Chapter 8

Flight

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Abstract

Most animal species fly. Insects, birds, bats and the extinct pterosaurs evolved powered flight independently, and each group has developed a wide range of adaptations, exploiting the many special opportunities that flight provides. Differing life styles need different flight capabilities and levels of performance. These require a variety of techniques, many employing aerodynamic principles unknown in orthodox engineering; and these in turn are reflected in the animals' physiology and design: overall structure, size, wing shape and proportions. Understanding the relationships between these variables and the behaviour, life histories, ecology and evolution of the animals is a difficult but fascinating challenge, involving a network of interconnecting experimental, observational and theoretical approaches.

1 Introduction

1.1 Which organisms fly?

Flight is widespread in the living world. Powered flight has arisen at least four times: in insects, pterosaurian reptiles, birds, and once – perhaps twice – in mammals; opinion is divided whether bats have a single or a dual origin [1, 2]. Gliding flight, or at least paragliding, has appeared in two families of fish, in several frogs, in snakes, at least five times in other reptiles, three times in marsupials, and at least three times among placental mammals [1, 3]. Gliding seeds, or strictly fruits, are found in some vines (e.g. *Alsomitra*), and samaras – fruits that rotate like the vanes of autogyros – have evolved independently in conifers, in maples, and in several other plant families [4, 5]. Furthermore many aquatic animals – pteropod snails, some squid, whales, turtles, some birds and many groups of fish – ‘fly’ through the water using tails or paired fins as flapping hydrofoils and employing the same fluid dynamic principles as aerial fliers. Aquatic locomotion is covered elsewhere in this series; the present account is restricted to flight in air.

Flight has unquestionably contributed hugely to the evolutionary success of the groups that employ it, allowing ready, fast dispersal and access to habitats and food sources in the three dimensions of space, with consequent niche diversification. This is reflected in the diversity of the

animals themselves: in terms of described species, insects are by far the largest class of animals, birds the largest class of terrestrial vertebrates, and bats the second largest order of mammals.

1.2 What is flight?

Animals and plants are heavier than air. To stay aloft they need to elicit from the air a vertically upward, supporting force at least equal to the force that gravity is exerting on them – their weight. Newton's first law of motion tells us that this would also be true if they were falling at a constant speed. In this case the upward force would be the *drag* – defined as the *aerodynamic force acting back along the direction of movement* (Fig. 1a). The high surface/volume ratio of many tiny animals and plant propagules ensures high drag values for their weight, and since drag increases with velocity these reach force equilibrium at low sinking speeds, and are often kept aloft and sometimes carried to high altitudes and over long distances by air that is rising faster than they are falling.

Bigger animals and large seeds, however, have relatively less drag for their weight, and their terminal falling velocities are much higher. To remain up in the air and travel horizontally they need to generate *lift* – defined as the *aerodynamic force operating perpendicularly to the direction of movement*. Contrary to common usage, which is influenced by our experience of fixed wing aircraft, lift does not necessarily act vertically upwards; and this is crucial to our understanding of animal flight. Lift on a sail is nearly horizontal, that on a stooping falcon may be more horizontal than vertical. Nonetheless it is the vertically upward component of lift that makes flight possible.

Lift is provided by aerofoils – wings. In conventional aircraft, gliding animals and winged fruits, the role of wings is to generate an overall aerodynamic force with a large enough vertical component to balance the weight. For this they need to be pulled or actively driven through the air.

Figure 1: (a) Forces on an animal falling at a steady speed: mg , weight. Forces generated by the wings in (b) an aircraft and (c) a flapping animal in mid-downstroke.

In gliding (Fig. 3) the propulsive force is provided by gravity; in powered aircraft (Fig. 1b) by jets or propellers. In powered animal flight the wings themselves are the propulsive structures, and propulsion is achieved by active muscular flapping: by cyclically oscillating, twisting and deforming the wings so that they provide not only sufficient net upward force, but also enough *thrust* in the direction of movement to counteract overall drag (Fig. 1c).

1.3 The generation of lift

Lift is created by accelerating air. By Newton's second law of motion, the magnitude of the force F is proportional to the mass m of air accelerated, and to the acceleration a .

$$F = ma.$$

Wings generate lift by creating vorticity in the air around them. In simplest terms, a vortex is a circulation of air around a linear axis: familiar examples are whirlwinds and smoke-rings. Both examples illustrate that vortices have their own momentum; once created, they are capable of travelling when detached from the agent which formed them, and they significantly influence the flow of the surrounding air.

When an appropriately orientated wing is accelerated in air the viscosity of the air immediately adjacent to the wing causes a linear *starting vortex* to develop along the posterior margin – the trailing edge (Fig. 2a). Such a vortex cannot exist in isolation, any more than a cogwheel can

Figure 2: Diagrammatic representations of vorticity and airflow around a (a) wing section and (b) gliding bird.

rotate without turning any other that may be engaged with it. Vorticity rotating in the opposite direction must simultaneously be created; and this takes the form of a *bound vortex*, circulating round the wing, backward over the upper surface, forward under the lower. The starting vortex is left behind, but the bound vortex remains with the wing, and serves to speed up the adjacent airflow past the upper surface, and to slow down that past the lower. This results in a reduction in the pressure on the upper surface and an increase in that on the lower: the wing is both sucked and pushed upward. Simultaneously, the air flowing over the wing is deflected downward behind it; the acceleration already mentioned as essential to the generation of lift. The distribution of pressure varies along the wing, and this leads to vorticity being shed along the trailing edge and winding up at the wing tips to form a pair of *tip or trailing vortices* that are left behind, and ultimately link the bound vortex with the remains of the starting vortex that was shed at the onset of lift generation (Fig. 2b). The tip vortices behind high altitude aircraft are familiar to us: the low pressure in their core causes the water vapour from combustion in the engines to condense out as vapour trails.

This account describes the situation where the wings are held still, as in a gliding bird. Even here, unless the flight is entirely steady and level the strength of the bound circulation, and hence the lift, will change periodically, and further vorticity will be shed by the wings to bring this about. In flapping flight, the wings are constantly accelerating, decelerating, twisting and changing shape, and the aerodynamics of flapping flight are complex and still being actively investigated [4–13]. Many of the same principles apply. In the downstroke the wing circulation creates lift with a strong upward weight-supporting component and usually some propulsive thrust, sometimes greatly enhanced by additional *unsteady* vorticity resulting from the wings' abrupt acceleration. However, the nature of the upstroke, the form of the wake, and the strength and direction of the forces generated vary considerably: both between species, and in an individual animal according to its current speed and behaviour – see Section 3.2.2.

1.4 Stability, and the control of manoeuvres

Flight needs to be stable. Overall flight paths must follow the intentions of the animal, and any significant departures must be correctable. Stability may be *physical*: built into the design, so that momentary deviations from the flight path automatically generate restoring forces. Physical stability governs the flight of an arrow, a dart, a chuck-glider. In animals it may be provided by a long abdomen, as in most dragonflies (Odonata), or long caudal filaments, as in mayflies (Ephemeroptera) and many Palaeozoic insects, or by a long tail, as in the Jurassic protobird *Archaeopteryx* and many early pterosaurs. Early flying animals, like traditional aircraft, seem to have made extensive use of physical stability, requiring only minor active adjustments to perform simple manoeuvres and to cope with transient air currents and gusts. Physical stability, though, tends to limit agility, since the passive restoring forces oppose any changes in direction; and in many more developed animals, as in modern high-performance aircraft, it is sacrificed in favour of *active* stabilisation [14–18]. The tails of bats and advanced pterosaurs were shortened or lost. The tail skeleton of birds became reduced to a compact pygostyle supporting actively movable feathers. Manoeuvrable insects, such as advanced flies, bees, wasps and moths, have relatively compact abdomens. Flight direction and velocity are now continuously monitored by sensors, feeding back via the nervous system to the muscles controlling the movements and orientation of the wings and of other surfaces and structures: the tail feathers of birds, the caudal patagium of bats. In most advanced insects the wings are the only effective controlling surfaces, and precise, often spectacular manoeuvres are achieved wholly by changes in the amplitude, timing, shape and symmetry of the stroke, under complex neurosensory control.

