How animals glide: from trajectory to morphology[1]

John J. Socha, Farid Jafari, Yonatan Munk, and Greg Byrnes

Abstract: Animals that glide produce aerodynamic forces that enable transit through the air in both arboreal and aquatic environments. The relative ease of gliding compared with flapping flight has led to a large diversity of taxa that have evolved some degree of flight capability. Glide paths are curved, reflecting the changing forces on the animal as it progresses through its aerial trajectory. These changing forces can be under control of the glider, which uses specific aspects of anatomy to modulate lift, drag, and rotational moments on the body. However, gliders share no single anatomical or behavioral feature, and some species are unspecialized for gliding, producing aerodynamic forces using posture and orientation alone. Animals use gliding in a broad range of ecological roles, suggesting that multiple performance metrics are relevant for consideration, but we are only beginning to understand how gliders produce and control their flight from takeoff to landing. In this review, we focus on the physical aspects of how glide trajectories are produced, and additionally discuss the range of morphologies and postures that are used to control aerial movements across the broad diversity of animal gliders.

Key words: animal gliders, biomechanics, gliding flight, trajectory.

Résumé : Les animaux qui planent produisent des forces aérodynamiques qui permettent le déplacement dans les airs dans des milieux tant arboricoles qu'aquatiques. La facilité relative du vol plané par rapport au vol battu a mené à une grande diversité de taxons ayant développé une certaine capacité de voler. Les trajectoires de vol plané sont courbées, reflétant les forces changeantes qui agissent sur l'animal au fil de sa trajectoire aérienne. Ces forces changeantes peuvent être contrôlées par l'animal planeur, qui utilise différents aspects de son anatomie pour modifier la portance, la résistance et les moments de rotation sur le corps. Les planeurs n'ont toutefois en commun aucune caractéristique anatomique ou comportementale unique, et certaines espèces non spécialisées pour le vol plané ne font appel qu'à la posture et l'orientation pour produire des forces aérodynamiques. Si les animaux utilisent le vol plané dans un vaste éventail de rôles écologiques, ce qui donne à penser que de nombreux paramètres de performance doivent être pris en considération, la compréhension de la production et du contrôle du vol du décollage à l'atterrissage par les animaux planeurs n'en est qu'à ses débuts. La présente synthèse est axée sur les aspects physiques de la production des trajectoires de vol plané et aborde l'éventail des morphologies et postures utilisées pour contrôler les déplacements aériens chez une grande variété d'animaux planeurs. [Traduit par la Rédaction]

Mots-clés : animaux planeurs, biomécanique, vol plané, trajectoire.

Introduction

Gliding is a fluid-based form of locomotion in which the animal moves horizontally without power, with the energy for movement provided by the potential energy of vertical position. In still air, the net vertical displacement of a glider is downward, with height passively traded for the kinetic energy of movement. Gliding requires only that the animal is denser than the surrounding medium and that it produces some force that propels it in the horizontal direction. The inability to produce sufficient force to overcome weight and move upward distinguishes gliders from true flyers, who produce additional force powered by muscle. A large range of animals can glide in air or water, but no analogue to an aerial glider exists underwater. All animals that glide aquatically (such as a shark cruising without body movement) can also move upward in the water column under power, excluding them from the classification of "glider". In this review, we focus on movements in the air, which traditionally defines the realm of animal gliders.

Gliding is indeed a form of flight, which has been broadly defined as any locomotor behavior in air that involves active control of aerodynamic forces (Dudley et al. 2007). As has been noted often, the evolution of powered flight, which provides the ability to move upward in still air, is decidedly rare, having occurred only in birds, bats, insects, and pterosaurs. Despite clear selective advantages, the paucity of such true flyers suggests that paired wings and oscillatory wingbeat kinematics are minimum requirements for powered flight. By contrast, gliders share no analogous set of anatomical features or kinematics. Most gliders deploy two "wings" in the air, but some employ four, and others none at all. Some gliders exhibit no morphological specialization and instead glide using behavior alone, employing position and orientation of body and appendages to control forces. Postures in the air are largely static compared with the movements used by flapping flyers, but many gliding taxa exhibit body movements during some portion of the glide trajectory, ranging from subtle movements to large oscillations of the whole body. Gliding has evolved numerous times and has so far been found to exist in mammals, lizards, frogs, snakes, squid, fish, and numerous wingless arthropods (Figs. 1A–1H).

J.J. Socha and F. Jafari. Department of Biomedical Engineering and Mechanics, Virginia Tech, Blacksburg, VA 24061, USA.
**Y. Munk.** Department of Biology, University of Washington, Seattle, WA 98195, USA.
G. Byrnes. Department of Biology, Siena College, Loudonville, NY 12211, USA.
Corresponding author: John J. Socha (e-mail: jjsocha@vt.edu).

Fig. 1. Diversity of animal gliders, representing most of the major types of gliders. All images except E and F were taken in the wild. Gliders use a wide range of morphologies and postures to create aerodynamic forces for stable gliding. The postures depicted are typical of mid-flight, but can be substantially modulated throughout the glide trajectory. (A) The rhacophrid frog *Rhacophorus nigropalmatus* Boulenger, 1895 (Wallace's Flying Frog), taken in the Danum Valley Conservation Area, Sabah, Malaysia. (B) The colugo *Galeopterus variegatus* (Sunda flying lemur), taken in Bako National Park, Sarawak, Malaysia. (C) The agamid lizard *Draco cornutus* Günther, 1864, taken in the Danum Valley Conservation Area, Sabah, Malaysia; identified by Jim McGuire. (D) The gekkonid lizard *Ptychozoon kuhli* (Kuhl's Flying Gecko), taken in Sarawak, Malaysia. (E) The colubrid snake *Chrysopelea paradisi* (Paradise Tree Snake), taken under experimental conditions indoors in Chicago, Illinois, USA. (F) The myrmicine ant *Cephalotes atratus*, gliding in a vertical wind tunnel. (G) The ommastrephid squid *Todarodes pacificus* (Steenstrup, 1880) (Japanese flying squid), taken in the Sea of Japan. (H) An exocoetid fish of the genus *Hirundichthys* Breder, 1928, likely *Hirundichthys affinis* (Günther, 1866) (fourwing flying fish), taken in the South Atlantic off the coast of Angola; identified by Mark Westneat. Photos courtesy and reproduced with permission of Tim Laman (A–D), Jake Socha (E), Yonatan Munk (F), Geoffrey Jones (G), and Jack Swenson (H). Figure appears in color on the Web.
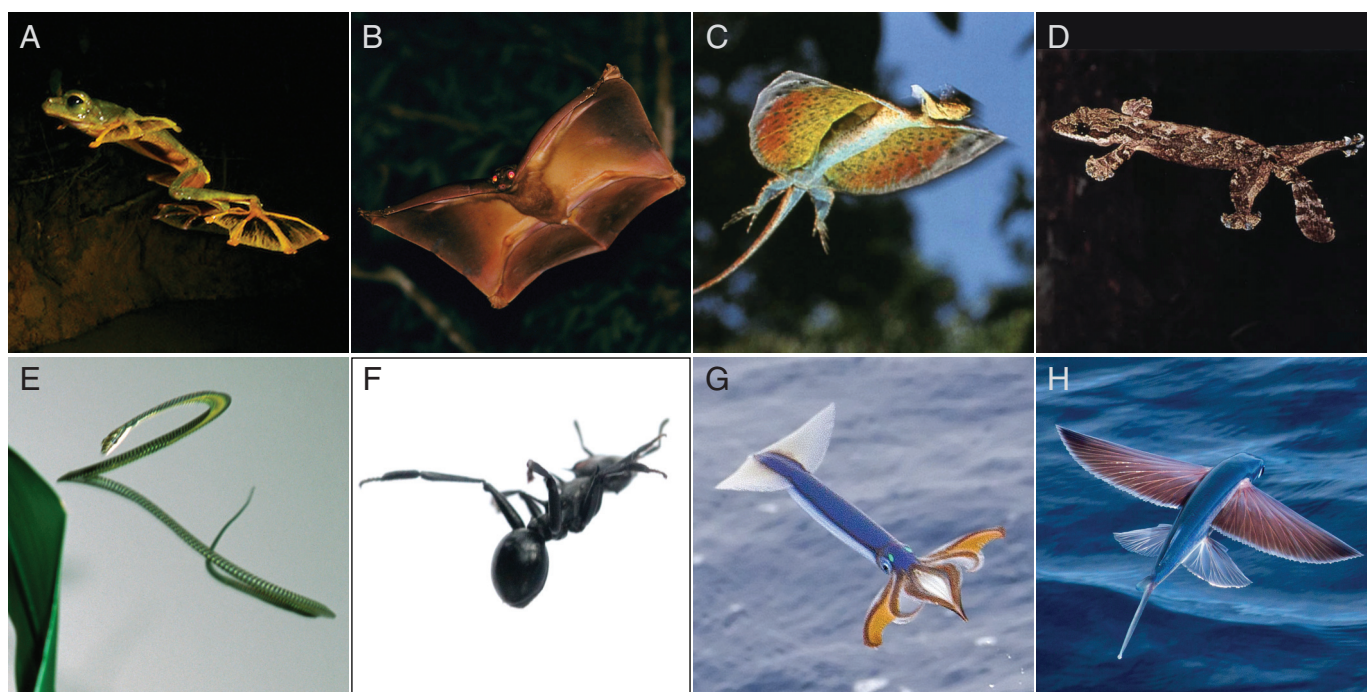
Historically, biologists have classified gliders by aerial performance according to Oliver (Oliver 1951), who categorized animals that travel along glide paths angled at <45° from horizontal as "gliders" and those whose paths were steeper (>45°) as "parachuters". Multiple authors have noted that these terms are physically arbitrary and not particularly useful for understanding gliding (Socha et al. 2005; Dudley et al. 2007; Dudley and Yanoviak 2011). The aerodynamic mechanisms that produce force do not change at 45°; moreover, individual gliders can behaviorally modulate force production to glide more or less steeply, blurring the line between these types. In the recent decade, the term "directed aerial descent" was introduced to refer to aerial locomotion in which wingless insects travel downward at a steep angle (Yanoviak et al. 2005). This term was used to indicate that such animals actively control their flight path and are not simply passive actors, as might be inferred from the term "parachuting". Dudley and colleagues later noted that both "directed aerial descent" and "gliding" refer to any controlled descent by an organism in which gravitational potential energy is used to produce useful aerodynamic force (Dudley et al. 2007). The defining feature of a glider is its ability to produce controlled forces that move it in a horizontal direction in air, regardless of the angle of descent. Here, we use this inclusive definition of gliding for its simplicity and clarity in identifying aerial behaviors of interest. In our view, any animal moving at an angle to the vertical (in still air) under the power of gravity is considered to be gliding. Parachuting involves vertical free fall (sensu Moffett 2000) that has been slowed via some morphological specialization or behavior.

