

Chapter 13

Convergence in Gliding Animals: Morphology, Behavior, and Mechanics



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Abstract Gliding locomotion has convergently evolved in multiple vertebrate and invertebrate taxa, spanning terrestrial and aquatic animals. The selective pressures attributed to the evolution of gliding include the topography of the environment as well as the capabilities for rapidly escaping predation, foraging over larger spatial areas, and landing safely after falling. Although gliding locomotion has likely evolved in response to these multiple factors in diverse lineages, extant taxa exhibit convergent morphologies and behaviors related to gliding. Understanding the relevance of specific gliding features is informed by the laws of physics: to successfully execute a glide, the animal must use a combination of body shape/size changes (morphology) along with attaining and modulating a favorable body posture (behavior) to generate sufficient aerodynamic forces to slow and control the descent. Gliding animals employ a diverse range of aerodynamic surfaces to generate lift and drag forces, from membrane wings in mammals, *Draco* lizards, fish, and squid, to smaller structures including skin flaps, flattened bodies, and appendages in geckos, snakes, frogs, spiders, and ants. These force-generating surfaces vary in their shape, size, and anatomical structure, but serve a common function of increasing the total body surface area of the animal compared to their non-gliding relatives, enabling them to produce significantly higher aerodynamic forces. Convergence is also observed in takeoff, gliding, and landing behaviors, necessary for the animal to execute a successful glide trajectory. Takeoff behaviors vary from jumping from vertical or horizontal substrates in terrestrial gliders, to launching from below or on top of the water surface in fish and squid. Once airborne, gliding animals produce

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and modulate aerodynamic forces of lift and drag through adjustments in their body-airfoil or posture, and/or interactive combinations of both. In some taxa, modulation of aerodynamic forces enables the animal to undertake aerial maneuvers to navigate spatially complex habitats and to land. The evolution of dedicated primary wings in mammalian gliders and *Draco* flying lizards allows them to substantially slow their descent and transition into a more upright position to land, mostly on vertical substrates. Gliders that lack wings, including snakes, geckos, ants, and spiders, use a landing strategy involving impact with the substrate without a significant reduction in speed, using a combination of the body and appendages to land. Flying fish and squid attain a more streamlined posture by tucking their fins to reduce drag while entering the water surface. In this chapter, we provide a broad overview of gliding in diverse lineages, highlighting the ecological and physical pressures that have shaped this form of aerial locomotion in the animal kingdom.

13.1 Introduction

The capability of moving through air is not common in the animal kingdom. Those that can fly reap tremendous ecological benefits - enjoying fast travel, with some migrating over long distances (including over the highest mountains and largest oceans), access to largely inaccessible resources, and means for foraging or avoiding predators. Muscle-powered flapping flight has convergently evolved only four times in the history of life, in birds, bats, insects, and pterosaurs (Rayner, 1988; Wigglesworth, 1973), but each of these groups has benefitted from access to vertical airspace, as reflected in the high diversity of their extant species.

Gliding (defined below) is also a form of flight, but an unpowered one in which the animal falls through the air in a controlled fashion, trading the potential energy of height for kinetic energy that drives horizontal travel (Dudley et al., 2007; Socha et al., 2015). Gliding is far less physically and biomechanically demanding than flapping flight, but entails its own set of challenges. Against the pull of gravity, the gliding animal must create aerodynamic forces of lift and drag that both help to support its weight and direct it horizontally, as well as distribute those forces in a way that keeps the body stable. Without the additional input of power, the frictional losses of drag dictate that the glider can only produce a net path that is downward, yet angled, in still air. With this capability, gliding animals can use rapid aerial locomotion to evade predators or hunt prey, forage, and engage with other conspecifics via mate-seeking or territoriality behaviors, each such behavior being essential for their survival. Because their source of energy is limited by their starting height, gliders are constrained to relatively short flights in comparison to flapping flyers, often balancing the requirement to cover horizontal distance with maneuvering around obstacles mid-air in often spatially cluttered environments (Khandelwal & Hedrick, 2020). Nonetheless, these short flights also enable them to cross otherwise limiting gaps in the environment (Graham & Socha, 2020), expanding the scope of available resources compared to their non-flying relatives. Overall, with fewer

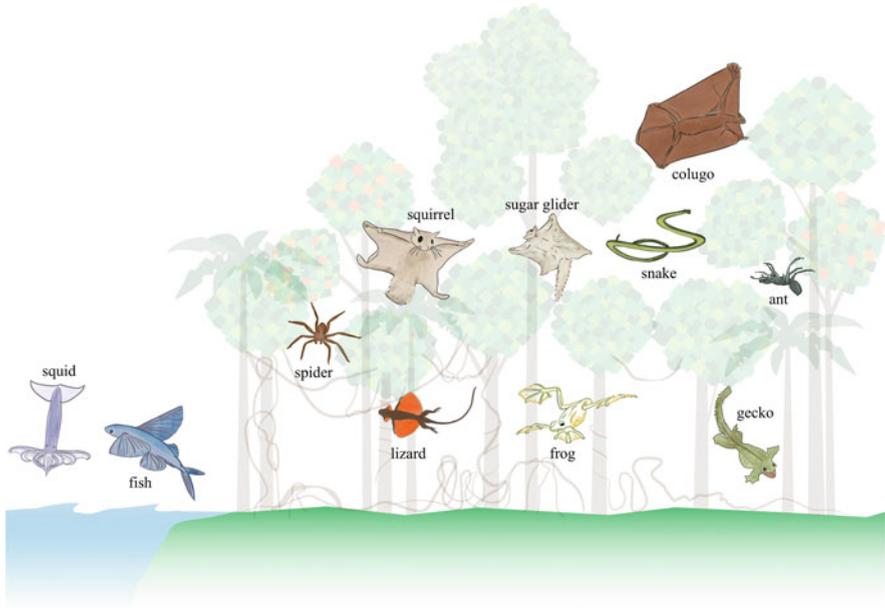


Fig. 13.1 Animal gliders of the world. Terrestrial gliders exclusively inhabit arboreal environments, including mammals (squirrels, sugar gliders, and colugos), lizards including *Draco* and the gecko *Hemidactylus*, snakes, frogs, spiders, and ants. The only known gliders that inhabit oceanic environments are fishes and squid. The animals in this figure are original illustrations by Dr. Mary Salcedo, inspired by images from multiple sources. Not to scale

physical and physiological requirements, gliding flight has convergently evolved far more often than has flapping flight, in groups that include mammals, reptiles, amphibians, insects, arachnids, fishes, and cephalopods (Fig. 13.1), with body sizes spanning over 4 orders of magnitude (from ~ 0.05 g in *Cephalotes atratus* (Yanoviak et al., 2005) ants to ~ 3.2 kg in the red giant flying squirrel (Jackson, 2000), *Petaurista petaurista*).

In this chapter, we discuss the morphological and behavioral convergences that underlie the ability of such a great diversity of animals to glide successfully. Perhaps the most common theme related to convergence in gliding is an increase of body surface area, usually through some dynamic action such as spreading of skin to form a wing, defined here as a morphological structure that functions to generate substantial aerodynamic forces in flight. But there is more to an airfoil than what might be seen in traditional bilaterally symmetrical wings: animal gliders also take advantage of morphological shape differences in flattened body structures relative to non-gliding relatives. Consequently, differences in morphology lead to convergence in specific aerial behaviors that the animals must employ on a day-to-day basis to become airborne, generate aerodynamic forces, and land successfully. We discuss such features in the context of the full repertoire of gliding, from takeoff to landing,

informed by the physics that strongly guide and constrain such behaviors. For a historical perspective, we also point the reader to previous reviews of gliding, including those that focus on adaptations (Rayner, 1981), evolution (Dudley et al., 2007), and morphology and trajectory (Socha et al., 2015).

13.1.1 *What Is Gliding?*

We consider gliding, following the conceptual framework of recent authors (Dudley et al., 2007; Socha et al., 2015), to be any aerial behavior in which the animal actively produces aerodynamic forces to effectuate horizontal travel in a controlled fashion. In doing so, animals must be able of at least partially supporting their body weight (thereby also slowing their descent), and also controlling their trajectory either by modulating aerodynamic forces or using inertial mechanisms. The underlying physical mechanism of aerodynamic force production is described by the equations for lift and drag:

$$L = \frac{1}{2} C_L \rho S v^2 \text{ and } D = \frac{1}{2} C_D \rho S v^2$$

where L and D are the lift and drag forces, C_L is the coefficient of lift, C_D is the coefficient of drag, ρ is the fluid (air) density, S is typically the effective surface area of the wing/airfoil, and v is the airspeed of the animal. Most gliders reconfigure a part of their body to form an airfoil that produces lift, but all morphological structures produce drag, important for the stability characteristics of the glider. The farther the center of aerodynamic pressure is from the center of mass of the glider, the greater the resulting rotational moment, meaning that even small amounts of drag can serve to topple the glider from a stable position, or be put to positive use for balance and to induce aerial maneuvers.

13.1.2 *Driving Forces of Convergence in Gliders*

A common benefit for all gliding animals is the ability to rapidly cover distance by moving through air instead of moving on the ground, climbing, or even swimming. Consequently, rapid aerial movement can help the gliding animal evade predators, forage, and cover a larger area of the habitat to perform behaviors, including the seeking of mates and establishment of territory. The evolution of gliding has been attributed to multiple factors including habitat structure, predator avoidance, foraging, injury avoidance, and energetic expenditure during locomotion (Fig. 13.2). It is highly likely that many of these factors collectively influenced the evolution of gliding across different taxa. We begin our discussion by examining terrestrial gliding animals with regard to each of the factors listed above and then extend it

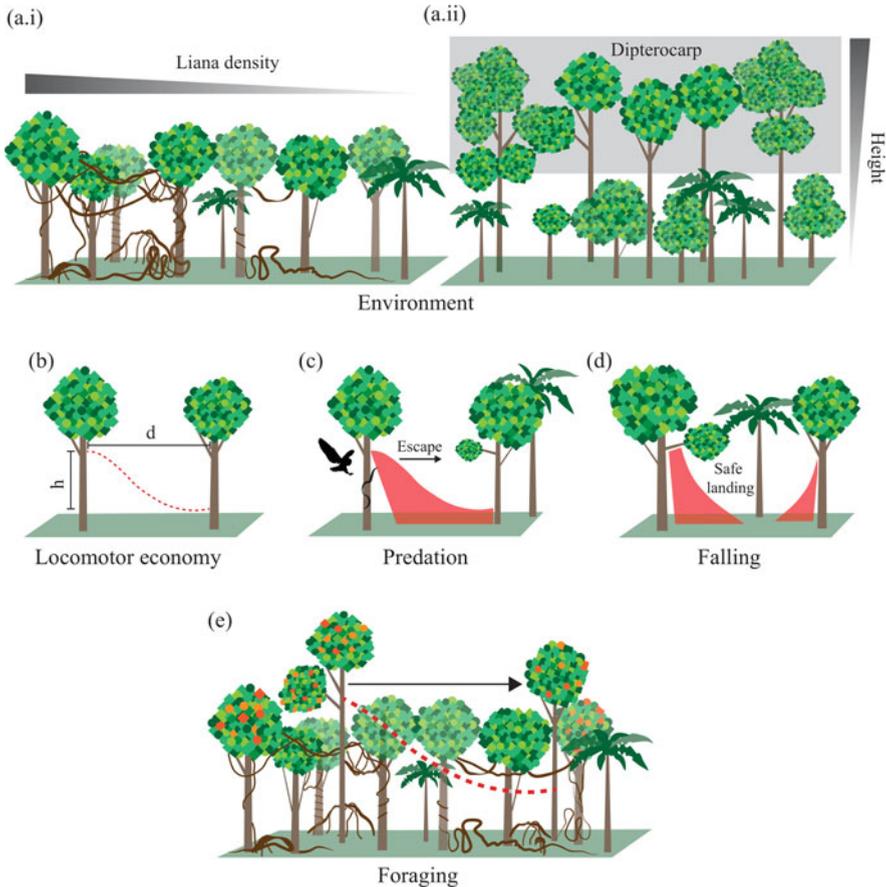


Fig. 13.2 Possible selective pressures that drove the evolution of gliding in arboreal taxa. Hypotheses include environmental conditions related to forest structure (**a.i**: density of vine-like lianas, and **a.ii**: tree height); energetics (**b**: locomotor economy); and behavior (**c**: predation, **d**: safe landing after falling, and **e**: foraging efficacy)

to the less frequently discussed selective pressures acting on aquatic gliders, including flying fish and squid.

