shapes, the combination of maximum flight speed and speed envelope, glide ratio, and manoeuvrability (see electronic supplementary material, table S1 for scoring criteria). Efficiency, speed and manoeuvrability are each attained by individual robots, but at the cost of other performance metrics. Among animal species, distribution in performance capabilities varies—pigeons perform moderately across all metrics, albatrosses have high glide ratios and fly efficiently, and falcons and swifts fly extremely fast. By contrast, hummingbirds have lower glide ratios, but have excellent manoeuvrability, including the ability to hover in place. Bats perform less well than high-performance birds, in several metrics, but they are mostly on par with pigeons [159]. Data for scoring from [14,141,159–163].

the wings of aerial robots. For instance, flap-bounding at higher speeds or flap-gliding may reduce energetic costs of flapping-wing robots. However, if intermittent flight is, in fact, largely a consequence of muscle activation costs, then it would not offer advantages to bio-inspired flying robots, which generally use actuators that do not incur similar activation costs [113]. A full assessment of the benefits and drawbacks of the different wingbeat kinematics will require a deeper understanding of their aerodynamic and energetic implications. In particular, more direct *in vivo* force measurements of vertebrate flapping flight are needed [124] to understand which aspects of vertebrate flight can lead to improvements for aerial robots.

Design choices also depend on the intended application and actuation constraints of the flying robot. For instance,

both inertial and aerodynamic control strategies enable rapid manoeuvres, but inertial control may be more advantageous for heavier wings and low-speed manoeuvring [145]. This underused method would be particularly useful for enabling larger robots with limited flapping frequencies to perform tight manoeuvres, such as turning in place. On the other hand, aerodynamic control would be preferable for fliers with lighter wings. Modifying the flapping amplitude or velocity of wings is more straightforward than changing their inertial properties. However, trade-offs would need to be made between using longer, high aspect ratio wings for more efficient high-speed flight, versus using shorter wings with high wingbeat frequencies for faster accelerations during low-speed aerodynamic manoeuvring [165]. For instance, the former is better-suited for



**Figure 11.** Biomimetic features have been incorporated into robots, enabling them to demonstrate a limited range of animal-like abilities. (a) Wing twist changes help control roll in a small aerial robot [166]. (b) The RoboSwift mimics the sweep and area changes that help the swift fly more efficiently at different speeds [141] (photo by Guy Ackermans). (c) A prototype wing uses two independent degrees of freedom in each wing [167,168]. (d) A robot with artificial feathers uses asymmetric morphing for roll control [157]. (e) The UMD big bird folds the wings during the upstroke to increase efficiency [169]. (f) The Nano-hummingbird controls its flight by adjusting flapping wing parameters and requires no tail for flight stability [13]. (g) A wing with six degrees of freedom per wing replicates the shapes of bat wings in a testbed [170]. (h) Another bat-inspired robot flies briefly using two degrees of freedom to replicate bat kinematics [164]. All these bio-inspired robots replicate limited aspects of bird and bat flight, and therefore none perform as well as their biological counterparts. Robot icons from [13,157,163,164,166,167,170] and Guy Ackermans.

delivery robots flying long distances, whereas the latter is preferable for search-and-rescue robots navigating cluttered environments. Therefore understanding the functional consequences of vertebrate wing morphology and flight behaviour helps drive judicious design choices that best suit the intended application of a flying robot.

#### 4. The future of bio-inspired flying robots

Replicating the flight capabilities of birds and bats in flying robots remains an open challenge for engineers. Current vertebrate-inspired flying robots incorporate certain aspects of bird or bat wings, and vary widely in complexity and flight ability (figures 10 and 11). We group these robots into two categories: those that generate thrust with a propeller (figure 11a–d) and those that generate thrust with flapping wings (figure 11e–h).