In this review, we focus on the physical aspects of gliding in animals, addressing how animals produce and control their glide paths in the air using a combination of morphology and posture. Across taxa, the scope of aerial performance and degree of agility is large, yet we have a relatively limited understanding of how gliders use different aspects of their glide system to generate specific flight characteristics. For other recent viewpoints on gliding, we refer readers to four sources. Dudley and colleagues (2007) provide a comprehensive review of terrestrial gliders and discuss the ecological and evolutionary context of gliding. Vogel (2006) considers the problems associated with coping with gravity in air more generally for all organisms from plants to birds. A recent symposium in 2011 focused on the biomechanics and behavior of most of the major types of animal gliders (including extinct taxa), providing the most comprehensive summary of gliding to date (Boistel et al. 2011; Byrnes and Spence 2011; Dudley and Yanoviak 2011; Jusufi et al. 2011; Koehl et al. 2011; McGuire and Dudley 2011; Socha 2011; Yanoviak et al. 2011). Lastly, Jackson and Schouten (2012) provide a comprehensive look at the diversity of gliding mammals in a beautifully illustrated book.

Motivations for gliding

Any discussion of gliding animals must begin with the question, why glide? What motivates an animal on an elevated substrate to take to the air or for an aquatic glider to leave the water? Although gliding by definition includes horizontal travel, the ecological relevance of gliding encompasses far more than the opti-

mization of horizontal distance. Gliding can be used for the following ecological roles:

1. To escape. An animal that can glide can leave the tree (or other elevated substrate) to avoid a predator (Howland 1974; Bonser and Rayner 1996), an act that is particularly effective if the predator is unable to follow in the air. Gliders may also potentially escape from adverse events such as fire.

2. To prevent injury. An accidental fall in the trees poses risks of injury due to impact forces of landing or crashing into objects (Schultz 1939; Nachtigall et al. 1974; Crawford and Baker 1981; Klem 1990; Schlesinger et al. 1993). The ability to glide provides a mechanism for controlling speed and orientation to reduce impact forces (Byrnes et al. 2008).

3. Intraspecific interaction. Gliding-related behaviors can play a role in male–male or male–female interactions, including sexual display, mate searching, or territorial defense (McGuire and Dudley 2011).

4. To travel among trees or to the ground. Gliding can be used as a form of travel to move both horizontally and downward and can be energetically more efficient under certain circumstances (Scholey 1986; Scheibe et al. 2006; Flaherty et al. 2010; Willis et al. 2011; Suzuki et al. 2012). Faster horizontal transit enables the animal to spend more time searching for food, mates, and less time climbing, crawling, and walking (Dunbar 1992; Byrnes et al. 2011a).

5. To avoid the forest floor or water surface. The forest floor can be dramatically different in composition from the understory or canopy, presenting unknowns that can be avoided by gliding. Some gliders cross small bodies of water, avoiding the surface by staying airborne until reaching a landing substrate. This is particularly relevant for invertebrates such as gliding ants, which are predated upon by fishes at a high rate when they land on the water surface (Yanoviak et al. 2011). Additionally, gliders can employ different forms of aerial locomotion depending on ecological context. For example, when the hylid frog *Agalychnis saltator* Taylor, 1955 (Misfit Leaf Frog) forms breeding aggregates of 25–400 frogs, they gather by gliding from the trees (Roberts 1994). But in the face of potential predators (e.g., snakes, monkeys), these frogs have been observed to simply drop from their arboreal perch into the water below, demonstrating that they might not use gliding for escape as might be expected.

For aquatic taxa that glide in the air above water, the most likely reason for gliding is to avoid predators that cannot become airborne. Squid are also known to exit the water while chasing underwater prey (Cole and Gilbert 1970). It is also possible that fish or squid use gliding as an energy-saving mechanism, but this hypothesis has not been tested quantitatively. As pointed out by O'Dor and colleagues (O'Dor 2013; O'Dor et al. 2013), the energetic hypothesis seem most plausible for migrating squid, which have little fat in reserve and are generally inefficient swimmers.

Although many of the preceding scenarios have been noted in the literature, the ecological context of gliding has not been well quantified for most taxa, largely because of the logistical difficulty of tracking climbing and gliding animals (but see Byrnes et al. 2008, 2011a, 2011b). The best understood systems are lizards of the genus *Draco* L., 1758, mammalian colugos, and ants, which will be discussed in more detail in the taxon-specific sections. The wide scope of motivation and utility of gliding suggests that multiple performance metrics should be considered when evaluating or comparing the effectiveness of gliding among different taxa.

Physical aspects of gliding

Gliding trajectories and aerial performance
Broadly, gliders create three types of trajectories, corresponding to those produced by terrestrial vertebrates, terrestrial inver-

tebrates, and aquatic gliders (Figs. 2A–2D). Terrestrial taxa have received the most experimental attention, thus the trajectories of some vertebrate and invertebrate gliders have been characterized in detail. Less is understood about the trajectories of aquatic taxa, likely due to the experimental difficulty of recording unpredictable glides that may be hundreds of metres in length on open seas.

Gliding is often considered to be the simplest form of flight, stemming from the physics of force balance during equilibrium gliding, which is sometimes called "steady" or "simple" gliding (Vogel 2013). By definition, a steady glide entails no net force on the glider, providing a constant velocity and a linear trajectory. This occurs when the lift and drag forces produced by the glider balance its weight. Specifically, the vertical components of lift and drag sum to equal the weight, and the horizontal components of lift and drag counterbalance. When this occurs, the ratio of lift to drag sets the glide angle:

$$(1) \qquad \gamma = \cot^{-1}\left(\frac{L}{D}\right)$$

where γ is glide angle, L is lift force, and D is drag force. All else being equal, increasing the mass of the glider should not appreciably change its angle of descent, but instead should make the animal glide faster (Vogel 1994).

This framework is often considered when discussing animal gliders, but the picture that is emerging from recent studies is that gliders are often not in equilibrium during flight (Socha 2002; McGuire and Dudley 2005; Socha et al. 2005, 2010; Bishop 2006, 2007; Bishop and Brim-DeForest 2008; Byrnes et al. 2008; Bahlman et al. 2013). In fact, unsteady gliding may be advantageous for shorter glides (Willis et al. 2011). There are at least two reasons why gliders are rarely observed in equilibrium. The first is that gliders that take off from a height (i.e., terrestrial gliders) begin the trajectory by accelerating under the force of gravity. In the Reynolds number regime of most gliders (~3 000 to 270 000; see Table 1), lift and drag are both functions of the square of speed, and therefore the resultant aerodynamic force on the body is small at slow speeds. The distance required to attain an equilibrium glide velocity may be considerable for some gliders, representing a significant portion of the trajectory. The second is that, even when moving at speeds that are great enough to produce equilibrium, many gliders can control the glide path by actively modulating aerodynamic forces. The result is that real glide paths contain at least some curvilinear portions; to our knowledge, no animal follows a completely linear trajectory. Such nonlinearity likely helps to explain the lack of strong patterns of performance across gliding taxa (Figs. 3A–3G).

Terrestrial vertebrates
Our best understanding of glide trajectories comes from recent studies of gliding dynamics in mammals, lizards, and snakes. These studies have tracked the two- or three-dimensional position of the glider (e.g., Figs. 4A–4C) throughout the entire trajectory (Socha 2002; McGuire and Dudley 2005; Socha and LaBarbera 2005; Socha et al. 2005) or part of the trajectory (Bishop 2006, 2007; Bishop and Brim-DeForest 2008; Socha et al. 2010; Bahlman et al. 2013). In some of these studies, multiple parts of the anatomy were tracked, enabling further analysis of body posture and orientation (Socha and LaBarbera 2005; Socha et al. 2005, 2010; Bishop 2006, 2007; Bishop and Brim-DeForest 2008). There have been two major efforts to record free-ranging gliders behaving under natural conditions. One on colugos used an accelerometer attached to the body to measure instantaneous acceleration throughout the glide (Byrnes et al. 2008, 2011a, 2011b); the other used high-speed cameras to track flying squirrels transiting to and from an artificial feeder (Bahlman et al. 2013). Takeoff has been examined in detail for snakes (Socha 2006) and mammals (Keith