13.1.3 Environment

Empirical evidence suggests that different forest structures across the world are correlated with different modes of locomotion by arboreal animals (Emmons & Gentry, 1983). Therefore, it follows that the variability in the structure of forests would have played a crucial role in the evolution of gliding in animals. Along these

lines, there have been two prominent hypotheses put forth to explain the evolution of gliding in terrestrial animals (Fig. 13.2a). The first deals with the distribution and density of vine-like lianas (Emmons & Gentry, 1983), and second with the presence of tropical rainforests dominated by members of the Dipterocarpaceae (Dudley & DeVries, 1990; Heinicke et al., 2012), discussed in detail below.

Emmons and Gentry (1983) hypothesized that the evolution of gliding flight was related to the distribution of lianas in forest canopies (Fig. 13.2a.i). Lianas are long, woody vines that climb trees to gain access to sunlight. By extensively covering trees and the forest canopy, lianas can provide arboreal pathways for canopy-dwelling animals. Emmons and Gentry surveyed liana density in Africa (Afrotropical realm), South America (Neotropical realm), and Asia (Indo-Malayan realm) and showed that Africa has the highest liana density, followed by South America, with the lowest density in Asia, leading to their hypothesis that the scarcity of lianas in tropical Asia favors the relatively long-distance strategy of gliding. Furthermore, the increase in liana density from Asia to America should also correspond to an increase in glider diversity. Indeed, this is the case, with Asian tropical forests home to a greater diversity of gliding animals compared to Africa, with the lowest in the Americas (Corlett, 2007). Even within the Americas, the southern flying squirrel, *Glaucomys volans*, is restricted to high-elevation deciduous forests consisting of oak and oak-pine, and is not found in liana-rich lowland Neotropical forests (Lambert & Halsey, 2015; Jackson & Schouten, 2012). Although the hypothesis of variation in liana density seems promising, it has faced criticism based on contrary results. Dudley and DeVries (1990) argued that the mean liana density is only 30% higher in Africa compared to the Neotropics, yet there are relatively few gliding animals found in either geographical region (Jackson & Schouten, 2012; McCay, 2003). Furthermore, Appanah et al. (1993) have shown that Asian forests are not poor in diversity and abundance of lianas compared to Africa and South America.

Dudley and DeVries (1990) extended the discussion of the evolutionary influence of the environment on gliding to include the height of the forests (Fig. 13.2a.ii). In particular, trees of the Dipterocarpaceae reach heights upwards of 60 m in the Indo-Malayan forests compared to the average forest height of 30–40 m in Africa and America. The presence of taller trees could provide gliders with opportunities to cover larger horizontal distances, reduce their energetic cost of transport, and provide vertical habitat stratification, which should promote diversification of gliding taxa. Furthermore, the presence of taller trees could favor the evolution of larger body size in gliding animals, with increased takeoff height enabling longer glide distances and lowering their cost of transport. Dudley and DeVries (1990) also hypothesized that gliding animals would climb as high as possible to increase their horizontal gliding distance and reduce their energetic costs. However, recent work by Khandelwal and Hedrick (2020) has shown that glide distances are independent of the takeoff height in glides performed by *Draco* flying lizards in their natural environment. A complementary evolutionary pressure arising from the ecology of dipterocarp forests is the prevalence of food patchiness and the supra-annual cycles of flowering and fruiting, which could promote spatially larger foraging bouts and gliding as an efficient energetic means of doing so (Corlett, 2007; Heinicke et al.,

2012). Further supporting the influence of the Diptero­carpaceae on the evolution of gliding, Heinicke et al. (2012) demonstrated a strong temporal overlap between the emergence of diptero­carp forests and the origin of gliding in at least six lineages.

Convergence of phylogenetically distant groups of animals upon similar gliding behaviors, coupled with the structural difference in glider habitats, highlights the evolutionary pressure imposed by the environment on extant gliders worldwide. Both hypotheses, that based on liana density and that based upon the Diptero­carpaceae, likely contribute towards our understanding of the evolution of gliding in animals. However, neither hypothesis can stand on its own, falling short of explaining how intermediate forms of gliding evolved into the variety of gliding lineages that we see today (Lambert & Halsey, 2015).

13.1.4 Locomotor Economy

The locomotor economy hypothesis (Fig. 13.2b) states that the energetic cost per unit distance is less for gliding in comparison to various forms of terrestrial or aquatic locomotion. Studies testing this hypothesis have been carried out primarily for mammalian gliders by comparing the cost of climbing and gliding a particular distance to the cost of quadrupedal locomotion for traveling the same glide distance horizontally (Byrnes et al., 2011; Dial, 2003; Flaherty et al., 2010; Scheibe & Robins, 1998; Scheibe et al., 2006).

Dial (2003) used a simplistic model derived from equilibrium gliding mechanics to show that an intermediate body size, in the range of 200–400 g, would favor gliding as an energetically efficient means of transport compared to animals of small or large body size. Dial (2003) further argued that the energetic advantage for mid-size animals would be evident in their home range size, with intermediate-sized gliding mammals having larger home ranges and exploiting calorie-poor diets compared to their non-gliding counterparts, as opposed to similar home range size for small and large-sized gliding mammals. Overall, the energetic calculations presented by Dial (2003) support gliding being favorable in open habitats, thereby corroborating the liana density hypothesis.

A true test of the locomotor economy hypothesis would require experimental measurement of the cost of locomotion and its comparison with the overall energy budget of the animal over a prolonged period of time. To this end, Flaherty et al. (2010) used an open-flow respirometry technique to calculate the resting and running energetics of the northern flying squirrel (*Glaucomys sabrinus*) and estimated that 64% energetic savings were accrued by gliding. Flaherty et al. (2010) showed that the net cost of quadrupedal locomotion for flying squirrels was significantly greater than the allometric estimates predicted, with the metabolic rate for horizontal travel increasing exponentially with velocity, and that extended bouts of quadrupedal locomotion in flying squirrels were energetically expensive compared to gliding. Studying a gliding mammal from a different order, Byrnes et al. (2011)

tackled the locomotor economy hypothesis by tracking gliding behavior in wild colugos using on-body sensors, providing an indirect estimate of overall energy budget during extended durations of time. Comparing bouts of climbing versus gliding showed that the energy required to climb was ~ 1.5 times greater than moving an equivalent glide distance using quadrupedal locomotion. The study further argued that the locomotor ecology of mammalian gliders shows that less than 10% of the animal's daily energy expenditure is expended in climbing, reducing its selective influence on the evolution of gliding in animals.

An alternative approach in support of the locomotor economy hypothesis and the liana density hypothesis is presented by Lambert and Halsey (2015), who argue that because gliding has evolved in an arboreal context, the added energetic cost of climbing has already been evolutionarily 'paid' and should not be considered in testing the locomotor economy hypothesis. Instead, if the energetics of an animal climbing and traversing horizontally (either through the treetops or by descending to the ground) are compared with the energetic cost of gliding the same horizontal distance, gliding is in fact an energetically efficient means of locomotion, especially in relatively open, liana-free environments.

Although there are opposing lines of evidence for the locomotor economy hypothesis, it remains unclear whether gliding was sufficiently efficient as a means of locomotion to act as a selective pressure for evolutionarily intermediate forms of gliders. Lambert and Halsey (2015) present an example wherein the benefits of gliding energetics are gained only after the animal is able to glide; in other words, the animals representing the intermediate phases that led to gliding animals would still drop to the forest floor and not have a selective energetic advantage compared to their conspecifics.

13.1.5 Predation

Emmons and Gentry (1983) proposed that predation is likely to be a selective pressure relating to the evolution of gliding (Fig. 13.2c). The three-dimensional structure of arboreal habitats provides the possibility of escaping in a variety of directions, potentially adding an element of uncertainty for the predator (Byrnes & Spence, 2011). Furthermore, falling followed by gliding can be a faster escape response compared to jumping (Socha, 2006) and/or sprinting. Because arboreal predators have different hunting strategies and may use different sensory cues, the escape benefits of jumping/escaping and gliding would largely be determined by the composition of predators present when gliding evolved (Lambert & Halsey, 2015). Gliding also allows the animal to avoid the forest floor or small water bodies and, in turn, the majority of non-volant predators. The rapid nature of a glide minimizes travel time, reducing the time gliders are exposed to potential predators (Byrnes & Spence, 2011; Dudley et al., 2007). In support of the predation avoidance hypothesis, flying animals have been shown to have lower mortality rates than non-volant animals (Pomeroy, 1990), and arboreality has been linked to greater longevity of

animals (except for marsupials) compared to their terrestrial relatives (Shattuck & Williams, 2010). Holmes and Austad (1994) compared the lifespans of gliding mammals with those of non-volant eutherians and showed that gliding mammals have significantly greater longevity. However, Stapp (1994) has urged caution with regard to the approach used by Holmes and Austad (1994) in comparing life spans of gliding and non-gliding animals, noting that a nocturnal and gliding lifestyle may not offer additional protection from predators relative to that already achieved by being arboreal and cavity-nesting (Fan & Jiang, 2009; Kavanagh, 1988; Stapp, 1994). For example, predation has been reported on giant flying squirrels by black-crested gibbons (Fan & Jiang, 2009) and on marsupial greater gliders by the powerful owl *Ninox strenua* (Kavanagh, 1988). The latter study suggested a staggering decline of ~80% in the marsupial greater glider population over a period of 46 months due to predation (Kavanagh, 1988; Fan & Jiang, 2009).