Propeller-powered flying robots are more like traditional aircraft, but morphing robots change the shape of their wings like birds and bats during gliding flight. Variable wing twist, for example, has been implemented in a flying robot (figure 8a) through the use of continuously distributed elasticity [166]. Even greater morphing capabilities have been demonstrated by the RoboSwift, a swift-inspired robot with

rigid overlapping feather elements that enable it to sweep its wings back and forth to change wing area (figure 8b) [141]. A prototype with a higher level of complexity incorporates more wing elements to make even more dramatic wing shape changes in flight, which improves performance in turbulence and crosswinds (figure 8c) [167,168]. Another vehicle (figure 8d) uses asymmetric wing sweep morphing to achieve roll control [157]. While these morphing features are advanced for robots, they are still far from matching the scope and performance achieved by birds and bats.

Flapping winged robots harness bio-inspired wing motion more faithfully to improve effectiveness. These wings typically have flexible membrane-based wings with simple up and downstroke kinematics inspired by insect flight [93,171,172]. Others offer more vertebrate-like features such as a hinge in the spar enabling wing folding during the upstroke, and increasing efficiency by reducing drag (figure 8e) [169]. Alternatively, a wrist oriented in the sweep direction enables recovery from obstacle impact [173]. The Nano-hummingbird, by contrast, does not actively change its wing span during flight. Instead, it changes its wing membrane tension and flapping motion patterns (figure 8f) [13]. These additional degrees of freedom represent state-of-the-art robotics that enable the Nano-hummingbird to hover and fly stably without a tail, but critically do not enable the fast forward flight of hummingbirds (figure 10). Biomimetic bat wings (figure 8g,h) integrate wing flapping and morphing. However, while these bat-inspired robots exhibit impressive ranges of motion and appear realistic, they have yet to achieve sustained flight [14,164,170].

These advances in biomimetic robots not only help improve the performance of robots, but also provide useful testbeds for studying animal flight. It is difficult to study the effects of specific adaptations in an animal because they often cannot be isolated without harming the animal. With a robot, this constraint is removed. Robotic models, for example, have been used to study the effects of different aerodynamic mechanisms in flapping animal flight [124,174] and to isolate effects of individual kinematic variables in a flapping wing [25]. Robotic platforms will enable testing how different materials perform as aerofoils, how different wing shapes perform in different flight conditions and how integrated filoplume-like sensors might enhance flight. With advances in sensors and control systems, it is even possible to compare different types of behaviour to examine their effectiveness across environments. This closed-loop inspiration [93] provides insight, both to biologists for better understanding animal behaviour and to engineers for improving aerial robot design.

#### 5. Summary and outlook

By improving our understanding of vertebrate flight and integrating the best solutions into bio-inspired designs, robustness and versatility of current aerial robots can be significantly advanced. We compare bird and bat forelimbs from the musculoskeletal level to the level of organism kinematics and performance to gain insight into how their flight capabilities are facilitated by unique morphological and behavioural adaptations. Many morphological aspects have been elucidated in recent years, but there remain functions that are still not well understood in a biomechanical and

physiological context, such as *in vivo* muscle function and skeletal mechanisms that coordinate motion between bones and their connected integuments. In engineering, aspects of vertebrate flight such as morphing and flapping wings have been incorporated in bio-inspired robots, but many morphological forelimb specializations have yet to be implemented. Whereas robots generally use rigid structures with separate actuators, bird and bat wings efficiently integrate flexible structures actuated by muscles that form aerodynamic surfaces and power flight. The bone and integument structures in bird and bat wings also have specialized characteristics at both the microscale and macroscale level. These hierarchical and repairable structures allow them to withstand loading specific to flight, sense their environment aerodynamically and actively tailor their wing shapes for different situations. As a result, birds and bats excel over current aerial robots in achieving efficient, robust and multi-modal flight, enabling effortless switching between hovering, gliding and fast forward flight. Engineering equivalents of hierarchical structures and high-performance actuators still need further development to help robotic flight achieve the same level of robust and adaptable performance. Capitalizing on the

work of generations of natural selection, additional biomechanical and physiological studies have the potential to provide the necessary inspiration for advancing engineering design. At the same time, these biomimetic robots also greatly aid studies of vertebrate biomechanics by providing a way to mechanistically test biological hypotheses in ways that are not possible *in vivo*.

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