Fig. 2. Schematized features of aerial trajectories for terrestrial (A, B) and aquatic (C, D) gliders. (A) The trajectories of terrestrial vertebrates, represented by glide paths of snakes (solid black line) and squirrels (broken blue line), can include an upward jump or a landing maneuver. (B) The glide path of terrestrial invertebrates such as ants is steep and can include a corkscrew-like initial falling phase prior to reorientation of the body. Vertebrates with few or no specializations for gliding (e.g., *Anolis* lizards) may exhibit similarly steep paths. (C) The sequence of events for most flying fish include a taxiing phases in which the tail is laterally oscillated to gain speed (also see Fig. 8C). Once fully airborne, glide paths can be close to level. (D) Gliding in squid includes an initial jetting phase in which the water in the mantle cavity is forcefully ejected through the funnel. Figure appears in color on the Web.
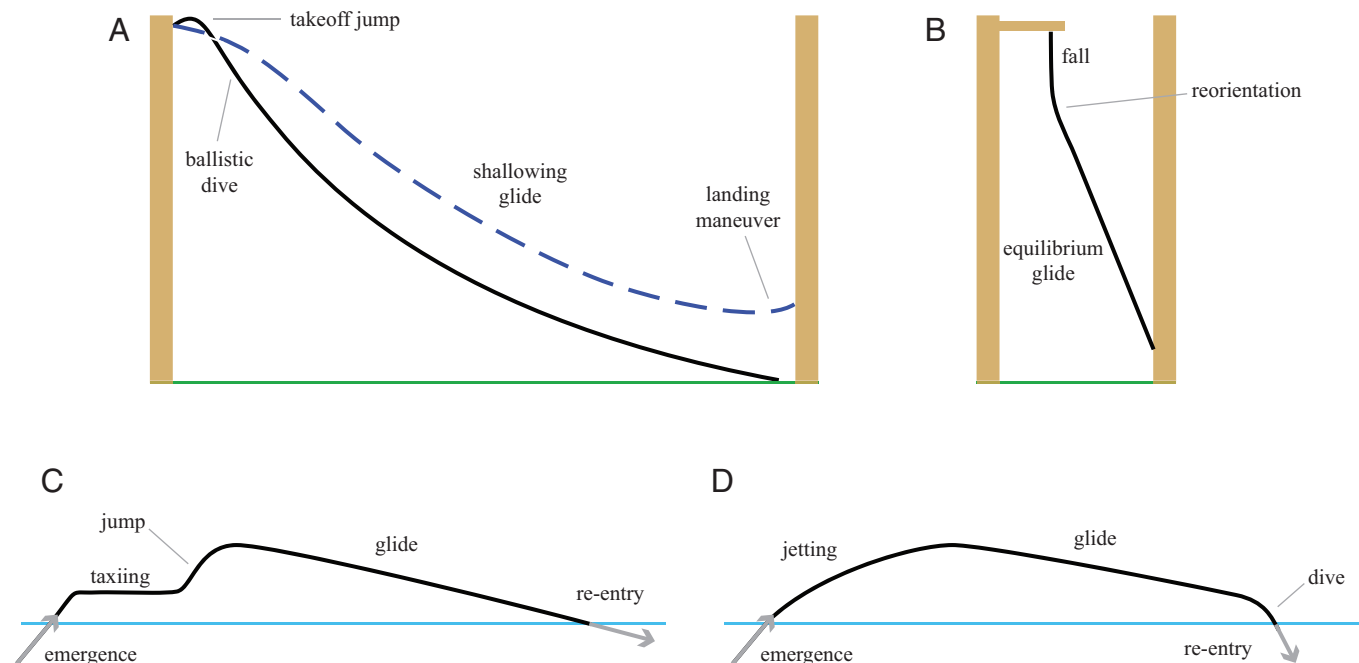
et al. 2000; Essner 2002; Paskins et al. 2007; Byrnes et al. 2008) and landing has only been examined in mammals (Paskins et al. 2007; Byrnes et al. 2008). Methodologically, position data are differentiated to yield velocity and acceleration; conversely, acceleration data are integrated to determine velocity and position. In addition to these basic metrics of glide performance, instantaneous glide angle can be calculated to indicate the direction of the local glide path.

These studies demonstrate that the trajectory of terrestrial gliders can consist of up to five phases: takeoff, ballistic dive, shallowing glide, equilibrium glide, and landing maneuver. Glides often begin and end on an arboreal substrate.

During takeoff, the glider pushes away or jumps from the substrate (Essner 2002; Socha 2006; Paskins et al. 2007); glides can also begin with a fall (Socha 2006). From horizontal substrates, flying squirrels (northern flying squirrel, *Glaucomys sabrinus* (Shaw, 1801), and southern flying squirrel, *Glaucomys volans* (L., 1758)) jump upward with angles in the range of 10°–35° (Essner 2002; Paskins et al. 2007), with smaller angles associated with longer glides, and reach speeds of 2.5 m/s (Essner 2002). Takeoff velocity has been measured to be 0.8–2.8 m/s in snakes (Fig. 5B) (Socha et al. 2005; Socha 2006), and estimated to be 3.3–8.4 m/s in the flying squirrel *Glaucomys sabrinus* (Fig. 5A) and 0.6–8.2 m/s in the colugo (*Galeopterus variegatus* (Audebert, 1799); also known as the Sunda flying lemur). Colugos tend to take off from a vertical posture (Byrnes et al. 2008).

The ballistic dive starts when the glider begins to move downward at the apex of the takeoff. During this phase, gravitational forces dominate and the local trajectory is parabolic. Essentially, the glider is falling, with the path determined by the velocity at takeoff. As the animal accelerates, aerodynamic forces increase, causing the path to deviate from ballistic. The end of the ballistic dive can be defined to occur when the glide angle begins to decrease (Socha et al. 2005). The maximum glide angle during the ballistic dive represents the steepest portion of the trajectory. For

snakes, it ranges from 52° to 62° in the Paradise Tree Snake (*Chrysopelea paradisi* H. Boie in F. Boie, 1827) (Fig. 5D) (Socha et al. 2005) and from 70° to 77° in Golden Tree Snake (*Chrysopelea ornata* (Shaw, 1802)) (Socha and LaBarbera 2005); it appears to be about 45° for the squirrel *G. sabrinus* (Fig. 5C) (Bahlman et al. 2013). The mean vertical distance dropped during the ballistic dive is 2.3 m for the snake *C. paradisi*; other values are not known precisely, but this depth appears to vary substantially among gliders. In fact, the ability to control the ballistic dive performance may be more important than is appreciated, particularly when considering the avoidance of objects or predators (see Fig. 4C). This may include postural adjustments to minimize drag to increase speed as rapidly as possible, which would increase lift production earlier in the trajectory.

The shallowing glide begins when the glide angle starts to decrease. During this phase, the glide path becomes more horizontal, increasing the horizontal distance traveled relative to vertical drop. The glide angle decreases at rates of 8°/s to 36°/s for the snake *C. paradisi* (Socha et al. 2005, 2010), 1°/s to 19°/s for the snake *C. ornata* (Socha and LaBarbera 2005), ~5°/s to 17°/s for the sugar glider (*Petaurus breviceps* Waterhouse, 1838) (Bishop 2007), and ~3°/m of height dropped for the squirrel *G. sabrinus* (Bahlman et al. 2013). As required to produce a curved glide path, the glide velocity changes throughout the phase (Figs. 5A, 5B). In *C. paradisi*, glide velocity increases and then levels off at ~9 m/s; vertical speed increases to ~6 m/s and then decreases. In *G. sabrinus*, glide velocity peaks at ~9 m/s within 5 m of horizontal distance traveled, and then decreases; vertical speed decreases throughout.

As previously described, in the equilibrium glide phase the forces are balanced and the glider moves at a constant velocity and constant glide angle. Equilibrium gliding has been observed repeatedly in glides by colugos (Byrnes et al. 2008) and in between poles 10 m apart by lizards (McGuire and Dudley 2005), and potentially in a single instance by a snake (Socha et al. 2005). Despite

experimental launch heights of 10–15 m and glide distances >20 m, most *C. paradisi* snakes have not been observed to achieve equilibrium (Socha et al. 2005, 2010). Similarly, *G. sabrinus* squirrels launching from a height of 15 m and traveling 18 m exhibited no instances of equilibrium (Bahlman et al. 2013). Comparisons with theoretical models of gliding suggest that snakes require greater vertical distance than ~15 m to reach equilibrium (Socha et al. 2010) or that snakes may oscillate about equilibrium (Jafari et al. 2014). In contrast, flying squirrels should be capable of reaching equilibrium within such heights; the lack of equilibrium that has been observed suggests that squirrels actively modulate aerodynamic forces throughout the glide (Bahlman et al. 2013). In both of these theoretical analyses, the dynamics of body movement were not considered and the differences between the species largely result from the effects of wing loading.

The final phase of the glide is the landing maneuver. When landing on a vertical substrate, mammals are known to pitch upward, rotating the body so that contact occurs feet first (e.g., Fig. 6A). In glides that reached equilibrium, colugos landed at a mean velocity of 4.0 m/s, a ~60% reduction relative to their mean glide velocity (Byrnes et al. 2008). Flying squirrels have also demonstrated a velocity reduction prior to landing in 18 m glides, but this appears to have occurred as part of a broader trend of velocity reduction throughout most of the trajectory (Fig. 5A) (Bahlman et al. 2013). For some of these glides, the squirrel was actually moving upward prior to landing, as demonstrated by the curved glide path with an upward-directed vertical velocity and glide angle (Fig. 5C). Snakes appear to drop the posterior body downward so that the tail contacts first when landing on the ground (Socha 2011), but show no evidence of slowing down for landing (Fig. 5B) (Socha et al. 2005, 2010).

Almost all terrestrial vertebrate gliders deploy their flight surfaces in the air or during takeoff. Aerodynamic force production increases as velocity increases in the trajectory (e.g., Fig. 7A). In short recordings located ~2 m from takeoff, the sugar glider (*Petaurus breviceps*) and the southern flying squirrel (*Glaucomys volans*) exhibited downward accelerations of ~1 to 5 m/s² (Bishop 2006, 2007); these values <1 g indicate that upward forces are generated early in the trajectory. Vertical accelerations can vary in large portions of the trajectory in snakes, colugos, and squirrels, demonstrating that force production varies substantially throughout the glide. In all three of these taxa, upward vertical accelerations on the order of 1–2 m/s² have been recorded directly (Byrnes et al. 2008) or calculated (Socha et al. 2010; Bahlman et al. 2013), indicating that the glider can produce more vertical force than is required to support its weight. Instances of reported equilibrium gliding indicate steady force production (McGuire and Dudley 2005; Socha et al. 2005; Byrnes et al. 2008), but it is possible that forces are actively modulated for control purposes at finer time scales than observed in these studies. A summary model of how forces on a flying squirrel change throughout a long glide is shown in Fig. 7B.