13.1.6 Foraging

The foraging efficiency hypothesis (Fig. 13.2e) has been addressed mainly through studies of mammalian gliders. The ability to glide allows animals to access patchily-distributed food and to forage over a larger area in a smaller amount of time, thereby potentially providing a selective advantage to gliding behavior compared to non-gliding arboreal animals. Byrnes and Spence (2011) showed that gliding originated independently in six lineages of mammals. Gliding evolved twice each in ancestors with folivorous, frugivorous, and exudivorous diets. Of these types, there were significant associations between changes in binary character (gliding versus non-gliding) for both exudivory and folivory. No significant association has been found between gliding and frugivory, despite gliding having evolved twice in ancestors exhibiting frugivory (Byrnes & Spence, 2011).

13.1.7 Falling

An open-space environment, gliding efficiency, predatory pressure, and foraging: all of these are possible selective factors relating to the evolution of gliding. However, it is unclear how each of these factors would have benefited the intermediate stages of gliding that preceded extant gliders. For example, for traversing between spatially distant trees efficiently, the lack of a well-evolved gliding apparatus and physiology could result in the organism falling to the ground in an uncontrolled fashion, making it prone to injuries and exposure to predators. Furthermore, the inability to glide long distances would prevent the organism from accessing sparsely distributed food resources.

Paskins et al. (2007) and Lambert and Halsey (2015) argue that controlling accidental falls in an arboreal habitat (Fig. 13.2d) would have provided a strong selective pressure for the evolution of gliding. Organisms with the capability of

safely landing after slipping in an arboreal environment would have a survival advantage compared to those unable to do so. Furthermore, what might be considered as an only partial or small degree of morphological specialization for gliding can still augment drag forces that slow down the falling animal, as has been observed for extant gliders with only small skin folds (Russell, 1979). Controlling accidental falls so as to land safely and reduce injury is likely of high relevance to intermediate forms of gliders. Caple et al. (1983) showed that an increase of up to 5% in the total lift force (relative to body weight) would allow significant control of the body around the pitch and roll axes, both necessary for correcting body orientation during a fall. Furthermore, it is plausible that intermediate gliding forms were able to generate up to 5% of body weight as lift force and thereby benefit from controlling body pitch and roll during a fall. Paskins et al. (2007) used force measurements at takeoff and landing for flying squirrels to demonstrate that, in the absence of aerial control or the ability to slow down, flying squirrels would sustain impact forces up to 28 times their body weight. A study on flying frogs also emphasizes the importance of body control and suggests that aerial maneuverability, rather than horizontal glide distance, could be an important driving factor in the evolution of flying frogs (Emerson & Koehl, 1990).

13.1.8 A Note on the Evolutionary Arguments for Gliding

As previously mentioned, it is highly likely that more than one selective pressure played a crucial role in the convergence of gliding-related morphologies and behaviors that we see today. Furthermore, the majority of arguments put forth in support of one or more of the hypotheses about the evolution of gliding are informed by studies and/or observations conducted largely on mammalian gliders (but see Dudley & Yanoviak, 2011; McGuire, 2003; McGuire & Dudley, 2005). Few studies describe or provide anecdotal evidence in support of the evolution of gliding hypotheses in gliding animals apart from mammalian gliders, highlighting our lack of understanding of the ecological and biomechanical context of the majority of extant gliding animals (Dudley et al., 2007; Emerson & Koehl, 1990).

Aquatic aerial gliders (flying fish and flying squid) have received even less attention. Like all of the other non-mammalian gliders, studies have been limited in number due to constraints relating to experimental methodology and data collection, which present particular difficulties for these open-water oceanic groups. Davenport (1994) described the evolution of gliding in flying fish in regard to the combination of enlarged pectoral fins and an asymmetric caudal fin. Together, these adaptations allowed the fish to swim near the surface in the high-drag zone where it could extend its pectoral fins to lift the front part of its body above the water surface, further reducing drag and, in conjunction with the ground effect, enable it to enact high-speed 'skittering' on the water surface. Taxiing on the water surface was thus a possible precursor to gliding flight seen in present-day flying fish. Here, we briefly mention two hypotheses that have been put forth for the evolution of gliding in flying fish and are likely applicable to flying squid.

The locomotor economy and predation avoidance hypotheses are generally used to explain the evolution of gliding flight in flying fish and squid (Davenport, 1994; Xu et al., 2013; Rayner, 1986). Explanations that undergird the predation avoidance hypothesis include the ability of the animal to exit the water and pass into the air, thereby resulting in the predator losing a clear line of sight and being faced with uncertainty about the point at which the potential prey might re-enter the water. However, observations of flying fish exiting the water surface in the absence of obvious sub-surface predators (Davenport, 1994), along with video recordings of both fish and birds catching flying fish mid-air and tracking them from beneath the water (Davenport, 1994; BBC footage: <https://www.youtube.com/watch?v=bk7McNUjWgw>), suggest that there could be multiple ecological reasons for the fish taking to the air. Rayner (1986) suggested that periodic flights of flying fish could be an energy-saving strategy, especially over long distances of travel. However, Davenport (1994) argues that the fish's muscle that likely contributes to the high-speed takeoff from the water surface is energetically expensive, and its use is not economical for frequent short-duration aerial glides.

13.2 Morphology

The vast majority of gliding animals have evolved morphologies that increase their total body surface area compared to their non-gliding counterparts, perhaps the largest convergence demonstrated amongst these flyers. The combined effect of change in total body surface area and its interaction with the surrounding air during descent allows the animal to generate lift and drag forces to control its glide trajectory. Gliding-specific morphologies range from dedicated and novel primary wing structures in mammalian gliders and flying lizards, to modifications of pre-existing body parts in ants, spiders, and flying snakes. Some taxa exhibit multiple specializations for gliding, combining flattened appendages and a primary wing membrane, as is the case in *Draco* flying lizards, further enhancing their gliding capabilities. To a lesser extent, flying frogs and geckos employ skin flaps and webbed feet that function to increase the total body surface area.

13.2.1 Membrane Wings

Membrane wings (often referred to as 'patagia'; a single membrane is a patagium) have convergently evolved in mammals, reptiles, amphibians, fish and cephalopods. Among mammals, the membrane wing has evolved at least six times, perhaps suggesting that the genetic modifications required to evolve a patagium are not complex. The developmental and genetic underpinnings of wing membranes in mammals is a rich target for research, particularly given the possibility that similar changes may underlie the evolution of flapping flight in bats (Bishop, 2008).

Membrane wings in reptiles are found only in *Draco* flying lizards, and in invertebrates, only in flying squid. Across these taxonomic groups, the membrane wings are extended/stretched once airborne to generate aerodynamic forces of lift and drag, and begin to retract just before landing, followed by complete retraction after the end of the glide. Mechanically, there is a distinction between the supported mammalian membrane wing and that of most other gliding wings, distinguished by the inclusion of some stiffened strut. In *Draco* lizards, frogs, and fish, the struts are bony elements (ribs or toes), whereas in squid they are tentacles. These struts provide additional mechanical integrity, but they also form small ridges on the surface that possibly influence the wings' aerodynamics. Unlike all the rest, the flying geckos (genus *Gekko*, previously *Ptychozoon*) possess lateral skin flaps on the trunk (Russell et al., 2001), which can be considered as unsupported membrane wings of low aspect ratio (the ratio of the wing span to the wing chord).

Mammalian gliders have a propatagium between the head and the forelimbs, a patagium between their forelimb and hindlimb, and variably a uropatagium extending from the hindlimbs to the tail (Panyutina et al., 2015). In colugos, an extensive uropatagium extends from the hindlimbs and incorporates the entire tail, contributing to the colugo's relatively larger aerodynamic surface compared to that of all other gliding animals. Anatomically, the membrane wings are only supported by distal attachments to the animal's body. For example, the patagium is supported at the leading edge, trailing edge, and the base of the wing where it joins to the body. Because there are no intrinsic muscles in the membrane (such as the plagiopatagiales proprii muscles in bats; Cheney et al., 2014), changing the shape of the membrane wing requires the animal to reposition its limbs and/or other body parts that connect to the membrane.

Squid possess two separate flight surfaces that help them glide once they jet beyond the water surface. The first is a pair of wings formed by the fins positioned towards the anterior of the body, and the second is formed by the spreading of tentacles along the posterior part of the body, with some sort of membrane between them. Azuma (2006) suggested that the tentacle/membrane wing provides greater lift force than does the fins. Squid also stiffen their mantle using muscle contraction during jetting, facilitating pitch-up control of the body. When re-entering the water, squid fold their fins and tentacles, which likely serves to streamline the body and reduce drag while entering the water surface.

For *Draco* flying lizards, the primary wing consists of a patagium supported by elongated thoracic ribs operated by specialized musculature (Colbert, 1967; Russell & Dijkstra, 2001). The opening and closing of the patagium are controlled by the combination of highly modified external and internal intercostal muscles, external oblique muscles, and a system of ligaments spanning the individual elongated thoracic ribs. The muscle actuation to rotate the ribs laterally is greatest for the first two anterior ribs. The large actuation to pull the first rib forward is achieved by the iliocostalis muscle extending far anteriorly to its origin on the anterior ribs and vertebrae. The great length of the muscle is necessary to allow a degree of contraction sufficient to rotate the ribs far out to completely stretch the patagium. The

anteriorly located second rib has a similar but less extensive development of the intercostal muscle. The remaining ribs are pulled anteriorly more by the ligaments that interconnect the ribs and less by the musculature, thereby completing the anterior extension of the ribs that consequently stretches the patagium open.

Mammalian gliders and *Draco* flying lizards are both proficient gliders that possess a specialized primary wing membrane to glide. However, the difference in the patagial anatomy between mammalian gliders and *Draco* flying lizards might also have an influence on the climbing speed and gait on trees in their natural habitat. The lack of connection between the patagium and the fore and hind limbs in *Draco* flying lizards might provide a higher degree of unconstrained motion compared to mammalian gliders.

The fully webbed feet of flying frogs and geckos also form membranous, bone-supported wings, significantly increasing the total lifting surface of the animal. The fully webbed feet of these gliding animals act as control surfaces that can easily be repositioned during descent to control the glide trajectory (Emerson & Koehl, 1990).

13.2.2 Skin Flaps

Gliding animals including flying frogs and flying geckos have evolved additional skin flaps instead of a primary wing membrane, along with fully webbed hands and feet. For example, flying frogs (genus *Rhacophorus*) have additional skin flaps on their legs compared to non-flying frogs (Inger, 1966). Flying geckos (*Gekko*) have cutaneous flaps extending laterally on either side of the body, and smaller ones around the hind limbs (Young et al., 2002).

In addition to the main membrane-strut wing, *Draco* flying lizards also have an additional set of lappets, small triangular structures on the lateral margins of the head that also extend immediately after takeoff and are retracted after landing. Because the surface area of these lappets is much smaller than the primary wing, their relative aerodynamic role is likely much smaller. However, their location far forward of the centers of mass and aerodynamic pressure mean that they could be influential in pitch control. The structure and function of lappets is potentially similar to the canards found in present-day aircraft in providing stability during gliding, but specific work is needed to understand this unique aspect of the lizard's morphology, which may also function to delay stall at high angles of attack (Wibowo et al., 2018).