Although highly agile flight may not have been possible until such neurosensory systems had evolved, the relative contributions of passive and active stabilisation are not a simple function of evolutionary ‘advancement’. Flight manoeuvrability is an aspect of overall lifestyle, and the degree of physical stability may vary substantially within a single group. In butterflies, for example, it is influenced by the relative positions of the centres of wing lift and of mass along the body axis, and is significantly correlated with the degree of distastefulness to potential predators [19].

2 The origins of flight

The beginnings of flight in insects and the flying vertebrate groups have been, and still are, extensively debated.

Flight is only possible if the wings move fast enough relative to the air to generate sufficient lift. In each group, the wings of the pioneering fliers would have been small and relatively ill adapted, and the minimum airspeed for flight correspondingly high.

The most obvious way for them to achieve flight speed would be to use gravity: to climb a tree or a high rock and to jump. Some lift can then be achieved even without wings, as do parachutists in free fall. A patagium of skin between the legs, as in several groups of mammals, or between the ribs, as in the lizard *Draco* and several Mesozoic relatives; or even the toes, as in the flying frog *Rhacophorus*, increases both lift and drag, slowing the fall and allowing significant forward travel, in the continuum between parachuting and gliding. Progressive elongation and specialisation of the forelimbs and patagium or feathers of flying vertebrate ancestors, and development of the thoracic muscles and nervous system would lead to fully established flapping flight. This route – the ‘trees-down’ hypothesis – seems adequate to account for flight in bats [20]. *Cynocephalus*, the colugo or flying ‘lemur’ (order Dermoptera), which has an extensive patagium extending between fore and hind legs and, bat-like, between the fingers, appears on genetic as well as morphological evidence to be the closest relative of the macrochiropteran bats at least [1] and probably of bats as a whole [2].

For birds, for the Mesozoic Pterosauria and for insects the evidence is more equivocal. For birds, the trees-down scenario, through parachuting and gliding to flapping flight, is again a strong candidate [21] but it has serious competition. A strong case can be made for bird flight developing in fast running, feathered dinosaurs with particularly long feathers on the forelimbs [22, 23]. These might initially assist in prey capture, but would progressively come to allow short glides over the ground, and eventually enlarge to become full-scale flapping wings. A weakness in this – the ‘ground-up’ hypothesis – is that the propulsive force would cease, and the bird would begin to slow down, as soon as its feet left the ground, but this does not rule out the theory. Running and gliding might still be advantageous over rough terrain. The take-off speed could be increased and maintained by active flapping [24]. Recent spectacular discoveries of small, feathered, dinosaurs in early Cretaceous rocks in China [25], including one ‘four-winged’ example, with fully-feathered hind legs [26], show that the question is still open; and indeed the two theories are perhaps less distinct than usually considered: a cursorial protobird using gravity to gain speed in gliding from rocky outcrops would have elements of both scenarios. For pterosaurs, too, both trees-down and ground-up theories have support, though the trees-down view predominates [27]. A small Triassic patagiate reptile from the Kirghiz Republic, *Sharovipteryx mirabilis*, may be close to the ancestry of the group [28].

For insects, the ground-up scenario is less probable, as their low mass and relatively high drag would slow them rapidly after take-off. The trees-down hypothesis is still perhaps the majority view [29–31], but a recently proposed alternative theory derives from observations on some

modern stoneflies (Plecoptera) and mayflies (Ephemeroptera) that skim on the surface of water, flapping their reduced wings to propel them. This ‘skimming theory’ proposes that the ancestors of winged insects behaved similarly, and that their wings became progressively enlarged to the point when they were able to leave the surface and fly [32]. Both theories have authoritative support. Their implications on the later development of insect flight are rather different [33] but either hypothesis seems plausible on the existing evidence.

3 Flight roles and techniques

3.1 The functions of flight

It seems clear that flight would initially have been limited to short journeys and excursions, escaping predators and competitors, seeking food, mates, shelter, and nesting and oviposition sites. As performance and techniques evolved and diversified, new roles would progressively have become available, and modern forms exploit flight in many ways.

Many birds and insects, and most bats, catch prey on the wing: by flying continuously (hawking) like swifts, martins, falcons, insectivorous bats, and many dragonflies; or by darting from perches like flycatchers (Muscicapidae), some bats, calopterygid and libellulid dragonflies, and some wasps and predatory flies. Many flying insects, birds and bats snatch prey from surfaces, often showing great precision and fine control in avoiding collision, as do some pseudostigmatid dragonflies and vespertilionid bats that take spiders from their webs. Some birds and bats snatch fish and pelagic invertebrates from the surface waters in flight; with beaks, like petrels and skimmers, or using feet, as do ospreys, fishing eagles, and *Noctilio* and some *Myotis* species among bats. Hummingbirds, some bats, and a variety of moths, bees and flies take nectar from flowers on the wing. Advanced flying insects, particularly among dragonflies, flies and butterflies, use flight in territory surveillance and defence, courtship display, aerial combat, mate guarding. Dragonflies mate in flight and fly ‘in tandem’, and males of some species attack tandem pairs in competition for the females, using tactics recalling the aerial piracy behaviour used by frigate birds and skuas to steal food from other birds on the wing. Improved efficiency has allowed many birds, some bats, locusts, some dragonflies, moths and butterflies to exploit the possibilities that flight offers for long distance migration, often making use of winds and thermal updraughts. Thermals and other upcurrents allow many raptorial and carrion-feeding birds to soar for long periods in search of food on the ground, and gulls and frigate birds, albatrosses and petrels to glide at length over cliffs, islands and the sea.

3.2 Categories of flight

Such a variety of flight activities and functions require a wide range of techniques.

3.2.1 Gliding and soaring

Gliding is powered by gravity alone. Lift from the wings is required; drag, impeding the movement, is inevitable; and the path of the glide depends on the ratio between these two. Figure 3 represents an animal gliding at a constant speed in still air. Its direction relative to the horizontal is given by the *glide angle* Θ . Its weight – its mass m multiplied by the gravitational acceleration g – must be equalled by the net aerodynamic force F_A acting vertically upwards. F_A is the resultant of the drag D , acting back along the glide path, and the lift L , at right angles to the flight path. L and D are the sides of a rectangle of forces, of which F_A is the diagonal. Examination will show that the

Figure 3: The forces acting on a gliding bird: F_A , net aerodynamic force; mg , weight; L , lift; D , drag; Θ , glide angle.

angle between L and F_A is equal to Θ , the glide angle, demonstrating that the latter is determined by L/D , known as the *glide number*. Using trigonometry, we find that:

$$L = mg \cos \Theta,$$

$$D = mg \sin \Theta,$$

and hence

$$L/D = \cot \Theta.$$

In consequence, a poor glider whose drag equalled the lift it was producing would fall at 45° to the horizontal. A glider with $L/D < 1$ would fall still more steeply, while $L/D > 1$ would give a more shallow glide path.