Terrestrial invertebrates

The ability of some wingless arthropods to glide has been recognized only within the past decade (Yanoviak et al. 2005). All known gliding arthropods engage in gliding behavior to avoid predation, and over the course of their trajectories, use visual information to identify potential target substrates before gliding towards and landing upon those targets.

Direct measurement of the trajectories of gliding arthropods is a difficult task, owing to the fact that these organisms are small (approximately centimetre scale) but may exhibit trajectories over 10 m in length. Hence, although gliding has been observed in diverse arthropod taxa (Yanoviak et al. 2005), including no less than three independent evolutions of gliding in ants (Yanoviak et al. 2011), trajectories have only been quantified for the gliding ant *Cephalotes atratus* (L., 1758).

In general, wingless insects exhibit trajectories with three phases: (1) a vertical drop of uncontrolled parachuting, often including aerial righting; (2) a rapid directional adjustment in which the body is aligned with a target tree; (3) a steep glide toward the tree, which may also include directional adjustments (Fig. 2B) (Yanoviak et al. 2005, 2009; Yanoviak and Dudley 2006). Two-dimensional trajectories for *C. atratus* were reported in Yanoviak et al. (2005) for ants gliding towards an artificial target in an experimental environment, revealing steep glide angles of 73°–79° and a mean equilibrium glide speed of 4.3 m/s. Recent work by Munk et al. (2011) has expanded upon this analysis, providing quantification of three-dimensional trajectories of *C. atratus* ants gliding towards tree trunks in a natural rainforest environment. This work shows that *C. atratus* ants reach terminal descent speed roughly within the first second of their fall, but are able to initiate lateral motions towards their target even before this stage. Furthermore, *C. atratus* ants perform most of their maneuvering in the early phases of their descent: analysis by Munk et al. (2011) demonstrates that mean trajectory curvature decreases as ants glide laterally farther from their drop point. However, no evidence exists to suggest that gliding *C. atratus* ants employ a landing maneuver as they approach their target; ants do not slow their trajectories on final approach, and if their first landing attempt fails, then they may bounce off the target substrate, re-stabilize, and make a second attempt at landing on the same trunk farther down.

For ants, glides become steeper with increasing body size, an effect seen both within and across species (Yanoviak et al. 2005, 2008). The origin of this size dependency has not been explained, but has been hypothesized to result from the shorter distance required for smaller insects to reach equilibrium velocity (Yanoviak et al. 2008), which is a consequence of their smaller weight-to-drag ratio.

In addition to work on gliding ants, which are secondarily wingless, glide performance has also been quantified for jumping bristletails (Archaeognatha), which are an ancestrally wingless insect order. Although the trajectories of these animals have not been quantified, field observations of natural glides have shown that these animals exhibit a mean glide ratio (ratio of total horizontal to vertical descent) of 0.4, with a maximum of 0.5 (Yanoviak et al. 2009). These figures would imply a mean glide angle of ~63°, but if the bristletails follow a J-shaped trajectory similar to those of gliding ants, then their glide angles in the latter phases of their trajectory may be substantially higher.

Aquatic gliders

Trajectories of aquatic gliders have not been rigorously quantified using modern techniques, and in general, these taxa are the least studied of the gliders. Most of our understanding of their flight behaviors derive from direct observations from ships at sea or from uncalibrated photographic evidence (e.g., Barrows 1883; Baird 1886; Adams 1906; Hubbs 1918, 1933, 1936; Breder 1929; Loeb 1936; Mills 1936; Edgerton and Breder 1941; Kawachi et al. 1993).

Flying fish jump out of the water to begin their aerial trajectories (Fig. 2C), whose characteristics are best summarized by Fish (1990), Kawachi et al. (1993), and Davenport (1994). Prior to becoming completely airborne, cypselurid species "taxi" across the surface by beating the tail at a high frequency (~50 to 70 beats/s; Fig. 8C), which serves to increase the forward speed from roughly 10 to 20 m/s (Hertel 1966; Davenport 1994). During taxiing, the pectoral fins, which are extended outward to the side to form wings, oscillate with small amplitude. This oscillation was the basis of extended debate in the late 1800s and early 1900s concerning whether or not these fish actively flap their fins to generate flight forces; for a historical perspective see Kutschera (2005). Because the oscillations stop at the same time that the tail stops beating, Rayner (1986) suggested that the oscillation of the pectoral fins results simply from a mechanical coupling to the tail beat; there is little evidence that flapping occurs once the fish is fully

Table 1. Compilation of characteristics of gliding species from the literature.

Species	Mean mass (g)	Maximum speed (m/s)	Wing loading (N/m²)
Mahogany glider, *Petaurus gracilis* (de Vis, 1883)	380[a]		
Sugar glider, *Petaurus breviceps*	110[a], 73.4[b]	5.1[b]	30*,[b]
Squirrel glider, *Petaurus norfolcensis* (Kerr, 1792)	190[c]		
Northern flying squirrel, *Glaucomys sabrinus*	92.7[d]	8.5[e]	58[f]
Southern flying squirrel, *Glaucomys volans*	81[g]	8.6[h]	45*,[g]
Japanese giant flying squirrel, *Petaurista leucogenys* (Temminck, 1827)		13.3[i]	
Red giant flying squirrel, *Petaurista petaurista* (Pallas, 1766)	1300[j]		120[f]
Siberian flying squirrel, *Pteromys volans* (L., 1758)			
Lord Derby's scaly-tailed flying squirrel, *Anomalurus derbianus* (Gray, 1842)			86[f]
Malayan colugo (Sunda flying lemur), *Galeopterous variegatus*	1100[n]	10[n]	60[f]
Paradise Tree Snake, *Chrysopelea paradisi* (mean±SD (min.–max.))	40.5±23.1 (3.0–82.7)[o]	10±0.9 (8.1–11)[o]	29±9 (12–46)[o]
Blanford's Flying Lizard, *Draco blanfordii* Blanford, 1878	11[q]	6.4[q]	14*,[q]
Crested Gliding Lizard, *Draco fimbriatus*	19[q]	6.4[q]	24*,[q]
Dusky Gliding Lizard, *Draco formosus* Boulenger, 1900	9[q]	7[q]	14*,[q]
Yellow-bearded Gliding Lizard, *Draco haematopogon* Gray, 1831	6[q]	5.2[q]	12*,[q]
Spotted Gliding Lizard, *Draco maculatus* (Gray, 1845)	4[q]	5.8[q]	13*,[q]
Giant Gliding Lizard, *Draco maximus* Boulenger, 1893	16[q]	6.5[q]	16*,[q]
Black-bearded Gliding Lizard, *Draco melanopogon*	4[q]	5.5[q]	9*,[q]
Dusky Gliding Lizard, *Draco obscurus* Boulenger, 1887	9[q]	6[q]	16*,[q]
Five-banded Gliding Lizard, *Draco quinquefasciatus* Hardwicke and Gray, 1827	7[q]	7.3[q]	11*,[q]
Common Gliding Lizard, *Draco sumatranus* Schlegel, 1844	6[q]	7.6[q]	15*,[q]
Barred Gliding Lizard, *Draco taeniopterus* Günther, 1861	3[q]	6.1[q]	10*,[q]
Burmese Flying Gecko, *Ptychozoon lionatum* Annandale, 1905	13.9[r]	8.7[r]	
Fish spp.	32.4[s]	20[s]	23[s,t]
Orangeback flying squid, *Sthenoteuthis pteropus*	4[u]	3.4[u]	
Gliding ant *Cephalotes atratus*	0.05[v]	4.3[v]	

Note: "Maximum speed" is the maximum reported speed from a glide; for *Draco*, only mean speed data were available and are reported instead. "Wing loading" is to horizontal, usually provided as a mean value for the entire trajectory, except for *Glaucomys sabrinus* and *Chrysopelea paradisi*, which are reported as minimum values was calculated using the reported values for the mass and wing loading. For the *Galeopterous variegatus*, wing-chord length (l_1) was calculated using the aspect ratio of the animal, whose mantle length was reported in O'dor et al. (2013). "*Re*" is Reynolds number and is calculated as Ul/ν, where U is maximum speed, l is length, and provided in this table. Socha (2011) provides a different lower bound (2500–3500), which represents that same small snake early in its trajectory, when the glide speed

[a]Jackson (2000).
[b]Bishop (2007).
[c]Flaherty et al. (2008).
[d]Vernes (2001).
[e]Bahlman et al. (2013).
[f]Stafford et al. (2002).
[g]Bishop (2006).
[h]Scheibe and Robins (1998).
[i]Ando and Shiraishi (1993).
[j]Lee et al. (1993).
[k]Scholey (1986).
[l]Suzuki et al. (2012).
[m]Corbin and Cordeiro (2006).
[n]Byrnes et al. (2011a, 2011b).
[o]Socha et al. (2005).
[p]Socha and LaBarbera (2005).
[q]McGuire and Dudley (2005).
[r]Heyer and Pongsapipatana (1970).
[s]Davenport (1994).
[t]Davenport (2003).
[u]O'Dor et al. (2013).
[v]Yanoviak et al. (2005).

airborne and gliding (Davenport 1994). The total distance of the taxi is on the order of 5–25 m. Some species do not employ this behavior and instead jump directly into the air, a trait that may be restricted to two-winged fishes (Davenport 1994).

At the end of the taxi, the fish becomes fully airborne, using a transition that is poorly understood. The fish then glides with either four or two fins extended, depending on the species. As summarized by Fish (1990) and Kawachi et al. (1993), the path of this portion of the trajectory has been described as flat or level with the water, implying a mean glide angle of 0°, but instantaneous trajectory data are needed to evaluate such observations. If the glide path is indeed level and the fins are static, then the flying fish must receive additional upward force from ground effect

(Kawachi et al. 1993; Davenport 1994, 2003; Park and Choi 2010) or upward drafts of air created by moving waves (Breder 1929; Fish 1990). A recent aerodynamic study of a four-winged flying fish model (Park and Choi 2010) reported a maximum lift-to-drag ratio of 4.37 (corresponding to a glide angle of 13°), which clearly indicates that a glide in still, open air would not be level. In fact, such a glide ratio would require a starting height of 11.4 m for a 50 m glide; the maximum height of a fish in a glide has been estimated at 8 m (Hertel 1966; Davenport 1994), suggesting that the fish must experience significant force enhancement due to the proximity to the water surface, which is a conclusion also deduced by Kawachi et al. (1993).