13.2.3 Flattened Body

For some gliders, the dorsoventrally flattened body itself provides the main aerodynamic force-generating surface. A flattened body employed in gliding has convergently evolved in flying snakes (Socha, 2011), the lizards *Leiolepis belliana* (Losos et al., 1989) and *Holaspis guentheri* (Arnold, 2002; Mertens, 1960; Schiøtz & Volsøe, 1959; Vanhooydonck et al., 2009), and the gliding spider *Selenops*

(Yanoviak et al., 2015). These taxa either employ behavioral flattening upon becoming airborne (discussed in detail in sect. 13.3.3) or are morphologically flattened at rest. *Draco* flying lizards may also exhibit a small degree of morphological flattening at rest, but this feature has not been well characterized within the genus. Recently, wandering salamanders (*Aneides vagrans*) have been observed to slow their aerial descent and change directions in a wind tunnel (Brown et al., 2022). This work suggests that they might glide in the wild, an ability attributed to their relatively flattened body, long limbs, and large feet, which were held in a skydiving posture in this experiment.

The flattened body of gliding spiders of the genus *Selenops* is also characteristic of the entire family *Selenopidae*, known commonly either as ‘flatties’ or wall crab spiders. Based on estimates from published images (Crews, 2011; Yanoviak et al., 2015), their degree of flatness is ~ 3.4 (length/depth) and ~ 1.5 (width/depth), contributing to the spider’s steep glide trajectories, with glide ratios (horizontal/vertical travel) ranging from ~ 0.2 to ~ 1 . The *Selenopidae* includes nearly 300 species, most of which have not been investigated for glide performance. Given that the flattened morphology is widespread amongst the group, which includes both arboreal and terrestrial taxa, this group may be amenable for testing evolutionary hypotheses about the acquisition of features related to gliding.

13.2.4 Limbs

Although limbs can be thought of as simple cylinders that mostly induce drag, their orientation and location can influence the centers of mass and aerodynamic pressure, and thus the balance of forces and torques on the glider. A wide range of terrestrial gliders have limbs that are unattached to membranes, including *Draco* flying lizards, flying frogs, and arthropods that glide. The effect of leg posture has been explored for some species. Physical modeling of the flying frog *Rhacophorus nigropalmatum* demonstrated that the positioning of the legs and feet have a strong influence on glide performance (Emerson & Koehl, 1990; Emerson et al., 1990; McCay, 2001), but the specific aerodynamic role of the legs (or any other part of the anatomy, for that matter) has not been studied. The gliding ant *Cephalotes atratus* has front legs that are dorsoventrally flattened (Yanoviak et al., 2005), but as with frogs, the aerodynamic effects of the legs have not been studied.

13.2.5 Sensory Structures

There is a paucity of studies on the role of sensation and sensory feedback specific to gliding animals. Consider the wings of bats: the membrane is very highly mechanosensitive (Swartz & Konow, 2015), with an average sensitivity greater or equal to that of skin of the human fingertip (Chadha et al., 2011). Only recently in bats have small, sub-millimeter projections on the skin surface been identified to

function as specialized airflow sensors, with directional asymmetry favoring sensitivity to flow from the leading edge to trailing edge (Sterbing-D'Angelo et al., 2011). There have been few reports of equivalent structures in gliding animals; the cutaneous mechanoreceptor sensilla found in the patagia of *Gekko kuhli* (Russell et al., 2001) may be one such candidate. However, gliding animals employ flight far less often than flapping flyers, suggesting that selection pressures that result in greater mechanosensory feedback are probably much lower in gliders. Alternatively, our lack of knowledge of gliding-specific sensory structures may reflect a dearth of focused studies. One starting point would be to examine the mechanical sensitivity of skin in gliders like lizards, snakes, and frogs to determine the spatial and velocity resolution of airflow that they can detect; such mechanosensitivity could be employed for feedback control.

Flying lizards and snakes are strictly diurnal compared to their mammalian counterparts. Therefore, it is likely that vision is a major sensory modality. For *Draco* flying lizards, Khandelwal and Hedrick (2020) modelled the glide trajectory based on a vision-based obstacle avoidance model and showed that real trajectories in the natural environment agreed well with the model's predictions. Their data also demonstrated that the initiation of landing behavior followed a relative retinal expansion velocity (RREV) model, previously seen in flapping flyers ranging from birds to insects (Lee & Reddish, 1981; Wagner, 1982). Furthermore, during landing, these flying lizards used a controlled collision approach to reach their desired target (Lee et al., 1993).

The vision of flying snakes has been preliminarily characterized in a recent study (Zamore et al., 2020). Using an optokinetic drum akin to that used in experiments conducted on flying insects (e.g., Mongeau et al., 2019), *Chrysopelea paradisi* was shown to possess a visual system that is broadly tuned and motion sensitive. These snakes also held an image fixed (i.e., maintained the image in view despite its movement), consistent with the observation that the head moves least of any body part during the snake's highly dynamic undulatory glide behavior (Socha et al., 2005, 2010; Yeaton et al., 2020). Three-dimensional head scanning and inverse perimetry (a method of ray tracing) suggest that the snake possesses a small region of binocular overlap in front of the snout, but that a much larger region of overlap extends above the head, which may be used for overhead predator detection (Socha & Sidor, 2005). Lastly, these snakes exhibit a sensitivity to light roughly equivalent to twilight, consistent with their ecology as diurnal gliders.

Although mammalian gliders are nocturnal, they too primarily rely on vision to glide in their natural habitat. Flying squirrels are known to lack the ability to form functional opsins in the eye, rendering them color-blind, but this visual trait may increase their spatial and temporal resolution for night-time vision (Carvalho et al., 2006; Niven, 2006). However, it is unclear if the trajectories of nocturnal gliders can be described using similar models as those employed for *Draco* flying lizards.

Because stability in the air is critical to successful gliding, the vestibular system has been recognized as a target of specialization (Boistel et al., 2011), capable of detecting accelerations in all three rotational axes (pitch, roll, and yaw). Boistel et al. (2011) used microtomography to study the three-dimensional morphology of the inner ear of many gliding and non-gliding lizards and snakes, and found differences

between gliders and those species that have only a climbing or terrestrial lifestyle. However, these differences did not involve the size of the semi-circular canals, as might be expected, but rather the angles of the connections between parts of the vestibular system. The mechanistic linkage to stability remains a target for future examination.

13.3 Behavior

Although gliding animals employ a range of behaviors that allow them to become airborne, change trajectory in air, and land, these behaviors typically involve actively changing the body posture, shape, and size, as well as recruiting other body parts during the process. Convergence in behaviors likely results from the limited number of body configurations, within the constraints of the morphology, that can generate sufficient aerodynamic forces for gliding.

13.3.1 Takeoff Maneuvers

Most gliding animals begin a glide with a takeoff, using thrust produced by the animal. Land-based gliders produce thrust by pushing from the substrate using their limbs or their body (in the case of flying snakes). Flying squid and fish generate thrust by pushing against water using jetting and body undulation, respectively (Davenport, 1994; Muramatsu et al., 2013; O'Dor et al., 2013). For arboreal gliders, the takeoff maneuver provides multiple advantages over simply dropping into the air: it can determine the direction of the glide, it transitions the body into a posture favorable for generating sufficient aerodynamic forces, and it can influence the net dynamics of the glide (Khandelwal & Hedrick, 2020).

13.3.1.1 Jumping Takeoffs

For mammalian gliders and lizards, jumping involves using the limbs to push off from the substrate and reorienting the long axis of the body so that it is almost parallel to the ground. In an arboreal environment, takeoffs can start from a vertical position on a tree trunk (Dehling, 2017; Khandelwal & Hedrick, 2020) or a more horizontal position from branches (Essner, 2002), although vertical takeoffs seem to be the predominant mode used in the wild. *Draco* flying lizards have been shown to modulate the direction of their jump based upon the complexity of the habitat in both the horizontal and vertical plane, to accommodate for obstacles in their path and the location of their desired landing tree (Khandelwal & Hedrick, 2020).

A typical takeoff from a vertical position, frequently performed by mammalian gliders (Fig. 13.3a) and *Draco* flying lizards, includes aerial twisting (Dehling, 2017; Panyutina et al., 2015). For these animals, takeoff requires them to generate adequate

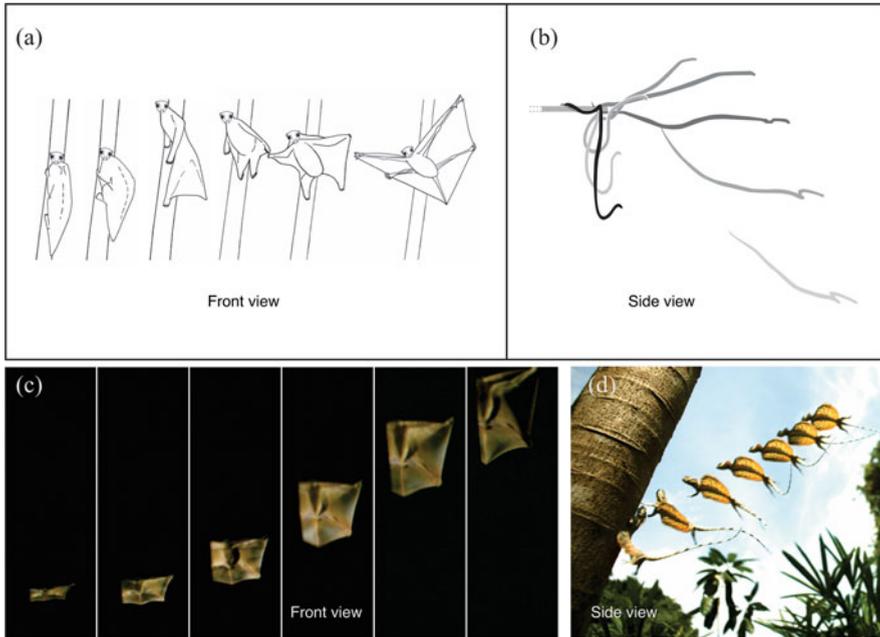


Fig. 13.3 Takeoff and landing in arboreal gliders. Mammals and *Draco* flying lizards employ a jump with a twist when taking off from a vertical tree trunk, illustrated in front view (a) in a colugo (modified with permission from Panyutina et al., 2015). The main takeoff used by flying snakes is the J-loop jump, shown in side view in (b) [modified with permission from Socha (2011)]. To land on a vertical substrate, mammals and *Draco* lizards enact a pitch-up maneuver that serves to reposition the legs for grasping while also avoiding direct contact of the head. The sequences in (c) are of a colugo (*Galeopterus variegatus*) and (d) a flying lizard (*Draco maculatus*) recorded by National Geographic television cameraman John Benam. Reproduced with permission from Socha et al. (2015)

thrust, deploy their wings, and correct their body orientation immediately after launching towards the landing target (Khandelwal & Hedrick, 2020). To accomplish this maneuver, the animal uses a combination of limb and tail movements along with dynamic wing and body morphing. *Draco* flying lizards rotate from a vertical to a horizontal orientation on the tree trunk and use their hind limbs to thrust themselves in the direction of the landing tree, accelerating at $\sim 9 \text{ ms}^{-2}$ and reaching a velocity of $\sim 2.5 \text{ ms}^{-1}$ by the time of complete wing deployment (Khandelwal et al., 2018). The main wing is extended and held in position independently of the limbs during takeoff. The forelimbs extend from the body and eventually are held parallel to the leading edge of the wing. Photographic evidence has been used to suggest that the hands grip the wing and aid in its deployment and modulation of aerodynamic force production (Dehling, 2017), but further experimental work is needed to test this hypothesis; the wrists may simply rest on the upper surface of the wings. Furthermore, pronounced tail movement along with changes in body roll, pitch, and yaw occur during takeoff, suggest that the tail may help control body orientation

(Khandelwal et al., 2018). *Draco* flying lizards complete their aerial twisting as they enter the ballistic dive phase of the glide.