While ‘flying’ frogs and some reptiles glide steeply, and are better described as parachuting, truly gliding animals operate at angles far below 45° in still air. How rapidly they descend, the *sinking speed* V_s , often the most important criterion, depends both on the glide angle and the *glide speed* V_g along the flight path. Figure 4 illustrates two different glide strategies. Bird A is a fast glider, with high lift, low drag wings, and hence a low glide angle. Bird B is a slower glider with a higher glide angle. Which has the lower sinking speed depends wholly on the values of Θ and V_g :

$$V_s = V_g \sin \Theta.$$

In still air descent is inevitable, and a descending glide is appropriate for a flying squirrel moving from tree to tree or a bird coming in to land, but prolonged gliding must recruit energy from rising air. This is usually distinguished as *soaring*, and it takes many forms. Air rises when wind is deflected upward by a cliff or the face of a wave. Air passing over a rock or an island can be thrown into standing waves, rising and falling in sequence down wind. A linear updraught forms where air masses converge and meet. Columnar thermals develop above hot ground, and

Figure 4: Two gliding strategies: V_g , glide speed; V_s , sinking speed; Θ , glide angle.

over towns. All these are exploited by birds. Many gulls, for example, *slope-soar*, gliding back and forth in the updraughts that occur when the wind meets a cliff. Condors and eagles do so in the mountains. Albatrosses and shearwaters slope-soar in the smaller upcurrents off the faces of waves. A variety of sea and land birds exploit frontal updraughts, and standing waves in the lee of large rocks. Vultures, eagles, buzzards, kites, storks and pelicans soar in thermals and travel with them downwind [34, 35], and frigate birds are able to exploit thermals that develop over the sea in the trade wind zones [36, 37]. The circumstances and lifestyle of the bird influence the gliding strategy, and hence the design; this is explored in Section 4.2.

In comparison with birds, bats make little use of gliding, flying mainly at night in situations where upcurrents are unimportant. Many pterosaurs, in contrast, must have made significant use of gliding and soaring. Several analyses of pterosaur flight have been published, and although these do not always agree in detail it seems certain that the giant Cretaceous forms at least were habitual soarers. The oceanic *Pteranodon* species, with wing spans up to 9 m, have been interpreted both as exclusively soarers with very low stalling speeds [38, 39] and as slow flappers with soaring capabilities [40], and the still more enormous terrestrial *Quetzalcoatlus northropi*, with an estimated span of around 12 m, must have been a specialised soarer; its muscles could surely not have coped with continuous powered flight [41]. By analogy with birds, many smaller pterosaurs must have made extensive use of both gliding and flapping.

Most prolonged gliders are relatively large. Many medium-sized birds, like crows, alternate between periods of flapping and gliding. The drag on smaller, lighter birds soon slows them down, and these glide, if at all, only briefly between bursts of flapping. Swifts and swallows, with their slender, high lift wings, are effective brief gliders, as are some bats, particularly those with high aspect ratio wings [42, 43]. Some large insects – locusts, some dragonflies and butterflies – similarly glide for short distances between periods of flapping, and dragonflies have been observed to soar on thermals [44]. Interestingly, gliding insects usually have moderately broad wings, apparently because on this scale slender wings are liable to stall before reaching their theoretically optimal gliding speed. The gliding seeds of *Alsomitra* and related plants also have moderate aspect ratios, probably for the same reasons [45]. The rule is not without exceptions: the huge pseudostigmatid damselflies glide well, despite their relatively slender, petiolate wings [46].

3.2.2 Powered forward flight

Provided metabolic energy is available, effective flapping allows flight to continue indefinitely, providing extra lift and hence weight-support and thrust to maintain altitude and speed. It also gives improved scope for accelerations and manoeuvres, greatly increasing the range of flight patterns and functions.

However the aerodynamic implications of flapping are considerable. The wing stroke cycle must again generate sufficient net upward force to support the weight. In moderate to fast flight, where the forward velocity of the animal relative to the flapping velocity of the wings is high, this may present no great problem, since the wings will be operating at a favourable angle of attack throughout much of the stroke. In fast flight, long-winged birds like falcons, gulls, swifts and martins, and many bats, generate weight-supporting force throughout the stroke-cycle, merely flexing their wings slightly in the upstroke [47, 48]. Visualisation of the flow behind a kestrel, flying at around 7 m/s, showed it to be leaving a wake that consisted of a pair of undulating vortices trailing behind the wing tips (Fig. 5a) [49]. Both upstroke and downstroke were generating weight support, but the upstroke produced less force – necessary as its horizontal component was

Figure 5: (a) Undulating vortex wake behind a fast-flying falcon. (b) Vortex ring wake behind a rising pigeon. Broad arrows represent the directions of mass airflow.

backward, reducing the overall thrust. Birds and bats with shorter wings, long-winged birds at low flight speeds, and most insects need to introduce far more asymmetry of shape or motion between the two halves of the stroke, so that the upstroke does not generate adverse forces countering the weight support and/or thrust provided by the downstroke. At low flight speeds, many birds and bats develop most of their useful aerodynamic force in a strong downstroke, and fold the wings close to the body in the upstroke, the birds twisting their primary feathers like the vanes of a venetian blind to minimise both lift and drag. Each downstroke generates and sheds a discrete ring vortex (Fig. 5b), so that visualisations of the animal's wake have shown it to consist of a series of such vortices projected downwards and backwards [50, 51].

These two flow patterns have long been regarded as distinct, discontinuous gaits, in the sense of the distinct walking, trotting and galloping gaits of mammals, but new work on thrush nightingales (*Luscinia*) flying freely in a giant wind tunnel, indicates that in this species at least they are actually extremes of a continuum of flow patterns, changing with increasing speed. Furthermore, even at their lowest speeds the nightingales generate a weak ring vortex in the upstroke, as well as the far stronger ring of the downstroke. If this last proves to be generally true, it solves a problem that has worried scientists for three decades: that calculated forces from the single vortex ring model are inadequate to support the bird's weight [52].

Insects do not actively fold the wings in flight, but the latter are twisted and often bent in the upstroke [53–59]. This may serve to 'feather' them, so that the upstroke generates minimal forces, but the wings of most insects are capable of being twisted enough for the upstroke to generate useful force, often including some weight support (Fig 6b and c). Since the wings have no internal muscles, this twisting, often accompanied by transverse bending, seems to be driven mainly by the inertial forces they experience as they accelerate [60]. Some insects are capable of altering the shape of the wings in the upstroke according to their flight speed, but bees, and by implication many other insects, appear to change speed simply by altering the angle of the body and with it the wings' stroke plane, tilting the body progressively more vertically and the stroke plane more horizontally as speed falls (Fig. 7).

Much attention has been paid to investigating how far flapping flight can be explained by conventional aerodynamic theory, and how far unconventional mechanisms are involved. Conventional theory was developed in association with fixed wing flight, and assumes that the airflow past the wings is relatively steady, with the wings maintaining a more or less constant velocity and orientation to the oncoming air. With oscillating wings this is clearly not so. Early investigations of insect flight [61, 62] treated the flapping cycle as a sequence of steady states, calculating the

Figure 6: Three insects showing the form of the wings in the upstroke. (a) A mantis. (b) A sawfly, showing wing tip bending and twisting. (c) A crane fly showing complete twisting. Traced from photographs: (a and b) from [63]; (c) from [64].