Glide angle (°)	Glide ratio	l_1, wing-chord length (cm)	l_2, square root of the wing area (cm)	Re	
				Using l_1	Using l_2
28[a]	1.9[a]				
30[a], 44[b]	1.8[a]		15		50 400
37[c]	1.3[c]				
27[d]	1.6[d], 1.9[e]		13		67 800
47[g]	1.5[h]	12.6[g]		41 000	
18[f]	1.9[f]				
12[k]					
	1.8[l]				
25[m]	2.1[m]				
		33	42	212 400	270 300
28±10 (13–46)[o]	1.06±0.27 (0.65–1.49)[o,p]	1.9±0.43 (0.9–2.5)[o,p]		11 800±3 700 (4 600** – 16 400)	
27[q]	2[q]		9		35 800
29[q]	1.8[q]		9		36 000
27[q]	1.9[q]		8		35 400
26[q]	2[q]		7		23 200
24[q]	2.3[q]		5		20 300
29[q]	1.9[q]		10		41 000
24[q]	2.3[q]		7		23 100
22[q]	2.4[q]		7		28 400
21[q]	2.3[q]		8		36 800
23[q]	2.3[q]		6		30 300
25[q]	2.2[q]		5		21 100
			12		155 800
		6[u]		13 000	
75[v]	0.2[v]	1[v]		3 020	

body weight divided by total body area; for some taxa, wing area was used in the calculation (indicated with by *). "Glide angle" is the angle of the glide path relative within a trajectory. "Glide ratio" is the ratio of the total distance traveled to the total height lost in a trajectory. Wing area (whose square-root l_2 appears in the table) reported by Stafford et al. (2002). For the squid *Sthenoteuthis pteropus*, the wing-chord length was calculated by finding the width and area of the body from an image ν is kinematic viscosity (15.68×10^{-6} m²/s). The minimum value for *C. paradisi*, 4 600 (indicated by **), was calculated from the smallest snake using the maximum speed is lower. The last three columns, except for *C. paradisi*'s minimum *Re*, were calculated for the first time in the present review.

Near the end of the trajectory, the glide speed apparently falls and the fish re-enters the water or lowers its tail to begin a new taxiing sequence, leading to a new glide. Such taxi–glide sequences have been seen to repeat multiple times, which enables the fish to travel relatively long distances above water, accounting for reports of glides lasting up to 400 m (see references in Fish 1990). Although mean glide speeds have been estimated to be as great as 20 m/s, it is not known how velocity and acceleration change throughout a flight, nor how the body and fins are oriented relative to the local airflow, which may be quite complex resulting from air movement in the wave-zone boundary layer (Melville 1996). Overall, new studies that track flying fishes using three-dimensional methods are needed to precisely quantify their glide behaviors.

Squid are among the most spectacular and least expected of the gliders. The flight of squid consists of four phases: launching, jetting, gliding, and diving (Fig. 2D); these phases best are understood from recent studies documenting chance observations (Macia et al. 2004, Muramatsu et al. 2013, O'Dor et al. 2013). In the air, squid employ fore and aft flight surfaces created by the fins and arms, respectively.

The squid launches from the water at a low angle by ejecting a water stream from its funnel, with initial body speeds in the range of 2–8 m/s. In contrast to most flying fish, the squid becomes

Fig. 3. Comparison of glide performance across taxa. Glide speed, glide angle, and glide ratio are plotted against body mass (A–C) and wing loading (E–G). Wing loading vs. mass (D) is also plotted to show how wing loading increases with body size. Wing loading for the orangeback flying squid (*Sthenoteuthis pteropus* (Steenstrup, 1855)) is estimated from data in O'Dor (2013) using mantle length = 6 cm, body mass = 4.3 g, and total area = 34 cm²; area based on the Japanese flying squid (*Todarodes pacificus*) from Fig. 1G. Wing loading for the myrmicine ant *Cephalotes atratus* is calculated using body mass = 4 g and total area = 0.35 cm². Speeds and glide ratios are maximum reported mean values, whereas glide angles are minimum reported values. Glide ratios are calculated using total distance traveled. Linear regression values for these plots are reported in Table 2. Source data are from Heyer and Pongsapipatana (1970); Lekagul and McNeeley (1977); Ando and Shiraishi (1993); Scheibe and Robins (1998); Jackson (2000); Russell et al. (2001); Vernes (2001); Stafford et al. (2002); Davenport (2003); McGuire and Dudley (2005); Socha et al. (2005); Yanoviak et al. (2005); Flaherty et al. (2010); Byrnes et al. (2011b); Suzuki et al. (2012); Bahlman et al. (2013); O'Dor et al. (2013). Figure appears in color on the Web.
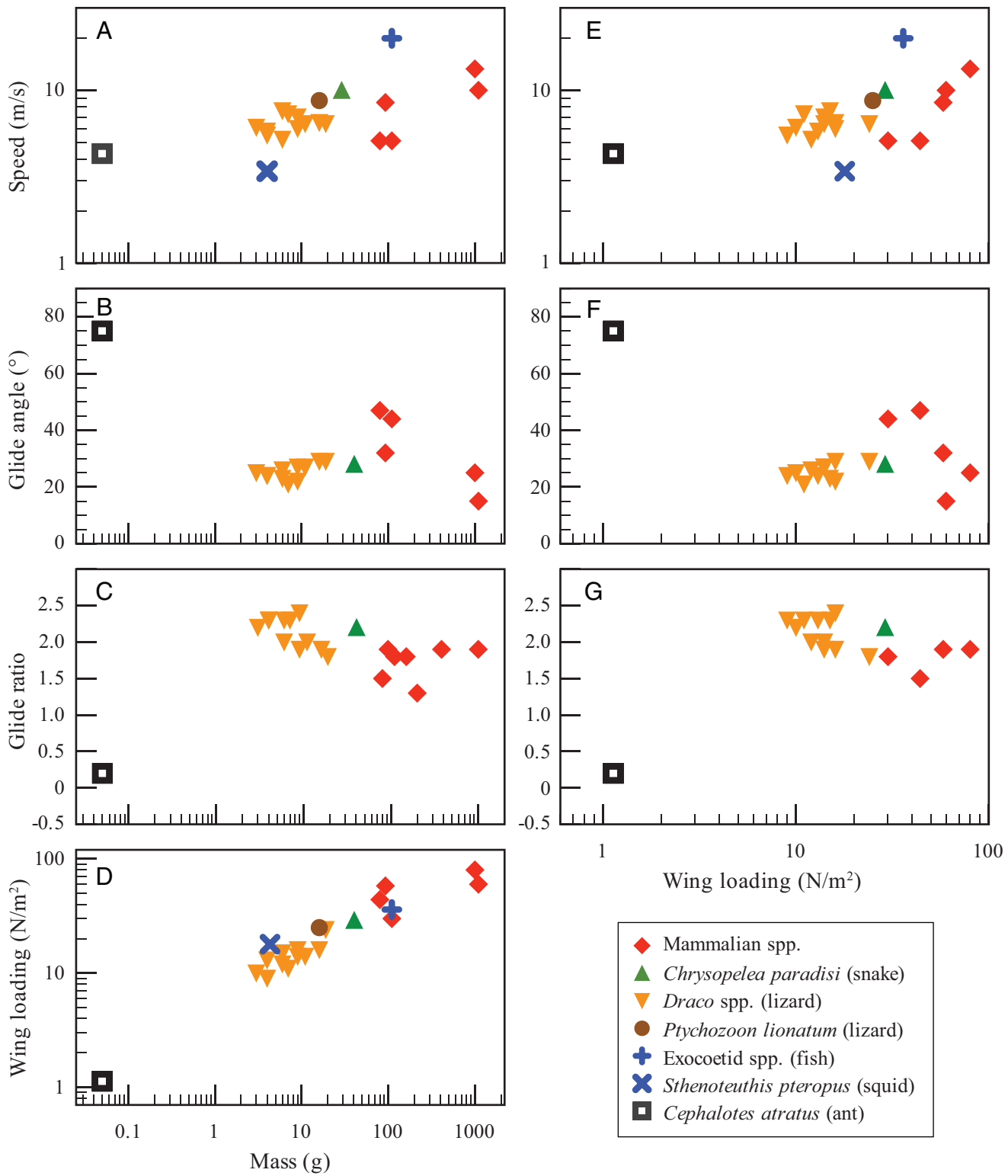
Table 2. Linear regression values for data shown in Figs. 3A–3G.

| | | | | | | *p* | |
| | | | | | | Slope | Intercept |
x variable	*y* variable	*Cephalotes atratus*	*y* intercept	Slope	R^2		
Log mass (g)	Speed (m/s)	With	4.71	1.04	0.32	0.01	0.0008
		Without	3.49	1.41	0.34	0.01	0.04
Log wing loading (N/m²)	Speed (m/s)	With	2.67	1.62	0.016	0.08	0.33
		Without	0.87	2.18	0.14	0.11	0.83
Log mass (g)	Glide angle (°)	With	37.2	−2.43	0.14	0.13	0.0001
		Without	21.4	2.39	0.27	0.04	0.0001
Log wing loading (N/m²)	Glide angle (°)	With	48.71	−6.28	0.19	0.08	0.0002
		Without	10.86	5.86	0.27	0.04	0.18
Log mass (g)	Glide ratio	With	1.74	0.05	0.05	0.32	0.0001
		Without	2.34	−0.11	0.43	0.02	0.0001
Log wing loading (N/m²)	Glide ratio	With	1.24	0.25	0.21	0.07	0.004
		Without	2.73	−0.23	0.36	0.01	0.001
Log mass (g)	Log wing loading (N/m²)	With	1.87	0.41	0.8	0.0001	0.0001
		Without	2.1	**0.33**	0.64	0.0001	0.0001