The force generated via jumping has been recorded for flying squirrels (*Glaucomys sabrinus*) and the Malayan colugo (*Galeopterus variegatus*) (Paskins et al., 2007; Byrnes et al., 2008). Using on-body accelerometers, colugos were observed to generate takeoff forces ranging between 1 and 13 times their body weight (Byrnes et al., 2008). Flying squirrels generated takeoff forces ranging from 1.08 to 9.57 times body weight when measured from force sensors mounted on a horizontal platform (Paskins et al., 2007). In a semi-natural study of glide trajectories of flying squirrels (*Glaucomys sabrinus*), the launch velocity was observed to be $5.4 \pm 1.0 \text{ m s}^{-1}$ (Bahlman et al., 2013).

Detailed body kinematics during takeoff have not been studied in mammalian gliders, but qualitative video observations suggest execution of aerial twisting similar to that of *Draco* flying lizards, including reorientation from a vertical to a horizontal body position, followed by a jump and the spreading of the patagium during the ballistic dive phase of the takeoff.

Possessing no legs, the takeoffs of flying snakes are distinctly different (Socha, 2006). The predominant mode of beginning a glide is the J-loop jump (Fig. 13.3b), in which the snake hangs from a branch, accelerates upward with the anterior portion of the body while gripping the branch with the tail and hind end of the body, and then releases the branch as it arcs up and away from it. The anterior portion of the body that participates in the loop undergoes an axial twist, such that the ventral surface faces to the side, but the head is oriented in a more horizontal plane. As the snake enters the air it releases its grip on the branch and untwists, contorting the body to bring the ventral surface into a horizontal orientation as it begins to undulate. A variation of this takeoff is the sliding J-loop takeoff, which entails a smaller loop and no static grip on the branch; instead, the body is in continuous motion throughout the takeoff. Both of these dynamic takeoffs entail maximum jumping accelerations of $\sim 20 \text{ ms}^{-2}$. In experimental glide trials, snakes were also observed to slide or deliberately fall off the branch (Socha, 2002; Socha et al., 2005, 2010; Yeaton et al., 2020). With little or zero preparatory movements or initial horizontal velocity, such takeoffs resulted in shorter glides than those initiated by jumps, and might be used as escape behaviors in the wild (Socha, 2006).

13.3.1.2 Launching from the Water

Flying fish and squid both shoot out of the water at an angle to begin their aerial trajectory (Davenport, 1994; Muramatsu et al., 2013). The many species of flying fish differ in their approach once emergent. Some fish gain height and begin gliding immediately, whereas others perform an intermediate tail-beating behavior, whereby the tail oscillates rapidly in the water with the body angled upward in the air. After a short tail-beating bout at the surface, the fish leaps into the air, deploys its fin-wings, and begins gliding. Unlike flying fish, which use undulatory propulsion to generate thrust and takeoff from the water surface, flying squid employ jet propulsion. Squid

fill their mantle with water and can completely empty it in less than 3 s (O'Dor, 1988), ejecting it at velocities up to 3 ms^{-1} through their funnel (Alexander, 2003) as they exit the water at a low angle, and continue to rise in the air before gliding at a slight pitch-up orientation. (Muramatsu et al., 2013; O'Dor, 2013; O'Dor et al., 2013). The squid ejects water only during emergence and the initial phase of the aerial trajectory, which may serve both to provide an impulsive force and to empty the body of water, reducing mass and wing loading (the ratio of body weight to airfoil area) for its glide, and ultimately resulting in a more energetically favorable force-to-weight (power-to-weight) ratio.

Even though squid move less water than fish, they can achieve similar thrust by accelerating less water at much higher speeds. Furthermore, squid can exceed the swimming threshold relative to body length of fish (~ 25 body lengths s^{-1}) and achieve speeds up to ~ 49 body lengths s^{-1} (Muramatsu et al., 2013). While airborne, squid benefit from jetting water to generate propulsion in a medium that induces much less drag than in water.

13.3.2 Tail Movement

Mammalian gliders, *Draco* flying lizards, and flying snakes exhibit tail movements during some or all components of the glide (Socha et al., 2015; Khandelwal et al., 2018). As a long appendage, the tail may provide both inertial and aerodynamic functions that influence the glide. Tails essentially consist of a flexible vertebral column surrounded by muscle, providing the capability for active control. However, as a long thin appendage, the tail is also subject to passive fluid-structure interactions, and so it is unclear how tail kinematics reflect active versus passive effects for these gliders. From video recordings, the tails of flying snakes give the appearance of passive and somewhat haphazard movements that result from the body's undulation (see supplementary video, Socha et al., 2010), and mammals and *Draco* flying lizards appear to exhibit more deliberate control (unpublished data, Khandelwal, P. C.). However, no direct electromyographic evidence exists to quantify the role of muscle activation.

The tail might be used for controlling movements during all three major components of the glide: takeoff, gliding, and landing. In *Draco* flying lizards, rapid tail movement can be seen during takeoff while the animal reorients, such that its ventral side faces the ground. This reorientation is likely causally linked to the tail. Previous work on the gliding gecko *Hemidactylus platyurus* (previously, *Cosymbotus platyurus*) demonstrated the use of tail as an inertial appendage for reorientation while falling (Jusufi et al., 2008, 2010). *H. platyurus* rotates its tail during the fall and, taking advantage of the conservation of angular momentum, reorients itself from ventral side up to the ventral side facing the direction of the fall.

Body reorientation may be a common feature of all gliders, part of an aerial righting reflex that adjusts the posture of the animal to one in which the dorsal side is uppermost and is advantageous for gliding or preventing injury during a fall (Jusufi

et al., 2011). During a glide, small tail movements could be used to effect changes in roll, pitch, or yaw; however, their use to control stability or the direction of the glide trajectory remains largely unexplored. During the landing phase, the tail of *Draco* flying lizard is positioned closer to the dorsal side of the body, which might facilitate attaining an upright body pose to land on a vertical surface such that the forelimbs make contact with the tree first. Recently, it has also been hypothesized that the tail might be used to modulate the center of mass with respect to the center of aerodynamic pressure to initiate pitch control in gliding animals (Clark et al., 2021). In simulations that modulated tail position to maintain a fixed angle of attack (the angle of incidence between the wing and the oncoming air/wind), the *Draco* flying lizard glided nearly twice as far than without tail control.

Some tails move but are far more constrained anatomically. The tail of the colugo is connected to the hindlimb by an additional skin membrane, which drastically reduces the degrees of freedom available for tail motion. Nonetheless, high frequency oscillations of the tail of colugos associated with landing have been noted (Socha et al., 2015). A previous study of colugos quantified glide kinematics using an on-body sensor to measure acceleration, but it was not possible to measure postural adjustments performed during gliding (Byrnes et al., 2011). Future studies should use a combination of motion capture and inertial sensing to investigate and compare the use of the tail in colugos and flying squirrels/sugar gliders.

13.3.3 Body Flattening

As mentioned previously, some gliders flatten their body facultatively to create a greater surface area for generating aerodynamic forces. Flying snakes display both the greatest degree of dorsoventral flattening and reliance on this behavior to enable gliding. The snake transforms from a round to flattened cross-sectional shape as it jumps into the air (Socha, 2006). Flattening occurs sequentially from snout to vent within 0.5 s, resulting in a triangular cross-sectional shape with the apex oriented dorsally and a flat base ventrally, with two small ventral protrusions at the lateral edges of the base (Socha, 2011). Flattening occurs by rotation of the ribs both dorsally and anteriorly. The tail does not have ribs and hence does not flatten. The body is not uniformly wide, and as it narrows posteriorly toward the vent, the ventral protrusions may be less prominent or even absent. The cross-sectional shape of the paradise tree snake (*Chrysopelea paradisi*) has been determined qualitatively from stereo photos (Socha, 2011), but more rigorous imaging is required to determine its shape quantitatively. The net effect of dorsoventral flattening of the snake results in an increase of the width (up to 2 \times) and a decrease in the height of the body, creating a shape that can generate favorable lift-to-drag ratios (Holden et al., 2014; Jafari et al., 2021; Krishnan et al., 2014) within the aerodynamic regime of the gliding snake.

Aside from flying snakes, a few other reptiles use body flattening. However, the effect seems to be small in comparison. The butterfly lizard *Leiolepis belliana* flattens dorsoventrally, increasing its surface area by 9% (Losos et al., 1989). In

experimental trials, its descent speed was found to be slowed by only 5%, a performance difference that suggests that while used when gliding, flattening did not evolve as an adaptation for gliding (Losos et al., 1989). In fact, this lizard may not even glide in the wild. Instead, flattening was suggested to function for thermo-regulation, communication, or escape. The sawtail lizard *Holaspsis guentheri* may flatten more than the butterfly lizard, and also glide in the wild (Schjötz & Volsøe, 1959), but its gliding has not been well studied; it appears to use flattening primarily to slow its descent (Vanhooydonck et al., 2009).

13.3.4 Airfoil Modification

Most gliding airfoils in the animal kingdom are soft, actuated, and compliant. These features allow changes in various airfoil properties including airfoil camber (curvature), surface area, and dihedral, the upward angle of the wing relative to the horizontal. Because a glider's airfoil typically offers fewer degrees of freedom than the flapping wings of birds and bats, airfoil modification is one of the primary ways by which the animal can modulate aerodynamic force generation during the glide. Such modulation is particularly crucial for gliding animals in spatially cluttered forest habitats for maneuvering around obstacles or performing evasive maneuvers in flight.

13.3.4.1 Camber Adjustment

The camber of a wing describes its curvature and shape, influencing the way it redirects airflow and therefore how it produces force. Typically, increasing camber increases force production, providing gliding animals with a mechanism for modulating flight performance (Pelletier & Mueller, 2000). Changes in camber during a glide have been observed for *Draco* flying lizards (Khandelwal, 2021; Khandelwal & Hedrick, 2022) and mammalian gliders (Bishop, 2006, 2007); however, it is unknown whether such changes are actively initiated by the animal or result passively from the material properties of the wing under aerodynamic load. The patagium of mammalian gliders and *Draco* flying lizards spans almost the entire length of the trunk and lacks muscles for actuation along the wing chord. Instead, it is possible that the animals use bending of the vertebral column to change the camber of the patagium.