Figure 7: Wing tip paths and wing and body orientations in a bumblebee, *Bombus terrestris*, at various speeds and advance ratios (J). Net aerodynamic forces are shown for representative downstrokes and upstrokes. The underside of the leading edge is marked by a triangle [65].

forces developed at each instant of the cycle, integrating these to estimate the total weight support and thrust, and comparing these with the weight and the total drag. However it has become progressively evident that unconventional mechanisms must often be involved, and several have been identified and analysed [8, 12, 13, 66, 67]. Some of these are transient departures from the steady states of orthodox aerodynamics, operating as the wings decelerate and accelerate around the top and bottom of the stroke. Many tiny insects, and some others make extensive use of the 'clap and fling' mechanism, in which the wings clap together at the top of the stroke and fling apart into the downstroke, generating high levels of lift-creating vorticity as soon as the stroke commences [68–70]. In the fruit-fly, *Drosophila*, high, unsteady lift appears to be created by rotating the wing backwards about its long axis as it begins to decelerate at the end of the downstroke, generating a kind of back spin like that on a sharply cut tennis ball [9, 12, 67, 71]. The timing of these transient events is probably crucial in the fine control of flight manoeuvres in these adept, precise fliers. Other mechanisms operate during the main sweeping (*translational*) part of the stroke. In hawkmoths, and by implication many other insects, extra lift is generated by the development of a low-pressure vortex behind and above the anterior edge that is sustained throughout the half stroke by spiralling out along the span, a steady-state but unconventional effect with some similarity to the flow pattern over the wings of delta-winged aircraft [8, 72]. The form, behaviour and occurrence of the leading edge vortex in insects, and its possible relevance to small birds [73–75] are currently being intensively studied. Two approaches are now usual: theoretical, using computational fluid dynamic analyses [11, 70]; and experimental, using flow visualisation, particularly particle imaging velocimetry. The former uses precise measurements of the shape and movements of the wings to compute the flow, the strength and distribution of the vorticity and consequent aerodynamic forces. The latter computes similar information from video recordings of the movement of suspended particles past flapping [9] or revolving [74, 76] or fixed [73] model wings, or past actual animals in tethered flight [77, 78] or flying freely [52, 75]. Models and tethers are normally instrumented to measure the forces actually generated.

The results from these investigations are at present conflicting, reflecting the diversity of the animals, the range of experimental approaches and the relative novelty of the techniques, which are still being refined. There is still much to learn.

3.2.3 Hovering

Many insects and some small birds and bats are capable of hovering. Many male dragonflies and flies hover in territory surveillance and mate location. Hummingbirds, some phyllostomid bats, hawkmoths (Sphingidae), many bees, bombyliid and syrphid Diptera, and various other moths and flies hover to feed at flowers. Most birds over 20 g, and many weighing less, can hover only briefly, if at all, in still air, though the African pied kingfisher, weighing about 100 g, hovers sustainedly over water in search of prey [79]. Kestrels and some other falcons, terns and some kingfishers can fly at zero ground speed into a wind – usually distinguished as wind hovering.

The majority of hovering insects do so by tilting their bodies towards the vertical, and beating their wings almost horizontally, twisting them extensively so as to generate vertical weight support on both half strokes, with any horizontal forces cancelling out. So do the nectar-feeding glossophagine phyllostomid bats [80, 81]; and so do hummingbirds, their short arms and long primary feathers allowing them to twist the wings to an extent unparalleled in other birds. Hummingbird flight technique appears astonishingly insect-like, and they have often been mistaken for large moths and *vice versa*. The curious back-tilted thorax of dragonflies allows them to hover without tilting the body. Hoverflies (Diptera, family Syrphidae) can do the same; but the latter [82], and most other hovering birds [83] and bats [6, 47, 84, 85] use an oblique stroke-plane, and generate most or all the necessary vertical force on the downstroke. Some butterflies can hover briefly by beating their relatively huge wings vertically downwards [86] – in effect operating them like fans or paddles and using pure drag for weight support – but others use the more conventional horizontal stroking method [87].

3.2.4 Special techniques for flight economy

Flight is metabolically expensive; a 100 g bird in cruising flight uses energy around twice as fast as a walking or running mammal of the same body mass [88]. Birds in particular have adopted a range of flight behaviours that serve to reduce energy consumption. Many species, particularly those of medium and large size, alternate between phases of flapping, rising as they do so, and gliding, in which they lose altitude. This is known as *undulating flight* [89]. Brief alternating bursts of flapping and gliding are also characteristic of the aerial manoeuvres of the slender-winged swifts and swallows, and many butterflies do the same.

The V-formation flying of geese, swans and cranes is again an economy measure. With the exception of the leader, each bird flies just outside the wing-tip vortex of the one in front, gaining support from the upwash that it causes. Theoretically this may save up to 15% of the total aerodynamic power expended [79].

The spectacular fishing technique of skimmers (*Rynchops*) which fly with a shallow wing beat in straight lines very low over the surface of water, snatching fish with an elongate lower bill, exploits the *ground effect*, in which the high pressure in the space between the bird and the water can save as much as a fifth of the necessary mechanical power [90, 91]. Waders and some other water birds, bats [92] and insects [10] often fly close to the water surface, and probably gain similar advantages. So may a variety of satyrid and other butterflies that fly close to the ground [10]. The Jurassic pterosaur *Rhamphorhynchus* is thought to have been a fish feeder, and may well have caught them, skimmer-like, by flying low over the water.

Many small birds with rather broad, short wings – small passerines like finches and tits, and woodpeckers, some parrots, and kingfishers – use *bounding flight*, in which flapping bursts alternate with periods in which the wings are folded close to the body. The flapping period accelerates the bird, and projects it into the folded phase, like a thrown pebble. This too has formerly been considered to be an energy-saving device, but is now seen as a means by which the bird can control its power output over a wide speed range by varying the length of the flapping periods [89, 93]. Bounding flight appears to be limited to birds with a body mass below *c.* 200 g.

4 Designs for flight

4.1 Basic morphology

4.1.1 Vertebrates

The wings of birds, bats and pterosaurs are/were modified fore-limbs, with bones, muscles, tendons, ligaments, and a vascular and nervous supply. The bat wing skeleton has a full complement of greatly elongate fingers, supporting a thin patagium of skin, muscle fibres and elastic ligaments, extending back to the hind limbs, and in most families to the tail. The patagium of the pterosaurs was principally supported by the arm and one extremely long finger, the other digits being free. Interestingly, the extent and structure of the pterosaur patagium are still controversial. Early reconstructions showed it continuing behind the hind wings to the tail, but this seems not to be true, though one interpretation of *Pteranodon* postulates that it may have been attached to extended tail vertebrae, bypassing the legs [94]. In general, though, opinion is divided as to whether the patagium arose from the side of the trunk, leaving the legs free [95, 96], or extended to the hind knee, or to the ankle. This would affect the area of the wings, and hence both wing-loading and aspect ratio (see Section 4.2.2) and has implications in calculating probable flight performance. In many specimens the patagium shows a close-packed series of fine ridges and grooves. These were earlier suggested to be wrinkles, resulting from the contraction in death of elastic filaments in the membrane whose function was to keep it taut, and allow it to function, in a wide range of flight positions. This would make pterosaur flight more bird-like than bat-like, and would have major implications on their capabilities and ecology [97]. However they are now believed to have been stiffening fibres, the so-called actinofibrils [98].

Another point of controversy is the position and function of the pteroid, a slender bony rod arising from the wing carpals. In most undisturbed fossils this points back along the wing towards the body, and evidently supported the propatagium, the relatively small area of the patagium lying anterior to the arm. However it may in life have been directed forward, supporting a far larger propatagium than has usually been assumed, and to have been capable of altering the basal profile of the wing. If this is the case, the wing area would have been significantly greater than has been believed, and wind-tunnel experiments on models have shown that flight versatility and overall performance would have been considerably enhanced [99].

The bird wing skeleton has a much reduced hand, and the main aerofoil surface is provided by the feathers: the primaries, extending to the wing tip and the distal part of the trailing edge, and the secondaries, forming the posterior part of the proximal region of the wing. The bases of these are overlaid by the shorter wing covert feathers, supplying much of the curved upper surface. The vestigial thumb bears a tuft of feathers – the alula – that can be actively lifted in many species and is believed to act like the ‘slot’ on an aircraft wing, deflecting air down over the wing’s upper surface and delaying stalling at low speeds and high angles of attack.