Note: Least-squares regressions were fit for each relationship. Data are based on raw species mean values and have not been adjusted to account for phylogenetic relatedness. Because of the large difference in body size between myrmicine ants *Cephalotes atratus* and all other gliding species, each regression was run twice, once including all taxa and once excluding *C. atratus*. The isometric relationship between log wing loading and log mass (slope = 0.33) is set in boldface type.

completely airborne after launch, but continues ejecting water from its funnel until the mantle is empty. This "jetting" phase occurs over a distance of roughly 1 m (O'Dor et al. 2013), and possibly longer (Muramatsu et al. 2013), with maximum heights reaching between 1 and 3 m. The function of jetting in the air has been attributed to propulsion (O'Dor et al. 2013), which would make squid unique among gliders in possessing a mechanism to actively generate thrust. The loss of water mass associated with jetting should also reduce the requirements for acceleration (Muramatsu et al. 2013) and is likely to be important for glide performance as well. O'Dor et al. (2013) estimate a total volume of ejected water of 4 mL from a squid with a mantle length of 6 cm. Using the density of water, this volume is equivalent to about 4 g of mass lost, which is roughly equivalent to the body mass of the animal itself. Such a large change in mass would dramatically alter the squid's wing loading and therefore its glide characteristics, particularly glide speed. After jetting stops, the squid glides along a path whose exact characteristics have not been described. Prior to re-entry, the squid's flight surfaces are folded up and the squid apparently dives at a nose-down angle into the water (Muramatsu et al. 2013). From recent studies, airspeed ranges from 2 to 11 m/s and total distance traveled ranges from 1 to 15 m (Macia et al. 2004; Muramatsu et al. 2013; O'Dor et al. 2013), but some historical observations suggest that longer travel might be possible (Macia et al. 2004).

Insights from physical theory

Based on Newton's second law, the following equations govern any gliding motion:

$$(2) \quad \begin{aligned} m\frac{dv}{dt} &= mg \sin\gamma - \frac{1}{2}\rho_{air}C_d S v^2 \\ m\frac{d\gamma}{dt} &= mg \cos\gamma - \frac{1}{2}\rho_{air}C_l S v^2 \end{aligned}$$

where *m* is the mass of the glider, *S* is wing area, *v* is the forward velocity, γ is the glide angle, *g* is gravitational acceleration, ρ_{air} is air density, and C_l and C_d are the time-varying lift and drag coefficients, respectively; for derivation see Willis et al. (2011). These equations can be used to predict the dynamics of any glider, but they require that the aerodynamic coefficients and wing areas be known; such data are not readily available for most gliding animals. Of these two parameters, the force coefficients are more problematic, as to date only a few studies have determined steady-state coefficients from physical or computational models (Song

et al. 2008; Miklasz et al. 2010; Holden et al. 2014; Krishnan et al. 2014). Furthermore, real gliders likely employ unsteady lift and drag, which has not been addressed. This may be the reason why theoretical models, in spite of their effectiveness, have so infrequently been applied to analyze glide performance in animals (Kawachi et al. 1993; Socha et al. 2010; Willis et al. 2011; Bahlman et al. 2013; Jafari et al. 2014). Among these, only Willis et al. (2011) and Jafari et al. (2014) used previously measured aerodynamic data in their modeling; Kawachi et al (1993) used an empirical relation for C_d as a function of C_l, while Socha et al. (2010) and Bahlman et al. (2013) used constant values for C_l and C_d in their simulations. Overall, these studies have provided new insights into the mechanics of glide trajectories:

1. For long glides, using a constant lift and drag coefficient throughout the trajectory may not be optimal, because smaller speeds are achieved, producing glides that are longer in duration and shorter in distance traveled. An optimum glide trajectory should include a ballistic phase in which the glider minimizes the aerodynamic forces to gain speed effectively and then uses a large lift coefficient to shallow the trajectory. This scenario appears to be reflected in experimental data (e.g., Socha et al. 2010; Bahlman et al. 2013). For short glides (Willis et al. 2011), it may be beneficial to employ the largest possible aerodynamic coefficients throughout the trajectory, especially the drag coefficient, to decrease the acceleration and stay airborne as long as possible. This strategy has the additional benefit that it minimizes the speed at impact, reducing the chance of injury.
2. Kawachi et al. (1993) and Willis et al. (2011) found that maximizing the lift-to-drag ratio does not optimize the range of trajectory, as would be predicted under equilibrium glide theory alone. This result demonstrates that the role of transient motions cannot be neglected.
3. Kawachi et al. (1993) and Bahlman et al. (2013) showed that flying fish and flying squirrels, respectively, continue to modify their lift and drag forces until the end of the trajectory, with no equilibrium gliding. These analyses assume that the animal is capable of modifying its aerodynamic properties independent of speed or glide angle, which could be accomplished by adjusting wing camber or angle. Kawachi et al. (1993) reported qualitative observations that supported their results. Bahlman et al. (2013) measured several glide trajectories by northern flying squirrels (*Glaucomys sabrinus*) and used eq. 2 to calculate force coefficients. They found that the squirrels systematically vary C_l and C_d to achieve higher glide ratios and larger speeds. Jafari et al. (2014) used aerody-

Fig. 4. Time-resolved position data for glide trajectories of terrestrial gliders. (A) Three-dimensional glide paths of the northern flying squirrel (*Glaucomys sabrinus*) under seminatural conditions. Glides were recorded in a forest in Maine, USA, using two high-speed cameras. Squirrels behaved naturally, launching from a height of ~15 m from a feeder on a building (represented by the origin 0,0,0) and volitionally gliding toward six trees ranging in horizontal distance from 7 to 20 m. Glides to each tree are color-coded; thin lines represent interpolations due to missing data. The gray lines are projections of the glide path onto the ground; multiple turns can be seen. A total of 56 glides from six squirrels are shown. (From Bahlman et al. 2013; reproduced with permission of J. R. Soc. Interface, vol. 10, issue 80, ©2013 The Royal Society.) (B) Three-dimensional coordinates of the Paradise Tree Snake (*Chrysopelea paradisi*) taken from the end portion of longer trajectories. Snakes were recorded in experimental conditions gliding between two constructed towers. The launch height was 15 m; only the lower ~8 m of the trajectory are shown. Glides are color-coded, with points representing five landmarks along the snake's body. The lateral spread of points through the trajectory results from the aerial undulation of the snake. The curved paths indicate turning, particularly in the brown and black traces. A total of eight glides from two snakes are shown. (From Socha et al. 2010; reproduced with permission of Bioinspir. Biomim., vol. 5, issue 4, ©2010 IOP Publishing.) (C) A comparison of glide trajectories from lizards (Black-bearded Gliding Lizard, *Draco melanopogon* Boulenger, 1877; Crested Gliding Lizard, *Draco fimbriatus* Kuhl, 1820), snakes (*Chrysopelea paradisi*), and squirrels (*Glaucomys sabrinus*) with launch points superimposed. For the snakes, the beginning of the sequence is the maximum height of the body after takeoff. All points represent the estimated center of mass of the animal. These plots are two-dimensional projections, representing a side view of the trajectory. Single trajectories are shown from two lizards and 14 snakes; multiple trajectories are shown from six squirrels (depicting the same data as in A). This comparison demonstrates the potential ecological relevance of differences in glide performance. Squirrels and snakes can achieve similar minimum glide angles, but snakes require a much greater ballistic dive and their glide paths shallow at a lower rate, resulting in large differences in horizontal distance traveled. The glide path of *Draco* lizards also shallows at a greater rate than in snakes. Although *Chrysopelea* snakes are known predators of *Draco* lizards, this plot suggests that the aerial pursuit by a snake chasing a lizard would be an ineffective strategy if the lizard is not intercepted early in the trajectory. For both *Draco* lizards and snakes, glide performance decreases with body size. The top trajectory of *Draco* lizards represents that of *D. melanopogon* with a body mass of 2.95 g and the lower trajectory is that of *D. fimbriatus* with a body mass of 21.6 g; for the snakes, the steepest trajectory is from the largest snake with a body mass of 83 g. Modified from McGuire and Dudley (2005; reproduced with permission of Am. Nat., vol. 166, issue 1, ©2005 The University of Chicago Press), Socha et al. (2005; reproduced with permission of J. Exp. Biol., vol. 208, issue 10, ©2005 The Company of Biologists), and Bahlman et al. (2013; reproduced with permission of J. R. Soc. Interface, vol. 10, issue 80, ©2013 The Royal Society).

namic force coefficients that were functions of angle of attack; their simulations resulted in trajectories that reached equilibrium when given sufficient time. However, as mentioned previously, equilibrium gliding has not been consistently observed in flying snakes (Socha 2002; Socha et al. 2005, 2010).

4. Jafari et al. (2014) have begun to consider the effects of the animal's body itself, whose rotations can change the force coefficients and alter its stability characteristics. They developed two theoretical models of a flying snake: one with rigid connections between "wings"; the other with springs and dampers to account for the postural reconfigurations of the snake body, and an external restoring moment to represent the effect of control movements. The first model possessed a locally passively stable equilibrium solution; the second model was inherently unstable but could be stabilized using a restoring moment. These results suggest that flying snakes may require active control for stable gliding; however, the passively stable trajectory of the first model provides an underlying "dynamical skeleton" for the closed loop control system of the snake to work with.

5. Simulations of gliding demonstrate that oscillations in velocity and acceleration are expected in a glide trajectory (Socha et al. 2010; Bahlman et al. 2013). Assuming constant force coefficients, these oscillations take on the order of 2–8 s to dampen, providing a lower bound on how long it should take a glider to reach equilibrium. This also may help to explain why equilibrium may not occur often in real glides in the wild, which can typically occur on these time scales (e.g., Byrnes et al. 2008).