Camber adjustment could be a way for gliding animals with low aspect ratio wings (<1.5) to increase aerodynamic force production at lower angles of attack, especially beneficial for animals inhabiting spatially cluttered environments (Pelletier & Mueller, 2000; Song et al., 2008). Wind tunnel tests have shown the advantage of a cambered airfoil for enhancing the force production ability of the airfoil; physical models of cambered airfoils of similar aspect ratio have shown changes of air flow on the curved surface, resulting in higher lift production at lower

angles of attack (Shyy et al., 2008; Song et al., 2008). Furthermore, such a strategy can help enable a more robust gliding behavior through which the animal can actively adapt to changing environmental conditions. That is, the animal does not solely rely on the modulation of aerodynamic forces through changes in angle of attack, but can also tune force production by changing its airfoil camber (Khandelwal & Hedrick, 2022).

Draco flying lizards have been shown to actively modulate their camber during the mid-glide phase, positively and significantly affecting their coefficients of lift and drag (Khandelwal, 2021; Khandelwal & Hedrick, 2022). The advantage of changing body camber continues in the landing phase, allowing the animal to maintain sufficient lift while increasing the drag forces to slow down before touch-down on the desired target, potentially avoiding a full aerodynamic stall (Khandelwal, 2021; Khandelwal & Hedrick, 2022). Previous measurements made on flying squirrels, sugar gliders, and colugos have also shown their capability to modify camber in flight (Bishop, 2006, 2007; Panyutina et al., 2015; Stafford et al., 2002).

The flying snakes can also change the overall airfoil camber (Socha, 2011), but the morphing appears to be binary, from the rounded state pre-glide, to the flattened state as it enters the air (Socha, 2006). The flattened state is held until the snake lands. It is unknown if the snake is able to make small adjustments to its camber during flight, or if it returns to the rounded state pre-, during, or after landing.

13.3.4.2 Wing Area

The ability to change wing area can have benefits based on the desired aerial behavior, including a reduction in wing area. For example, reducing wing area can reduce drag and thereby increase airspeed.

In *Draco* flying lizards the patagium is not attached to the fore and hind limbs (Colbert, 1967), allowing lizards to potentially control wing opening during the takeoff phase of the glide. An advantage of such an approach could be to maintain a more streamlined body shape to increase airspeed and ultimately increase aerodynamic force when entering the mid-glide phase. This behavior can provide increased aerodynamic control earlier in the glide phase, which can be beneficial for maneuvering around obstacles in the glide path. Furthermore, anecdotal evidence also suggests the capability of these flying lizards to undertake asymmetrical wing opening during the takeoff phase (Khandelwal, P. C., unpublished data). Such control can lead to unbalanced aerodynamic force production, providing a mechanism for the animal to initiate roll response in the air.

Mammalian gliders have a patagium connected to the forelimb and the hindlimb (Jackson & Schouten, 2012). Here, wing area is modulated by changing the position of the fore- and hind- limbs; the patagium of gliding mammals is not supported by the ribs, in contrast to *Draco* flying lizards, nor does any other skeletal structure intrude into the web of the patagium. Furthermore, among mammalian gliders, colugos have an additional skin membrane connecting their hindlimbs with the tail

(Panyutina et al., 2015). The additional lifting surface may help to augment force production given the colugo's relatively large body mass, but the ability of the colugo to change this additional lifting surface is unknown.

13.3.4.3 Body Undulation

Flying snakes are the only gliders that employ large, full-body movements while gliding, an aerial undulation that gives the appearance of swimming through the air. Their net motion can be considered as the sum of two waves of motion, a large-amplitude horizontal wave and a much smaller vertical wave (Yeaton et al., 2020). In essence, the largest displacement occurs in the side-to-side direction, but vertical undulations also occur. Yeaton et al. (2020) first identified these small vertical movements, which are coupled at a 90° phase offset from the horizontal wave. Surprisingly, the vertical wave exhibits twice the frequency of the horizontal wave. Coupled horizontal and vertical waves of bending have only been identified in one other snake (sidewinders; Marvi et al., 2014), but at a 1-to-1 ratio of frequencies. The net effect of aerial undulation is to move the centers of aerodynamic pressure and mass in a way that increases the stability of the snake during gliding. In this way, the snake's aerial undulation functions in a unique fashion, both among gliding animals and all other locomoting animals.

13.3.5 Aerial Maneuvers

Maneuvering can be defined as any deliberate deviation from a constant, straight path, representing any acceleration or directional change of the flying animal (Dudley, 2002). By this definition, it is likely that most gliders exhibit the ability to effectuate aerial maneuvers.

13.3.5.1 Pitch Control

The amount of aerodynamic force generated by a wing depends on the angle of attack, the angle of incidence between the wing and the oncoming air/wind. Most gliding animals have wings that are anatomically restricted and cannot be easily moved beyond the dorsal plane of the body (Endo et al., 1998; Gupta, 1966; Panyutina et al., 2015; Russell & Dijkstra, 2001; Russell et al., 2001). In such cases, varying the angle of the wing with respect to the oncoming airflow is linked to body orientation, specifically body pitch, which can be thought of as the nose-up or nose-down angle. Controlling body pitch thus plays a crucial role in allowing the animal to generate sufficient aerodynamic forces to perform a successful glide (Nave et al., 2019). Khandelwal and Hedrick (2022) showed *Draco* that flying lizards continuously change their body pitch to maintain an angle of attack of ~25° during

the mid-glide, allowing them to operate close to their maximal lift-to-drag ratio. However, how gliders control pitch is not well understood. Some theoretical modeling has been conducted to understand pitch control in flying snakes (Jafari et al., 2014), and measurements of kinematics have demonstrated some correlates of pitch rotation with fine adjustments in sugar gliders. For example, movements of the forelegs away from the head were associated with nose-up rotations in sugar gliders (Bishop, 2007).

Flying squirrels, sugar gliders, and *Draco* flying lizards have a prominent tail that has been hypothesized to facilitate pitch control during gliding, whereby the tail is used as an inertial appendage to change the body pitch by changing its position in the sagittal plane of the body (Clark et al., 2021). Because aerodynamic forces are proportional to the square of the airspeed, the tail might play a larger aerodynamic role towards the latter part of the glide. However, the contribution of the inertial versus aerodynamic effects of the tail in pitch control remain untested.

Flying frogs and geckos (*Gekko*) possess enlarged webbed feet that can be used as aerodynamic control surfaces that can be moved independently to potentially change body pitch and consequently the body-airfoil angle of attack. In the absence of a tail, gliding ants, spiders, and frogs rely on drag-based limb movements to change the pitch of the body during gliding.

13.3.5.2 Rolls

Body roll—rotation around the transverse axis of the body—allows redirection of the aerodynamic lift force vector, enabling lateral movements in air. *Draco* flying lizards (Fig. 13.4a, b) and mammalian gliders have been observed to perform body rolls to change their glide direction (Khandelwal & Hedrick, 2020; Stafford et al., 2002). Stafford et al. (2002) observed that body rolls in the flying squirrel *Petaurista leucogenys* were induced by the adduction and ventral flexion of the forelimb, leading to asymmetrical left-right aerodynamic force production about the longitudinal axis of the body. Modelling of roll angle in *Draco* flying lizards has shown that they can maneuver around obstacles that lie directly in-line with their target by achieving a roll angle of approximately 21° while only losing roughly 7% of their total upward lift force (Khandelwal & Hedrick, 2020). However, the means by which they achieve body roll is unclear. It may be initiated by the use of the tail, or by the asymmetric extension of one side of the patagium relative to the other, or both.

Body rolls have also been investigated in the flying frog *Polypedates dennysi* using a wind tunnel (McCay, 2001). The tunnel was tilted to 45° to match the glide angle of this species, and the airspeed (12–14 ms⁻¹) was set so that the frog glided in place, enabling observation of body and limb orientation. Maneuvers were induced by revealing a plastic plant outside the tunnel that the frog would try to turn to reach. During rolls, the frog's feet were held at equal levels relative to the body, so it is unclear exactly how left-right force asymmetries were created. These frogs also exhibited a non-rolling maneuver called a crab turn, in which one rear foot is held higher than the other, inducing a yaw turn (a turn where the body rotates around the

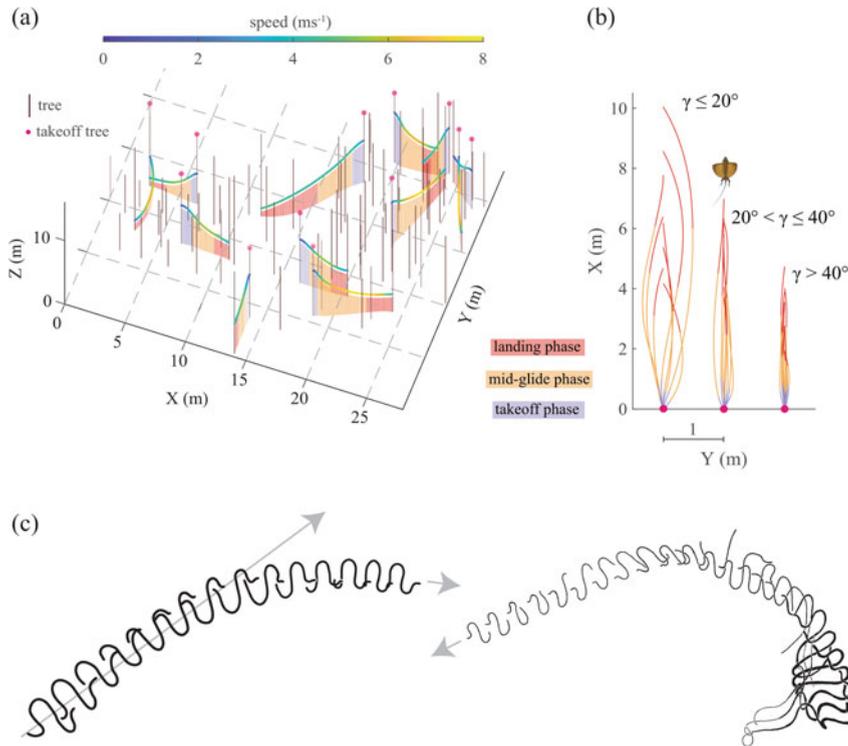


Fig. 13.4 Aerial maneuvering in *Draco* flying lizards and flying snakes. (a) Glides performed by the flying lizard *Draco dussumieri* in its natural environment. (b) Top view (X–Y plane) of glides grouped by the obstacle angles γ . The obstacle tree is defined as the tree closest to a straight glide path between the takeoff and the landing tree. The obstacle angle is the angle subtended by the obstacle tree on the takeoff tree in the X–Y plane. The figure highlights the maneuvering capabilities of the lizard around obstacles and the influence of obstacles on the glide path; the path curvature increases as the obstacle angle decreases. Note that the X and Y axes are not to scale in (b). Modified with permission from Khandelwal and Hedrick (2020). (c) Flying snakes appear to turn without banking. The sequences shown here were traced from video stills recorded at 60 Hz, depicting a gentle turn (left) and a sharper turn (right) that occurred just after takeoff. In both sequences, the snake appears to become smaller as it moves closer to the ground because recording took place using a top-view camera. Modified with permission from Socha (2011)

dorsoventral axis in the frontal plane). Both types of maneuvers are possible with only slight adjustments because the frog possesses only a small amount of positive stability in pitch and roll, and negative stability in yaw.