The tail feathers of birds form an additional aerofoil, providing some lift, and particularly stability and active control [100, 101]. The shape and length of bird tails vary enormously, reflecting different modes of flight but also showing a range of special adaptations in association with courtship and other display.

In both birds and bats, the thoracic muscles powering the wing stroke are inserted via tendons on the humerus bone of the upper arm. In both groups the downstroke is powered by the large pectoralis muscles, arising on the sternum, which in birds is broad and keeled – familiar enough to anyone who has ever carved a chicken. The sternum in bats is relatively narrow, and the pectoralis muscles pull against each other, separated by a sheet of tough membrane. The upstroke in vertebrates is powered by smaller muscles, assisted by the aerodynamic force on the wing. In birds this muscle is the *supracoracoideus*, inserted on the sternum and covered by the pectoralis; with a tendon which passes through a hole between three bones to attach on the upper side of the humerus. In bats the wing elevator is the deltoid muscle attached, more conventionally, to the scapula – the shoulder blade. Pterosaurian flight musculature had features of both patterns. The broad, rather bird-like sternum indicates the presence of a large pectoralis for the downstroke, but the upstroke seems to have been powered by both a *supracoracoideus* from the sternum and a deltoid from the scapula [95].

We have seen that flapping flight requires the wings to undergo significant, often extreme cyclical changes in shape, during the stroke-cycle, and when the wings are stowed at rest. In all three groups of flying vertebrates, these deformations are/were brought about directly by the muscles of the arm and hand, flexing and extending the arm; and spreading and apposing the feathers in birds, and the fingers in bats and pterosaurs. Not so in the insects.

4.1.2 Insects

The flight system of insects is fundamentally different from those of flying vertebrates. The skeleton of insects is topologically external, and insect wings are skeletal structures, with no internal musculature, and very little other internal tissue. They consist largely of *cuticle*, a highly structured complex of organic polymers whose physical properties – stiffness (resistance to deformation), strength, toughness (resistance to fracture and tearing), resilience (springiness) – vary greatly from place to place according to the cuticle's local chemistry and ultrastructure [102]. Typical wings consist of thin membrane, supported by and continuous with a framework of *veins*, usually hollow tubes containing blood and air-filled respiratory tubes. Most insects have two wing pairs, not one as do vertebrates, and these may beat in or out of phase. In many insects the two wing pairs are coupled together, forming a single effective aerofoil. In several groups one or other pair is lost, or modified to protective structures (the fore wings of beetles and earwigs) or special sense organs (the hind wings of flies).

The muscles powering flight are restricted to the thorax, and in most insects are remote from the wings themselves, although in dragonflies, cockroaches and Orthoptera the downstroke is wholly or partly powered by muscles inserted at the wings' extreme base. Elsewhere these 'direct' muscles are concerned only with modifying the wings' angle of attack and the shape of their base in flight, and in folding them at rest. The aerodynamically useful deformations that the wings undergo in flight are brought about by the inertial and aerodynamic forces that act on them, modulated, often with great precision, by the muscular forces at the base. How these interacting forces influence the shape of the wing through the stroke cycle depends largely on the detailed architecture of the wings themselves: the distribution of stiff and flexible components and areas, whose properties are influenced both by their macrostructure and by the chemistry and ultrastructure of the cuticle (Section 4.2.2).

4.2 Morphological variables

The extensive range of flight functions and techniques that animals adopt is reflected in a wide variety of designs, and discovering the relationships between design, performance capabilities and behaviour is a major challenge to students of flight. Conventional engineering analyses based on orthodox aerodynamic theory have been helpful, but the theoretical framework for analysing flapping flight is still incomplete, though advancing rapidly. Actual measurements and observations are essential; and the results are sometimes surprising and thought-provoking.

Some design features are readily quantifiable, and their association with particular types of flight performance and behaviour can be theoretically predicted and tested against actual observations. A variety of body characters may influence performance, adversely or favourably. A bulky head or long, unwieldy legs will increase drag. Tail size and design are very important in birds, and a recent analysis of microbats has shown that tail and ear lengths and areas, as well as wing variables, may contribute to flight performance and manoeuvrability, and assist in predicting foraging strategies and habitat preferences [103]. Nonetheless most attention has properly been focussed on wings.

4.2.1 Wing loading and aspect ratio

The wing loading of an animal is the weight carried by unit area of wings. Small wings on a heavy animal need to generate more lift per unit area, and this is most readily achieved by moving faster through the air: by more rapid flight, or by flapping at a higher frequency or at higher amplitudes, or any combination of these. Orthodox aerodynamic theory predicts that, for animals of similar design, characteristic speeds such as minimum speed, the speed at which minimum power is expended, and that at which the *cost of transport* (energy consumed in transporting unit weight of the animal through unit distance) is lowest, should vary approximately as the square root of the wing loading (see Section 5.2). Animals with high wing loading values might be expected to fly fast and/or flap rapidly, and to have high take-off and landing speeds. Since wing loadings tend to increase with size (in a range of similarly shaped animals weight will vary as length^3 , wing area as length^2 , so wing loading will increase directly with linear dimensions), one would expect larger animals to fly faster and to expend more effort in getting into the air, or to have disproportionately large wings.

Clearly, the designs of flying animals vary enormously, but in birds, which include the largest extant flying animals, these predictions are very broadly correct, though at any given mass or wing loading the range of speeds is wide. Many of the highest reliable estimates of sustained flight speed, between 17 and 21 m/s, are recorded for swans, geese and large ducks, whose wing loadings are among the highest, while recorded speeds for small passerines and, unexpectedly, swifts, with the lowest wing loadings, are generally below 12 m/s [79]. A peregrine falcon has been reported to exceed 70 m/s in a dive, but its wings would have been folded, and the wing loading thereby greatly increased. Flight speed data on bats are relatively scarce, but there appears again to be a broad correlation between speeds, wing loading and body mass. High wing loading can reduce manoeuvrability, as the radius of turning is proportional to wing loading, and insectivorous and carnivorous bats all have relatively low values [42, 47].

Few insects have wing loadings approaching those of even the smallest birds and bats, and most are several orders of magnitude lower [104]. Bumblebees, whose loadings are among the highest, are capable of hovering; and the ability, or lack of it, for insects to fly slowly and to hover depends on other factors of design and physiology. Low wing loadings, however, certainly limit top speeds, and although very few reliable values have been published, the majority of insect species – most of which are tiny – appear incapable of exceeding 1 m/s [10]. A significant factor allowing the evolution of small flying insects has been the origin, several times independently, of

an unique type of muscle whose operating frequency is not limited by the need to be excited by a nerve impulse at each contraction. These *asynchronous* muscles are activated by being stretched by the muscles which oppose them, so that the thorax and wings are able to operate at or near their physical resonance frequencies, which may be several hundred cycles per second. Some tiny biting midges have been recorded at over 1 kHz [105], though this needs confirmation. High frequency flapping accelerates more air, and asynchronous muscle allows insects to function with relatively smaller wings and higher wing loadings, and hence perhaps at higher flight speeds for their size [10]. However even the fastest insects seem to operate at the lower end of the speed range of flying vertebrates. A queen bumblebee of the species *Bombus terrestris* has been recorded at 7.6 m/s in a wind tunnel [106], and foraging bumblebees can fly still faster in the field [107]. Some dragonflies may fly at higher speeds, though the evidence is largely anecdotal.

The aspect ratio (AR) is a measure of the slenderness of wings. It is properly calculated as $4(\text{wing length})^2/\text{wing area}$, though often as $(\text{wingspan})^2/\text{area}$, including the width of the body; the two values may be rather different.