In these studies, the aerodynamic force coefficients represent the total effect of the air on the body, but it is also possible to consider gliding from first principles of fluid mechanics. Gliding behavior can be considered one form of the problem of free fall of a solid object in a fluid, which has been studied recently both in theory and in experiment (e.g., Pesavento and Wang 2004; Andersen et al. 2005; Paoletti and Mahadevan 2011; Ern et al. 2012; Varshney et al. 2012, 2013; Huang et al. 2013). Paoletti and Mahadevan (2011), inspired by gliding insects, developed a comprehensive model of an elliptical cylinder falling through a fluid and found different solutions for gliding strategies that optimize time or energy. Inspired by the motion of falling tulip seeds, Varshney et al. (2013)

determined the motions of a falling parallelogram and found coupled tumbling–helical patterns with horizontal displacement, but no net horizontal drift. Huang et al. (2013) studied the effect of nonuniform mass distribution on the trajectory of a freely falling plate and observed tumbling patterns, but with a net horizontal displacement. Ern et al. (2012) summarized our understanding of the wake-induced oscillatory paths of freely falling objects in fluids, which is important for determining the stability characteristics of objects moving within a fluid. Together, these studies demonstrate that, in the absence of control, even a symmetric bluff body with nonuniform mass distribution can move horizontally, providing plausible templates for the evolution of gliding without morphological specialization. However, these studies have focused on simple geometries and the applicability of their results to real gliders has not yet been investigated.

Future work on gliding theory would benefit from an increased understanding of time-varying forces on the glider, incorporating three-dimensional and aeroelastic effects (i.e., interaction between materials and airflow), and a greater consideration of inertial mechanics and stability of the glider's body.

Aerodynamics of gliders

Although the aerodynamic properties of flapping flyers have been studied extensively, among the gliding animals, only snakes (Miklasz et al. 2010; Holden et al. 2014; Krishnan et al. 2014) and mammals (Song et al. 2008) have been examined for aerodynamic performance. Miklasz et al. (2010) and Holden et al. (2014) measured the lift and drag forces produced by a two-dimensional airfoil resembling a flying snake's body shape, with Holden et al. (2014) using a more anatomically accurate geometry. These two studies found that the snake's airfoil is able to produce lift up to high angles of attack and has a gentle stall region. In addition, Holden et al. (2014) observed two different vortex-shedding patterns depending on the angle of attack, which resulted from the flow separation point shifting from the apex of the cross section to the leading edge. Similar results were obtained by Krishnan et al. (2014), who used immersed boundary methods to computationally study the aerodynamics of the snake's airfoil; their results help to explain the physical basis of the peak in lift at the angle of
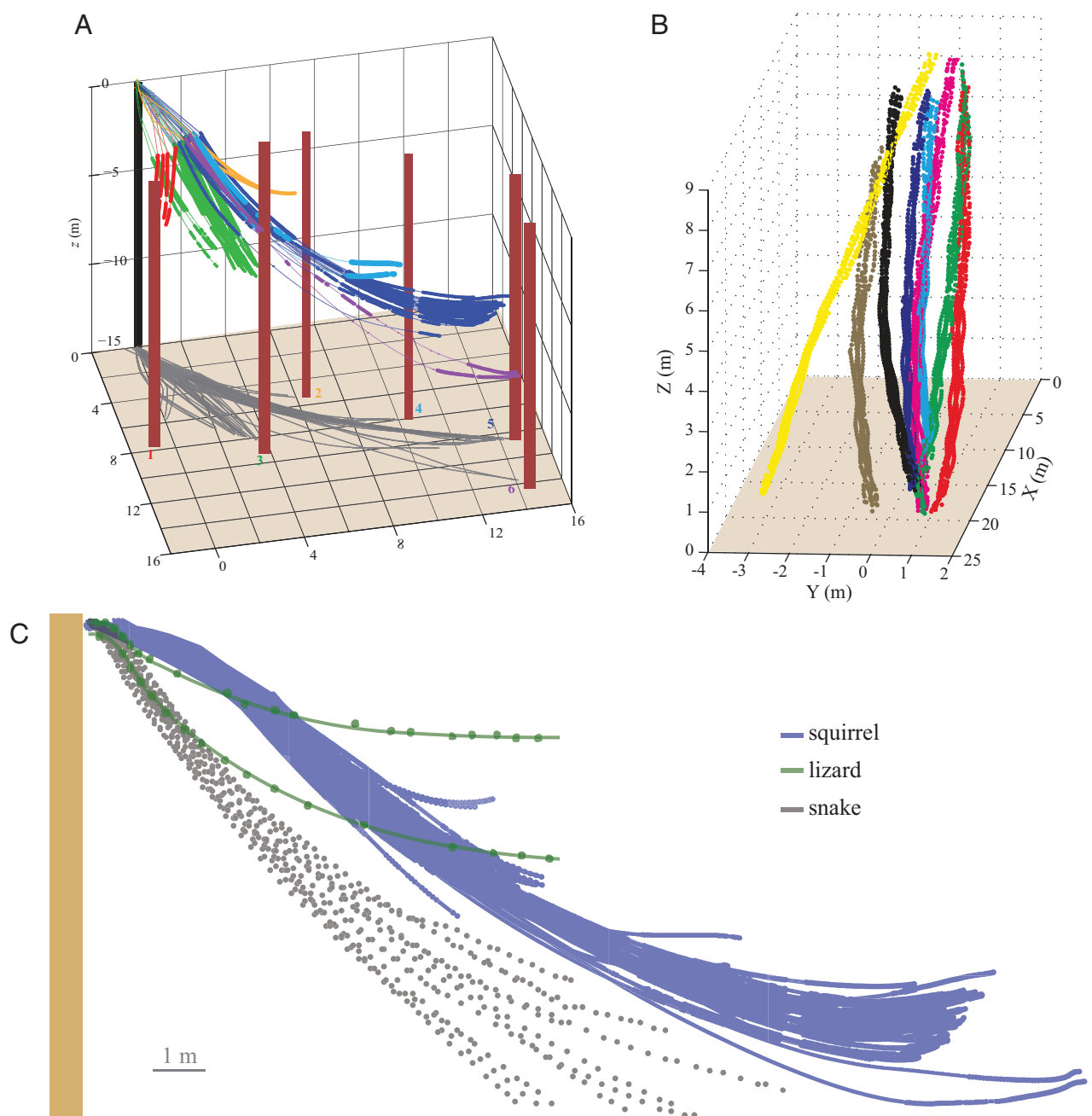
attack of 35°. In a preliminary test of interactive effects of body sections, Miklasz et al. (2010) tested two snake models placed in tandem. They found enhancements in the overall lift (30%) and lift-to-drag (50%) relative to solitary models with a specific configuration. However, further work is needed with anatomically accurate models to understand the tandem aerodynamic effects and to determine if the snake takes advantage of such effects while gliding.

Song et al. (2008) explored the aerodynamic properties of mammalian patagia using rectangular compliant membranes, testing effects of aspect ratio, angle of attack, compliance, and Reynolds number. The membrane wing models stretched under higher loads (either due to an increased airspeed or angle of attack), creating larger cambers that resulted in larger lift production and delayed stall in comparison with rigid wings. Furthermore, the compliant membrane wings exhibited higher drag coefficients, although the overall lift-to-drag ratio was generally improved. Wings with

lower aspect ratios had better lift and drag behavior for large angles of attack; i.e., they maintained near-maximum lift coefficient for higher angles of attack, and the drag coefficient increased with a smaller slope. Compared with two gliding mammals whose force coefficients were calculated by Bishop (2007) using trajectory data, the compliant membrane wing models had smaller lift-to-drag ratios than in southern flying squirrels (*Glaucomys volans*), but performed similarly to sugar gliders (*Petaurus breviceps*). The superiority of flying squirrels was attributed to the leading edge of the membrane extending to the pollex, a morphological specialization that allows them to control the leading-edge angle of their wings by forelimb rotation; this specialization is absent in sugar gliders (Bishop 2008).

Most gliding animals use low aspect-ratio wings. A key feature of the lift-producing mechanism of low aspect-ratio wings is the presence of tip vortices, which generate low-pressure regions over a significant portion of the wing and enhance the overall lift