13.3.5.3 Drag-Inducing Limb Movement

All gliders experience drag forces while gliding, a consequence of frictional losses due to viscosity. Limbs can be considered as cylinders that create drag forces that influence the balance of forces on the animal. Changes in posture of the limbs can

also be used to induce a moment that rotates the body in pitch, roll or yaw, thereby inducing an aerial maneuver. Gliders with free limbs include frogs, lizards, and arthropods. For frogs, the main gliding surface is the splayed webbed foot (including both fore- and hind- feet); therefore, postural changes of the leg also relocate the main aerodynamic surface, complicating analyses of the effects of leg movement. Gliding geckos (*Gekko*) present a similar situation, except that their foot surface is relatively smaller and therefore should have a weaker effect. Nonetheless, Young et al. (2002) have shown that bound feet in the flying gecko *Gekko kuhli* inhibited aerial maneuvers and prevented the gecko from entering the glide phase, demonstrating the importance of the feet as aerodynamic control surfaces. In contrast to the frogs and other gliding lizards, *Draco* flying lizard hangs its rear legs from the body; the front legs are held parallel to the leading edge of the wing. The relative role of the legs has not been rigorously studied in most gliding vertebrate taxa, including the movement of *Draco* flying lizards' front legs into the leading-edge position at the beginning of the trajectory.

For arthropods, legs represent a major aerodynamic surface. Asymmetrical leg movements in gliding ants result in the production of yaw turns, effectuated by a single hind leg raised dorsally on one side of the body (Yanoviak et al., 2010). Similar movements that lift the leg above the body axis are involved in aerial righting behaviors in ants (Yanoviak et al., 2010). In response to a threat, newly hatched stick insects (*Extatosoma tiaratum*) become airborne and tuck the legs against the body, which should reduce drag and increase speed through the air, helping to avoid predation (Zeng et al., 2020); these insects use a multitude of leg movements to change position in the air (Zeng et al., 2017). With eight independently actuated legs, gliding spiders possibly possess the greatest opportunity for aerial maneuvering using their jointed appendages. The gliding spider *Selenops* effects a stereotyped splayed posture in the air, with the two forelegs held laterally and anteriorly, and the remaining legs splayed posterolaterally (Yanoviak et al., 2015). Yanoviak et al. (2015) also report observing repeated twitching of the legs of *Selenops* while airborne, but the physical consequence of such vibration is unknown. They also note that these spiders steer with their forelegs; with the legs held anteriorly it is possible that such movements induce pitching moments as well. Overall, detailed kinematics and mechanical study are needed to understand how gliders use limb movements to manipulate drag forces.

13.3.5.4 Body Inertia

Despite the lack of obvious control surfaces, flying snakes are able to change direction in the air (Fig. 13.4c, d), an ability that likely varies with species. The paradise tree snake (*Chrysopelea paradisi*) has been observed, via kinematics studies, to turn while airborne (Socha, 2002; Socha et al., 2010; Yeaton et al., 2020); the golden tree snake (*Chrysopelea ornata*) has been reported to turn in one instance only, when takeoff was from a very high launch point (41 m; Heyer & Pongsapipatana, 1970), although no kinematic details were provided. Snakes appear

to turn without banking. Although a rigorous mechanistic explanation of turning is still lacking, it is likely that snakes use an inertial mechanism, shifting body mass and taking advantage of principles of conservation of angular momentum. Yeaton et al. (2020) proposed that turns could be initiated using modifications to the large-amplitude horizontal waves during gliding, timed to occur when the inertial yaw moments are large.

13.3.5.5 Landing Maneuvers

Terrestrial gliding animals are strictly arboreal. Landing is potentially the most critical part of the glide and perhaps the most understudied aspect of gliding in animals. It involves the greatest risk of injury through impact with the arboreal or ground substrate, but it allows the animal to reach its target to perform various ecologically relevant behaviors. Generally, two types of landing are recognized: a pitch-up maneuver that orients the animal into a more vertical, head-up position prior to contact, or no maneuver at all (Socha, 2011), meaning that the animal essentially crash-lands with a direct impact.

Most glides of *Draco* flying lizards and mammals recorded in the wild have shown that they preferentially land on vertical tree trunks (Bahman et al., 2013; Byrnes et al., 2008; Khandelwal & Hedrick, 2020; Krishna et al., 2016). To successfully land on a vertical substrate, these animals perform a landing maneuver involving large pitch-up rotation such that the ventral aspect of the body faces the vertical landing substrate (Fig. 13.3c, d), which serves both to move the legs and feet into a position favorable for gripping the substrate and also to avoid direct collision with the head. During a pitch-up rotation, the animal changes the angle of attack of the airfoil, causing a large increase in drag; if lift production ceases completely, aerodynamic stall occurs. This pitch-up maneuver allows the animal to expend kinetic energy in the form of drag, slow down, and perform a controlled landing. In *Draco* flying lizards, just before landing, the head is elevated toward the dorsal side and the forelimbs are extended forward, bringing them in contact with the landing substrate first (Khandelwal, 2021). Movement of the tail dorsally might also serve as a control movement. Overall, the mechanisms used by mammals and lizards for pitch-up landing maneuvers are not well understood.

In the absence of a primary enlarged wing surface, it appears that gliders including flying snakes and the gliding gecko *Hemidactylus platyurus* are unable to slow down sufficiently and/or rapidly to initiate a controlled landing maneuver (Siddall et al., 2021; Socha et al., 2005). Instead, they impact the landing substrate without significantly reducing their glide speed and use their body and/or tail to stick the landing. Recent work by Siddall et al. (2021) has shown that *H. platyurus* slams into the substrate and uses its tail to stabilize its landing. In experimental trials recorded in the forest, geckos approached the landing tree at speeds up to 7 ms^{-1} and crashed head-first with some part of the torso into the tree trunk. The high impact at landing led to a pitch-back movement with the torso bending dorsally, forcing the forelimbs to lose contact with the substrate. To prevent a fall, the gecko pushed its

tail against the substrate to counteract the bending of the torso and stabilize the landing.

Landing in snakes has been described only qualitatively (Socha, 2011). When landing on the ground, they appear to contact the surface with the tail first and then ‘roll’ into the landing, with head contacting last. Such kinematics would serve to increase total impact time and reduce forces on the head. However, it is unclear if snakes preferentially use these landings when targeting the ground, or if there is a minimum trajectory distance needed to properly position the body for such a landing. Landing on arboreal substrates is even more enigmatic. Snakes appear to contact branches at a location somewhere along the body, and then the forward momentum of the remainder of the body results in a wrapping motion. It is not clear if or how flying snakes land on a vertical substrate.

13.4 Mechanics

Here, we provide an overview of the underlying physics that governs gliding in animals. Each animal has to counteract the pull of gravity by generating sufficient aerodynamic forces to slow and control its descent for the ecological task at hand. Specific aerodynamics result from a combination of body shape, size, and posture of the animal interacting with the surrounding air. Most or all of these factors can be actively modulated by the animal during the glide, which contributes to the greater complexity of analysis and prediction of mechanics compared to a rigid, fixed-wing glider of similar size moving through air. Convergent gliding morphologies and behaviors are likely dictated by these complex body-fluid interactions, with limited combinations of morphology and aerial behaviors leading to desirable aerodynamic output.

13.4.1 Aerodynamics

A large portion of the aerodynamic force produced by a gliding animal functions to support the animal’s weight. As the animal glides, it experiences an airflow along the direction of the glide trajectory. The aerodynamic force is the resultant of the lift force, which acts perpendicularly to the glide path, and the drag force, a pressure- and friction-based force that acts to slow the glider along the glide path (Fig. 13.5). The cross-sectional shape and orientation of the airfoil plays a major role in determining the magnitude of lift and drag. The relatively large aerodynamic surfaces of mammalian gliders and *Draco* flying lizards allows them to generate significantly more lift than drag, resulting in relatively shallow glide trajectories (Fig. 13.6). However, smaller marsupial gliders, such as the feathertail gliders, have a much smaller aerodynamic surface along with a long feather-shaped tail, which must influence how they produce glide forces (Pridmore & Hoffmann, 2014).

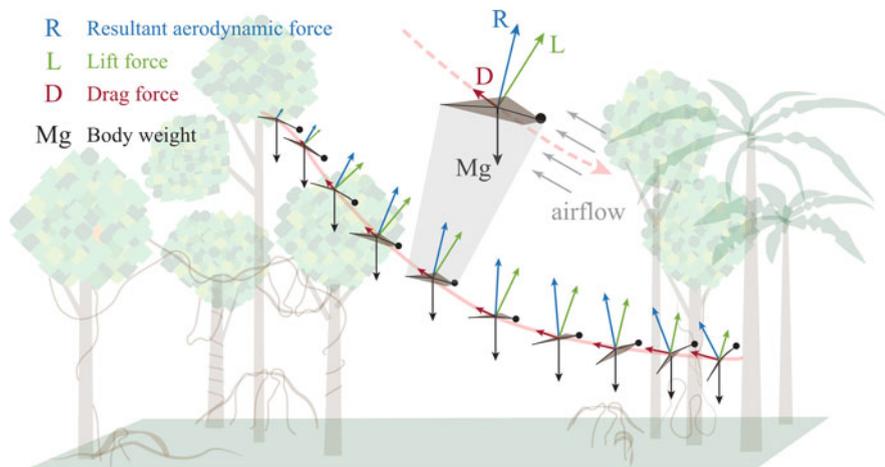


Fig. 13.5 Aerodynamic forces acting on a glider throughout its trajectory. The drag force (red) acts anti-parallel to the direction of travel, while the lift force (green) acts orthogonally. The relative magnitude of these two forces determines the resultant aerodynamic force (blue). The body weight of the glider determines the gravitational force (black), which acts downward. The changing direction and magnitude of the resultant aerodynamic force can result in a non-linear trajectory. Modified with permission from Khandelwal and Hedrick (2022)

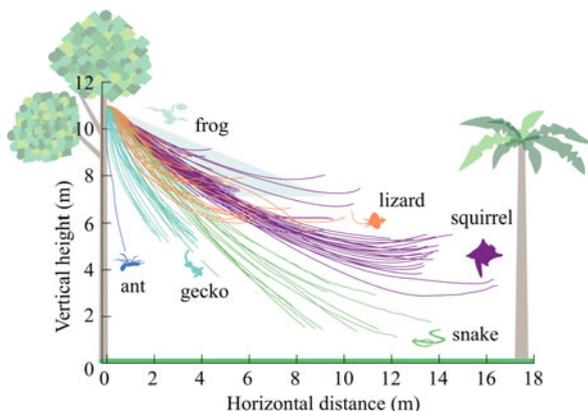


Fig. 13.6 Comparison of glide trajectories of some arboreal gliders. Trajectories shown are from experimental kinematic data from flying snakes (Socha et al., 2005), *Hemidactylus* geckos (Siddall et al., 2021), *Draco dussumieri* flying lizards (Khandelwal & Hedrick, 2020), *Cephalotes atratus* ants (Munk et al., 2015), *Glaucomys sabrinus* flying squirrels (Bahlman et al., 2013), and *Rhachophorus* frogs (Emerson & Koehl, 1990). Frog trajectories are depicted as minimum and maximum horizontal distances covered from a fixed height, as reported in the study

Conversely, gliding arthropods lack large flat surfaces and exhibit steep glide trajectories (Munk et al., 2015; Yanoviak et al., 2005, 2015), and so drag must dominate their force production profile.