Aspect ratio, at least in aircraft, birds and bats, can be thought of as an approximate measure of aerodynamic efficiency. High aspect ratio wings have lower induced drag (the drag associated with lift generation, (see Section 5.1)), so that the lift/drag ratio is high, and energy costs relatively low. Virtually all man-made gliding aircraft have high aspect ratios, and so do marine gliding birds – albatrosses (AR 15–20), gannets (AR c. 13), fulmars (AR c. 11), operating in open spaces, often close to the water in situations where upcurrents are chancy and relatively slight and shallow glides are essential. So too do frigate birds (AR c. 15), which are also capable of thermal soaring in the trade wind zones [36, 37]. In these, and also in swifts, terns, martins and many migratory bats high aspect ratios allow long periods of sustained, economical flight. Long wings also generate large turning moments, and can hence aid agility, the ability to perform rapid banked turns on the wing. Birds and bats that catch insects on the wing in open spaces tend to have high aspect ratios. Most insects change direction without noticeable banking, but long-winged butterflies like the heliconiid *Dryas julia* and some swallowtails are relevant exceptions.

Low aspect ratio wings, though less efficient aerodynamically, are by no means uncommon. Considerable structural and mechanical strength is needed to support and flap long wings, and breadth is often necessary to limit wing loading, and hence to allow slower flying and higher manoeuvrability. Most terrestrial soaring birds have a low aspect ratio, a lower lift/drag ratio, and a correspondingly steep glide angle. Steeper glide paths matter less to birds exploiting strong upcurrents, and broad wings can have a large area and hence low wing loading without excessive mechanical stress. Slower flight aids the tight turning circles that may be necessary to stay in narrow thermals. Fast gliding is still possible when necessary, by partly flexing the wings, so that the bird has considerable control over speed, and Rüppell's griffon vultures (*Gyps rüppellii*), for example, can glide huge distances by soaring slowly in thermals and gliding fast between them [34, 35].

Long wings can also hinder flight within small spaces, and many woodland birds and insectivorous bats have short, broad wings, relatively low wing loadings, and the capacity for versatile, manoeuvrable flight in dense vegetation [42, 43, 48].

The influence of aspect ratio in insects is less clear-cut, because of the presence in most groups of two pairs of wings. Where fore and hind wings are physically coupled, or at least beat in the same phase, it is reasonable to calculate a single value for the aspect ratio of the four wings together, but this is less logical where fore and hind wings, often quite different in size and shape, beat out of phase.

For a given body size, long wings sweep out a larger area through which the air is accelerated. This should particularly favour slow flight and hovering, and indeed many slow-flying insects,

like zygopterous Odonata (damselflies), myrmeleonid Neuroptera (ant-lions) and nematoceran Diptera (midges and gnats), have high aspect ratios; but this is by no means invariable, and most skilled hoverers have medium aspect ratio wings. Recent work with model wings suggests that aspect ratio may not be particularly influential in determining the lift/drag ratio in the insect size range [76].

The relationship between flight performance and design is complex, with many interacting variables. Statistical analysis of such situations needs a multivariate technique; and for flying vertebrates principal component analysis (PCA) has proved particularly useful. PCA allows the relative overall influence of individual variables to be computed. Analysis of a wide range of birds [48] and of bats [42] shows size to be overwhelmingly important in accounting for overall variation, followed by wing loading and aspect ratio. It is then possible to examine the relationship between loading and aspect *corrected for size* in a two dimensional scatter plot of these variables for the individual species, and to interpret the results in terms of their flight capabilities and behaviour. The results are illuminating: the plots conveniently and encouragingly tend to bring together many species, often in different families, with similar flight habits.

A combination of high aspect ratio and relatively low loading minimises the power requirements and cost of transport (Section 5.1) and favours animals that fly continuously for long periods (albatrosses, swifts, terns, gulls) and long distance migrants, including some bats. In helping slow, economical flight it also assists aerial predatory birds (swifts, swallows and martins, bee-eaters, falcons, harriers, kites, skuas).

High aspect ratio with high loading still minimises cost of transport, but allows higher speeds. This favours animals that commute long distances, like the molossid Mexican free-tailed bat *Tadarida brasiliensis* which flies many kilometres each night to feed on distant moth swarms. Birds with this combination tend to be fast-flying migrants, like eiders and other arctic ducks, or shore birds, flying rapidly between feeding grounds; or wing-swimmers, like auks and diving petrels, whose wings are a compromise between hydrofoils and aerofoils [48].

Low aspect ratio with low loading would tend towards slow flight, which is potentially costly. This combination characterises a large number of woodland birds and bats operating in situations where long wings would hinder movement, and manoeuvrability is useful. Here too are the terrestrial soaring birds, where energy expenditure is minimised by gliding, and the ability to fly slowly and turn tightly is often valuable (Section 3.2.1).

Low aspect ratio with high loading tends to fast expensive flight. Birds with this combination are generally poor fliers – ground-living galliforms (grouse, pheasants, partridges), tinamous and rails, that fly mainly for escape, where speed is more important than economy. No bats live like this; bats with relatively low aspect ratio and high loadings tend to be insectivores, or fruit- and nectar-feeders, operating in close habitats, capable of fast but agile flight and also hovering. Hummingbirds too combine hovering and nectivory with fast flight between plants, but have higher aspect ratios than their bat equivalents.

A similar PCA of Pterosauria, using estimated values for mass, places all species studied in the high aspect ratio, low loading category, occupied in birds by the marine gliders and aerial predators [108]. This conforms well enough with both morphological and geological evidence. The fact that *Quetzalcoatlus* and some other late Cretaceous pterosaurs are found in continental deposits merely confirms that a high aspect ratio is excellent for terrestrial as well as marine soaring, no surprise to glider-pilots. There is no reason to suppose that all pterosaurs were soarers; active, falcon-like flight is entirely probable for smaller species.

Analyses of this kind are less easily applied to insects. The ambiguity of aspect ratio as a concept in four-winged animals, their frequent reliance on unsteady aerodynamics, the uncertain influence of very small size and low wing loadings, their far more varied wing shape, all introduce problems

of practical analysis and interpretation. In a PCA of butterflies it was far harder to distinguish the influence of wing loading and aspect ratio from that of other morphological factors, and the relationships between design, flight habit and habitat were far less clearly defined than in comparable studies on vertebrates [87].

4.2.2 Wing shape and proportions

One consequence of flapping, as opposed to flying with fixed wings, is the need to expend energy in accelerating and decelerating the wings against their inertia at the end and beginning of each half stroke. This *inertial power* (energy consumed in this way in unit time) is a function not only of the mass of the wing but also of the *moment of inertia* of the wing about its base, a measure of the distribution of mass along its length. The effect of the mass of any component of the wing increases as the square of its distance from the base, so for minimum energy expenditure it is logical to concentrate the mass of the wing close to the base, keeping the distal part as light as possible. This is evident in all animal wing designs: in the reduction of the bony component of bird wings, with the distal area supported by feathers made of the significantly lighter keratin; in the ultra-slender digits of bats, and their reduction to one supporting finger in pterosaurs; and in the tapering, thin-walled distal veins of many insect wings. It also partly accounts for some major differences in wing design within these groups. Figure 8 compares the wing proportions of three birds with high aspect ratios. The bones of the albatross (Fig. 8a) extend *c.* 65% the length of the wing, those of the hummingbird (Fig. 8b) *c.* 35%, and of a swift (Fig. 8c) a mere 28%. Albatrosses glide extensively and flap slowly, and the long bony skeleton is necessary to support the wing against the high bending moments associated with large size. Swifts alternate gliding with periods of rapid flapping. The short arm and long primary feathers are stiff enough to cope

Figure 8: Three narrow bird wings, showing the extent of the bony skeleton: (a) an albatross, (b) a hummingbird and (c) a swift.

with the bending moments, and the moment of inertia is relatively far lower. Hummingbirds flap continuously at high frequencies, up to 52 cycles/s in the case of the ruby-throated hummingbird [79]. Besides ensuring a low moment of inertia, the long primaries assist in the extensive wing twisting that characterises their insect-like flight technique. Hummingbird hands are as long as their arms; and a high ratio of hand length to arm length and consequent low moment of inertia also seem advantageous for hovering bats [42, 43] though the moments of bat wings average twice those of comparable birds [109]. Minimising the moment of inertia, and hence the inertial power, may also be an incidental advantage of the relatively short, broad wings of many woodland birds and bats, and of the short, pointed, broad-based wings of many shorebirds.

A second feature of flapping flight is the presence of a velocity gradient along the span of the wing: the tip is always moving faster than the base. For a given flapping frequency the importance of this gradient increases with decreasing flight speed, and this relationship is conveniently expressed by the *advance ratio*, the ratio of forward velocity to flapping velocity. Many insects that habitually fly at very slow speeds, with a low advance ratio, have narrow-based, even stalked wings whose area is concentrated distally, in the part of the wing where the airflow is fastest. This is true of zygopterous Odonata (damselflies), some Neuroptera and nematoceran Diptera (midges and gnats), and reaches extremes in some fossil insects of the Carboniferous and Permian periods [110]. In contrast, the individual wings, or coupled fore and hind wings, of the majority of insects capable of flying fast have broad bases.

A third important consequence of flapping flight, already touched on in Section 3.2.2, is the frequent need for the wing to deform in flight. Much of this deformation is concentrated in the distal part of the wing: the spreading, closing and twisting of primary feathers and the hands of bats; torsion and bending in insect wings. The length and area of the distal, deformable part of the wing relative to the whole can significantly influence the flight capabilities of the animal, particularly its manoeuvrability and versatility.

4.2.3 Structural detail

The wings of each of the three flying vertebrate classes are rather uniform in basic structure, and their variations are essentially those of proportion. An exception is provided by the wingtip primary feathers of birds. Primaries vary slightly in number, from 9 to 12 but typically 10, but they differ more obviously in the extent to which they are emarginated, and spread in flight. Many seabirds, shore birds, falcons and aerial insectivores have pointed wings, but the majority of birds are capable of spreading their primaries at need, and in many owls and soaring birds they are habitually widely spaced in both the horizontal and the vertical plane, like an array of small individual wings. In larger birds the vanes are usually emarginated, increasing the gaps between them. The aerodynamics of spread primaries are far from straightforward, but they appear to reduce the drag by acting as a series of individual slender wings, and to delay stalling at low speeds [111]. Spread primaries are typical of low aspect ratio wings, but are not limited to them. Some storks and pelicans have aspect ratios in excess of 10 – much the same as gulls – but their tip feathers are widely spread in flight.

Insect wings are bewilderingly varied: in shape, venation density and pattern, in the relative size of fore and hind wings, in the presence and arrangement of lines of flexibility, and in many other features of detail [112]. The functional significance of these variations is progressively becoming understood, and one can recognise some design features occurring widely and convergently in association with particular flight techniques and skills. The broad, fan-like hind wings of Orthoptera and Dictyoptera (grasshoppers and crickets, cockroaches and mantises) for example, are associated with rapid forward flight, with limited versatility; most of the aerodynamic force being generated on the downstroke. Wings of this kind are incapable of significant twisting in

flight [113] (Fig. 6a). Many insect wings, though, have adaptations that allow twisting, at least of the distal areas. Twistier wings can create useful thrust and even some weight-support on the upstroke, and this facilitates flight at low speeds, and in many cases extends the insects' speed range and overall versatility. Torsion is often accompanied by some ventral bending, and the wings of many insects, like the sawfly in Fig. 6b, have a transverse, or obliquely transverse line of flexible cuticle, like a one-way hinge, that allows the tip to bend and twist in the upstroke, even when the wing base itself is incapable of much torsion. The most versatile fliers of all – dragonflies, many flies, some lacewings – have astonishingly twisty wings, with a soft posterior margin that allows the entire wing to rotate about its long axis, in effect turning upside down for the upstroke (Fig. 6c).

These deformations are facilitated and limited by the wings' architecture: the distribution of flexible and rigid components; and they are also influenced by the muscles at the extreme base – a combination of automation and remote control which is without parallel elsewhere in the animal kingdom [114]. Not all wing characters, however, are flight-related. Insect wings have come to assume many secondary functions: camouflage, signalling, armour, thermoregulation; and these may influence or even dominate their adaptive design.

5 The energetics of flight: power, speed, size and behavioural ecology

Powered flight is an expensive activity [115]. The potential for high speed means that the cost of transporting unit mass of animal over unit distance is generally lower than that of terrestrial locomotion, but the metabolic power requirements (energy consumed in unit time) are extremely high. Cruising flight in a 0.1 kg bird uses between 7 and 10 W – compare about 4 W for a walking/running mammal of the same size [88]. Bat flight may be slightly more expensive, and insect flight is more costly still: bumblebees in flight consume up to 400 W/kg body mass over a wide speed range [116].

5.1 Power, and the power curve

The *metabolic power input* is the rate at which fuel is consumed. The *mechanical power output* is the power delivered by the muscles in flight. The ratio of the latter to the former is the *efficiency* of the system, taking account of energy lost as heat in muscle contraction, and other flight-related metabolic processes.

The power output can be further divided into the *inertial power*, used in overcoming the wings' inertia in flapping, and the *aerodynamic power*, used in overcoming drag. In this context we may distinguish three kinds of drag. These are *induced drag*, the drag incurred in generating the lift-producing vorticity; the *profile drag*, the drag on the wings; and the *parasite drag*, the drag on the body and legs. The aerodynamic power spent in overcoming these three drag components can similarly be divided respectively into *induced power* (P_{ind}), *profile power* (P_{pro}) and *parasite power* (P_{par}). Figure 9 shows the relationships between these power components, in the form of a flow diagram.

The inertial power component should vary with the square of the maximum flapping velocity, with the frequency, and with the moment of inertia both of the wing and of the *virtual mass* – the mass of a volume of air around the wing that is accelerated with it. In practice the cost of overcoming inertia is lower than might be expected. In insects most or all of the inertial energy is thought to be stored elastically in the cuticle or the flight muscle and given back in the next

Figure 9: Flow chart of energy expenditure in flight.

half stroke, and in vertebrates too a significant proportion seems to be converted into useful aerodynamic work [47, 109].

The three components of aerodynamic power can be combined in the *power curve*, which has been very influential in the study of animal flight, particularly that of vertebrates, as it is a useful tool for comparing flight patterns and behavioural strategies. The curve and its components are extremely difficult to determine experimentally for any species, and are normally obtained by modelling. The modelling process is complex, however, as many factors are involved, and the literature is controversial [117–123]. In gliding flight the three types of aerodynamic power are expected to vary in different ways with flight speed. Induced power is highest at low speeds, and falls off thereafter. Parasite power and profile power probably increase as the third power of the animal's forward velocity. Flapping horizontal flight is expected to increase both the induced and the profile power components. Induced power will then be highest in hovering and at low speeds, and will rise again somewhat at higher speeds, and some profile power will be expended even when the forward speed is zero. In insects, at least, the flapping velocity may sometimes be more important than the forward velocity in determining profile power [10].