Airfoil-like surface areas alone cannot result in production of aerodynamic forces if they are not held in an appropriate aerodynamic configuration. Convergent aerial behaviors are likely an outcome of the requirement of gliding animals to modulate their body posture and simultaneously control the relative position of their body parts, within the constraints of their evolved morphology, to ensure production of sufficient aerodynamic forces during descent. One of the primary ways to control aerodynamic force production is by changing the angle made by the animal's airfoil with the oncoming airflow, referred to as the angle of attack (AoA). Generally, increasing the AoA will increase the lift force on an airfoil at the expense of increasing drag force, up to certain point (Abbott & Von Doenhoff, 1959). At large AoA, the airfoil experiences turbulent airflow on its upper surface, leading to a drastic loss of lift force and potential dire consequences for the animal. This loss of lift is referred to as aerodynamic stall; many fixed rigid-wing airfoils experience it at AoA of less than 15° (Abbott & Von Doenhoff, 1959). Mammalian gliders and *Draco* flying lizards have been observed to operate at an AoA greater than 40° (Bishop, 2006, 2007; Khandelwal, 2021; Khandelwal & Hedrick, 2022), especially during the landing maneuver. At such high AoA, the animal is able to remain aloft without a significant loss in lift. Studies on gliding mammals have suggested that the ability to maintain lift generation at extreme AoA is likely due to camber (Khandelwal, 2021; Khandelwal & Hedrick, 2022). Field measurements of gliding behavior in *Draco* flying lizards have shown their ability to actively modulate camber during the glide and influence the production of lift and drag forces (Khandelwal, 2021; Khandelwal & Hedrick, 2022). These findings have been further corroborated through modelling studies, which have shown that cambered wings can delay stall (e.g., Song et al., 2008), and have also suggested the contribution of wing aspect ratio as a facilitator in lift production at high AoA (Torres & Mueller, 2004).

The magnitude of aerodynamic force production and how it varies with AoA also depends strongly on Reynolds number (Re), the non-dimensional number that indicates the relative role of inertial to viscous forces (Vogel, 1994). Reynolds numbers vary widely across gliders, from the small and slow arthropods to the large and fast mammals, ranging by three orders of magnitude from approximately a few thousand to more than 200,000 (Socha et al., 2015). The vast majority of gliders appear to glide at $Re \sim 10,000\text{--}100,000$, a fluidic regime that is understudied compared to high-Re fixed wings (Shyy et al., 2008), but is receiving increasing attention in recent years related to interest in engineering micro-aerial vehicles (MAVs). The flexibility of gliding surfaces in animals is also a topic of increasing interest (e.g., Shyy et al., 2010).

Clearly, the ability of animals to change their body posture, shape, and size during gliding has important consequences for their aerodynamic force production and the control of their glide trajectory. Moreover, modern data collection techniques, including on-body sensors, motion capture systems, and video, have shown that gliding animals do not often use equilibrium gliding (Bahlman et al., 2013; Byrnes

et al., 2008; Khandelwal & Hedrick, 2020; McGuire & Dudley, 2005; Socha, 2002; Socha et al., 2005, 2010; Yeaton et al., 2020), a condition in which the aerodynamic forces exactly balance the weight during gliding, resulting in the animal descending at a constant velocity. Instead, gliders have been mostly observed to exhibit non-equilibrium dynamics (Yeaton et al., 2017; Khandelwal & Hedrick, 2020), whereby they modulate their aerodynamic forces during takeoff, mid-glide, and landing. During takeoff, the animal rapidly gains speed along with attaining a gliding pose to generate aerodynamic forces. Post-takeoff, the animal transitions into the mid-glide phase and may actively modulate the aerodynamic force production to navigate its spatially complex habitat and reach its desired target. Finally, the landing phase may involve slowing down and/or aligning the body with the landing target to safely land.

13.4.2 *Inertial Mechanics*

For gliding animals, maintaining an upright orientation during the glide is important due to the sensitivity of aerodynamic forces to orientation of the airfoil-body. Muscle activation is used in gliding animals to move their body parts as control surfaces, as well as to shift the mass distribution to maintain orientation and rotational stability. As the glider changes its shape during a glide, there is continuous redistribution of aerodynamic forces as well as of mass. The effect of shifting mass results in inertial effects that are not always intuitive, but play an important role in both rotational stability and maneuverability while airborne. Among gliders, the relative role of such effects is not well studied. For shifting mass, the effects could be considered to be very small or even negligible in gliders that maintain a relatively stable posture, to very large in flying snakes, which continuously move the body in three dimensions. Nonetheless, mass effects might be more important than previously considered, given that almost all gliders seem to make postural adjustments such as the previously discussed tail movements and changes in wing camber of *Draco* flying lizards and gliding mammals.

The strong coupling of control, force production, and body posture during gliding in animals requires a change in the conceptual framework to accurately understand a glide. The current framework is based upon fixed-wing aircraft theory for describing rotational stability, but given that gliding animals can be considered as living, morphing wings, a rigid-body approximation, common for aircraft, is inappropriate.

Consider instead a variable-geometry model (Garrido de Matos & Lino, 2013). In this approach, a gliding animal is considered not as a rigid body but as a “quasi-rigid body” (Goldreich & Toomre, 1969); that is, we can use some simplifying notation from the dynamics of rigid bodies, but consider that even in a frame co-moving with the animal’s center of mass, the mass distribution is changing. This conceptual framework allows us to formulate general equations of motion for gliding animals that can be decomposed into inertial and aerodynamic components (Yeaton et al., 2020). The rotational dynamics are of special interest, as the inertial terms can be

further decomposed into rigid-body terms and inertial moments due to the changing mass distribution,

$$\underbrace{\mathbf{M}_{aero}}_{\text{aerodynamic term}} = \underbrace{\mathbf{I} \cdot \dot{\boldsymbol{\omega}} + \boldsymbol{\omega} \times (\mathbf{I} \cdot \boldsymbol{\omega})}_{\text{rigid-body terms}} + \underbrace{\dot{\mathbf{I}} \cdot \boldsymbol{\omega} + \dot{\boldsymbol{\gamma}}}_{\text{variable-geometry terms}}$$

where M_{aero} is the aerodynamic moment, obtained from integrating over the body, I is the 3×3 inertia tensor, $\boldsymbol{\omega}$ is the angular velocity, related to changing rates of yaw, pitch, and roll, and $\boldsymbol{\gamma}$ is an angular momentum-like term due to non-rigidity. Over-dots refer to time-rates of change. Because the mass distribution is changing in time, I is time-varying in a co-moving body frame due to the reconfiguration of the glider's shape, such as those brought about by relative body or tail movements. If the body were rigid, the mass distribution would not be changing and the inertial moments would vanish.

When starting from a low-speed jump, inertial moments always dominate at the beginning of a glide. Gliding animals can also maneuver in the air to achieve rotations and changes in direction of motion in any axis. Here we consider turns, which redirect the forward path in the lateral direction. We will refer broadly to two categories: low-speed turns, where aerodynamic effects are negligible due to the velocity squared dependence of lift and drag, and high-speed turns, where aerodynamic effects should dominate. Examples of low-speed turns are the aerial righting via tail movement seen in *Hemidactylus platyurus* geckos (Jusufi et al., 2011) and greater than 90° turns of flying snakes that occur in the space of a few body lengths (Socha, 2011). Such 'sharp' turns and reorientations likely occur when aerodynamic forces are negligible and are due primarily to internal moments, when the animal moves some part of its body (e.g., an appendage) relative to the main body, causing the body to rotate the other way (Jusufi et al., 2010). The rotation of the main body is independent of the speed of the appendage's rotation, and mathematically it is known as 'geometric phase' (Marsden et al., 1991), closely related to conservation of angular momentum (the rigid-body terms) because the aerodynamic moment is small. On the other hand, high-speed turns are those that depend largely on the aerodynamic moment, wherein the animal banks to redirect aerodynamic forces to achieve turns (Shin et al., 2019). The role of the variable-geometry moments, due to the time-varying mass distribution, is still relatively unknown and difficult to isolate, although they may be related to the vibration-induced and undulation-induced stability seen in insects (Taha et al., 2020) and flying snakes (Yeaton et al., 2020), respectively. Flying snakes may be a special case in which inertial reorientation is used more than, or in place of, banking (Yeaton et al., 2020), but a rigorous analysis of snake turning is needed to understand its mechanics.

13.4.3 Control

Some gliding animals control their glide primarily via aerodynamics by morphing their wing-body, although control authority may be enhanced via inertial moments like those seen in the tails of *Draco* flying lizards (Clark et al., 2021). Rapid tail movements have been observed during takeoff in flying mammals and lizards, though their contribution as an inertial appendage remains unclear. Control of inertial dynamics is significant for those animals that appear to have no large wing-like surfaces to create or direct flight forces, such as ants, spiders, or flying snakes, which can nonetheless reconfigure their bodies or appendages to redistribute aerodynamic forces or to take advantage of large inertial effects. For gliders that can use both aerodynamic-dominated and inertial-dominated control, it is possible that some degrees of freedom can be controlled with one, but not the other. For example, horizontal undulation alone may not be capable of providing any control of a flying snake's yaw degree of freedom (Jafari et al., 2017), which can only be effected indirectly, via aerodynamic moments influenced through pitch and roll degrees of freedom.

Gliding in many animals may be actively controlled; that is, a system of 'closed-loop' feedback incorporating sensory feedback to redirect aerodynamic forces to achieve desired objectives. Such feedback has not been rigorously investigated, but is evidenced in small control movements observed in kinematics studies (Bishop, 2006, 2007). But there is still a possible role for 'open-loop' control with no feedback, for example, via periodic changes in shape such as vibrations or undulations. For flying snakes, whose undulations have been well-documented (Socha, 2002; Socha et al., 2005, 2010; Yeaton et al., 2020), the closed-loop control system may need to work around a passively stable trajectory (Yeaton et al., 2017). Undulation may in fact lower the demand for a complex closed-loop control system in flying snakes (Jafari et al., 2017), but more dynamical modeling needs to be done. Overall, the use of an open- or closed-loop control system (or both) during gliding is largely understudied. Convergence in control strategies can be expected in gliding taxa with similar gliding morphologies and behaviors and/or based on the biological complexity of the animal.

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