Figure 10 shows these general relationships, and illustrates how the total aerodynamic power P_{sum} should follow a U-shaped curve. The graphs shown have no values attached, and the curves will vary in detail between species according to their morphology and physiology and also their ecology. Information on these can be used to predict the flight capabilities at least of birds and bats, and the interacting effects of a wide range of design features on the various components of the power curve and on other aspects of performance have been extensively analysed and discussed in the literature [42, 118–120, 122, 123].

The power curve has been particularly useful in indicating certain characteristic speeds that may have behavioural significance (Fig. 10). That at the lowest value of P_{sum} is clearly the *minimum power speed* (V_{mp}), at which the animal can fly most economically. That at the point where the curve meets a tangent drawn from the origin is the *maximum range speed* (V_{mr}), where the power/speed ratio and the cost of transport are lowest, and the animal can maximise its flight distance per unit energy expended. Many useful predictions about the effect of design features on performance emerge, and these can be compared with the actual flight characteristics

Figure 10: The power curve: how the aerodynamic power requirements for flight should vary with speed. P_{sum} , total aerodynamic power; P_{pro} , profile power; P_{par} , parasite power; P_{ind} , induced power; V_{sm} , predicted optimum speed between stopping places for migrating birds; V_{mp} , minimum power speed; V_{mr} , maximum range speed; V_{ot} , optimum transportation speed. Modified and generalised after [122] and [129].

of particular species. The high aspect ratio wings of swifts, for example, can be expected to minimise both induced and profile drag values, and favour economical flight at all speeds; those of hummingbirds, by reducing induced power expenditure, assist in sustained hovering – at zero airspeed, where P_{ind} will be highest.

It is crucial to realise, though, that these are curves of power *required* for flight at particular speeds. Equally important to the animal are the mechanical power *available* from the muscles, and the rate of energy consumed by them: the metabolic power. This last has been determined for a number of species, by measuring the mass lost in flight, or the oxygen consumed, or the rate of decline of radioactively labelled water. For some bird and bat species the plots of metabolic power against flight speed indeed appear U-shaped but others tend to be rather flat [122, 123]. Most of these results do not include data for low speeds, where P_{ind} would be highest, so the flat trajectories may represent the broad shallow part of the U-shaped curve around V_{mp} , but for some hummingbirds [124], small bats [125] and insects the curve is better regarded as J-shaped, where the power requirements of hovering, low and moderate speeds are similar, and costs only rise at high speeds [121]. Aerodynamic power output curves have been calculated for relatively few insects: bumblebees [116], two dragonflies [126], two moths [127, 128]; and these too appear best to fit a J-shaped model [10].

5.2 Speed and size

If indeed the curve of the mechanical power required for larger animals to fly is U-shaped, we may use it to revisit the relationship between size and available flight speeds. Limiting our discussion

to birds and bats: in general, the larger the animal, the higher will be its power requirements, and the faster it will tend to fly – the power curve is shifted upwards and to the right.

The power *available from the muscles*, however, depends on the morphology and physiological state of the animal, and will be largely independent of speed, though there is some evidence from starlings that the overall efficiency (mechanical power output/metabolic power input) may increase somewhat with speed [122]. Again, the larger the animal, the more power will be available; but the available power rises far more slowly than the power required, and larger birds will be progressively incapable of flight at the lower, more costly part of the speed range [117, 118]. This is very evident when one considers birds taking off. Small birds can rise directly from their perches, but many large birds need to run, or to taxi on the water surface to gain flight speed. The upper size of flying animals seems to be imposed partly by available power, but probably also by the mechanical strength of bones, tendons and muscles. The largest today – swans, bustards, albatrosses, pelicans, the Californian Condor – have a mass of around 15 kg. However fossils show the actual limit to be far higher: estimates put the mass of the Pleistocene condor *Teratornis* at around 40 kg, and the enormous Cretaceous pterosaur *Quetzalcoatlus northropi* and the Miocene condor *Argentornis magnificans* may have been twice as heavy [41, 48].

The huge diversity of insects in size, morphology and flight kinematics makes performance predictions from power curves far harder than in vertebrates. Almost all are smaller than the smallest vertebrates, and some of the largest – hawkmoths, dragonflies – are capable of sustained hovering and flying at a wide range of speeds, while others, of widely different sizes – grasshoppers, many Hemiptera, halticine beetles – need to jump to gain airspeed, and most of these are incapable of hovering. It is indeed not yet wholly clear whether the limits to flight performance in insects are determined by available metabolic power, or by aerodynamic constraints [10, 121].

5.3 Flight strategies, and appropriate speeds

Animals fly for a variety of purposes (see Section 3.1) and the power curve allows us to make some more predictions about the most appropriate speeds [129] (Fig. 10). The minimum power speed V_{mp} , allowing the animal to stay in the air for the longest time without refuelling, seems appropriate for swifts flying at night without feeding; for harriers, kestrels, ospreys and hunting wasps quartering the area in search of a single prey, or frigate birds waiting about to steal food from other seabirds [129, 130] for female insects searching for oviposition sites [10]; for nectar-feeding bats waiting for access to flowers [43]. Other kinds of foraging flight, where many prey items are taken, would be better suited by flying at a speed where the net energy gain is highest – probably rather above V_{mp} , but limited by the animal's ability to recognise prey at speed. This would apply among others to martins and swifts, and to bats [43] feeding on the wing. Speed adopted searching for prey with a patchy distribution would vary with the distance between patches, but should approximate to the maximum range speed V_{mr} . Flight at the food source would be slow, close to the minimum possible. Birds, bees and molossid bats foraging over long distances to bring back food or build up milk for their brood theoretically need to fly faster than V_{mr} [129, 131], at a speed – the optimum transportation speed (V_{ot}), found by drawing a tangent to the power curve from a point on an extended ordinate representing the rate of net energy gain in foraging. Optimal speed between stopping points (V_{sm}) for a migrating bird is found where this same tangent crosses the abscissa (Fig. 10) [129]. For escaping a predator or pursuing prey the best speed is sensibly the highest available, but for vertebrates might be the highest anaerobic (sprint) or aerobic (stamina) speed, depending on circumstances. Insects are not known to use anaerobic metabolism in flight.

Flight speed is notoriously difficult to measure in the field, but there is a useful body of data tending to confirm some at least of these predictions. Many bird species searching for food have been observed at speeds between V_{mp} and V_{mr} . Kestrels, *Falco tinnunculus*, tend to wind-hover at airspeeds close to the predicted V_{mp} [132]. Swallows travelling between food patches operate well above their feeding speed and above V_{mr} [133]. Pipistrelle bats *Pipistrellus pipistrellus* range around their calculated V_{mr} when foraging, but are significantly faster when commuting [134]. Bumblebees operate well above their calculated maximum range speed when commuting to food patches [106, 107].

6 Conclusions

Flight is a frequent method of locomotion for the great majority of animal species. Though their designs are ultimately constrained by the laws of aerodynamics, the astonishing diversity of flying forms reflects the huge range of lifestyles that flight allows. Habitat and distribution, food preferences and feeding behaviour, generation time, breeding situation and habits, whether sedentary, migrating or commuting, and many other ecological and behavioural factors interact with each other, and indeed with phylogeny: the morphological and physiological heritage of each separate evolutionary line on which later diversification has built. Seeking general principles and common solutions in a field with so many variables is a fascinating but daunting task, and so indeed is accounting for the variability; particularly in insects – why are some groups so variable despite having apparently similar flight capabilities, while others with recognisably different flight behaviours are comparatively uniform? Theoretical and experimental aerodynamics, muscular, circulatory, respiratory and neurosensory physiology, functional morphology and structural mechanics, ecological modelling, all have parts to play, but there is still a major need for field observation and measurement of flight behaviour and performance of the greatest variety of animals under natural conditions. Whatever our models may predict – the animals still fly.

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