Fig. 5. A comparison of instantaneous velocity and glide angle in the glide trajectories of squirrels (A, C; northern flying squirrel, *Glaucomys sabrinus*) and snakes (B, D; Paradise Tree Snake, *Chrysopelea paradisi*). Note that performance metrics are depicted across distance for squirrels and through time for snakes. Plots represent summaries of multiple glides, 23 for squirrels and 14 for snakes, with error bars representing 1 SD and 10th and 90th percentiles, respectively. For the snakes, the sequences commence at the maximum height of the body after takeoff. Both species show continuously changing velocities and glide angles, demonstrating glides that generally lack equilibrium. For the squirrels, an upturn in the glide path from horizontal can be seen at ~16 m. Modified from Socha et al. (2005; reproduced with permission of J. Exp. Biol., vol. 208, issue 10, ©2005 The Company of Biologists) and Bahlman et al. (2013; reproduced with permission of J. R. Soc. Interface, vol. 10, issue 80, ©2013 The Royal Society).
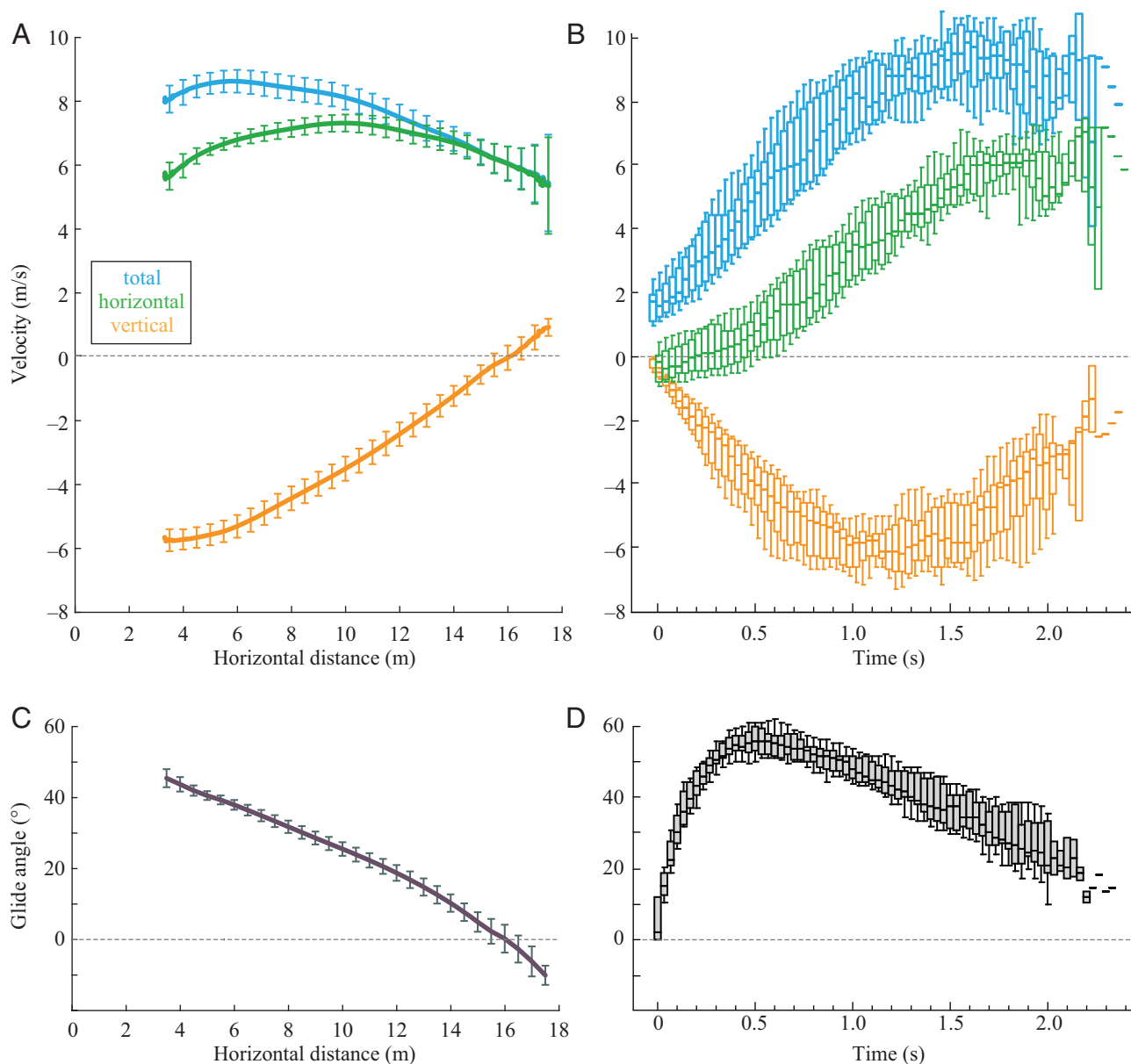

relative to high aspect-ratio wings. Moreover, tip vortices are considered to be responsible for delayed stall (Torres and Mueller 2001). Both of these effects may be vital for gliding animals, as they need to produce large lift forces to overcome their weight, particularly while in steep portions of the glide trajectory. The tip vortex may have strong interactions with a leading-edge vortex, if the latter indeed exists. Based on membrane deflection (but without visualizing the actual flow), Song et al. (2008) conjectured that a strong vortex was formed at the leading edge of the compliant membrane wings, which would likely become unstable at larger angles of attack. The resulting separated flow on the upper surface of the membrane would decrease the pressure difference between

the surfaces of the wing, and therefore the strength and core size of the tip vortex and its contribution to lift would diminish.

Despite the commonalities of the wings of gliders as flexible and having low aspect ratio, it would be misleading to generalize the aerodynamic properties of gliders across species. Aerodynamic properties are highly dependent on the specifics of shape, angle of attack, and Reynolds number, which vary substantially among gliders. Therefore, despite the relatively large literature on the kinematics of gliding animals, there is currently a gap in our knowledge regarding their aerodynamics, limiting our ability to understand the physical mechanisms that gliding animals use to generate lift, maintain stability, and maneuver.

Fig. 6. Landing maneuvers by a colugo (A; Sunda flying lemur, *Galeopterus variegatus*) and a flying lizard (B; Spotted Gliding Lizard, *Draco maculatus*), composited from high-speed video records. Duration between stills is 40 ms. In A, the colugo was gliding toward the camera and then angled upward to position itself vertically for landing. Time progresses from left to right. The tree is not directly visible but can be seen in shadow to the left. The last frame represents the time just prior to contact of the tree. This sequence occurred at the end of a natural glide in the wild. In B, the lizard pitches its head upward just prior to landing, apparently to avoid contact with the tree. The front feet contact the tree first; the posterior body then rotates downward; the rear feet follow with contact. This sequence, which started with the lizard jumping from a perch under its own volition, occurred at the end of a short trajectory (height, <3 m) and therefore likely represents the end of a nonequilibrium glide. More than one landing of this type was observed from this specimen, but no further analysis was conducted. Although it is unclear if such landings occur in the wild, this sequence demonstrates the capability of the lizard to re-orient during landing. Both sequences were recorded in Penang, Malaysia, by John Benam; courtesy and reproduced with permission of ©2014 National Geographic Creative. Figure appears in color on the Web.
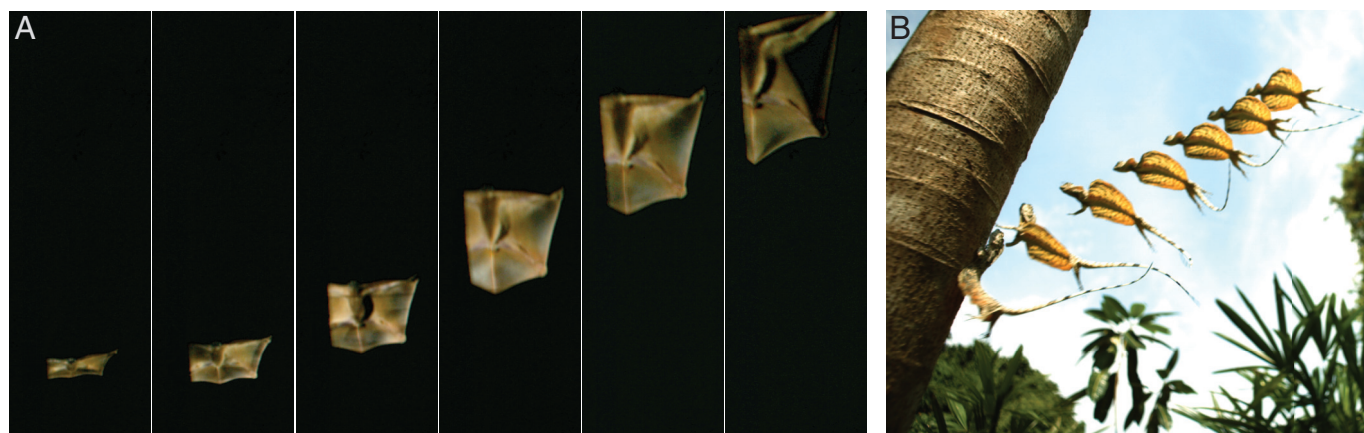
The influence of morphology and posture on terrestrial gliders

In this section, we discuss the morphological specializations that influence glide performance for the major groups of terrestrial gliders. To place these specializations in a phylogenetic context, we begin each discussion by documenting the broad diversity of gliders within each of these groups.

Mammals

Diversity

Gliding mammals are a diverse group containing at least 65 species from six phylogenetically distinct families (Jackson and Schouten 2012). In addition to these extant groups, at least three extinct groups of mammals once glided through ancient forests. Each of these groups is described from fossils, consisting of skeletal elements and evidence of soft tissues including the patagium. These fossils indicate two distinct groups of extinct gliding rodents, the Eomyidae (Storch et al. 1996) and the Gliridae (Mein and Romaggi 1991). The third is a Mesozoic mammal, *Volaticotherium antiquum* Meng, Hu, Wang, Wang and Li, 2006, dated to at least 125 million years ago (Meng et al. 2006, 2007), roughly contemporary to the early flying birds.

The six extant groups of gliding mammals include three distinct families of marsupials and three independent lineages of placental mammals. The gliding marsupials include the greater glider (*Petauroides volans* (Kerr, 1792)) (Pseudocheiridae), the tiny feathertail glider (*Acrobates pygmaeus* (Shaw, 1794)) (Acrobatidae), and six species of lesser gliding possums, including the well-known sugar glider (*Petaurus breviceps*) (Petauridae). Most species of gliding marsupials are native only to Australia, with only the sugar glider having a broader range, extending to New Guinea and the surrounding islands. Two other lesser gliding possum species are endemic to small regions of New Guinea (northern glider, *Petaurus abidi* Ziegler, 1981) or surrounding islands (Biak glider, *Petaurus biacensis* Ulmer, 1940) (Jackson and Schouten 2012). The gliding eutherian mammals include the two lineages of rodents, the scaly-tailed squirrels (Anomaluridae) and the flying squirrels (Sciuridae: Pteromyini), as well as colugos of the order Der-

moptera. Six species of anomalurids inhabit the forests of tropical Africa (Wilson and Reeder 1993). The flying squirrels are the most taxonomically and geographically diverse group of gliding mammals, with 48 species inhabiting forests throughout Asia, Europe, and North America (Jackson and Thorington 2012). Despite this coverage, the majority of species are restricted to south and southeast Asia. Similarly, the two described species of colugos are also native to southeast Asia and the Philippines.

Due to the great richness of species of gliding mammals and other vertebrates in southeast Asia, several authors have suggested hypotheses to explain the global pattern of diversity, most of which are based on differences in structure of tropical forests. Two prominent hypotheses suggest that lower density of lianas (Emmons and Gentry 1983) or greater canopy height (Dudley and DeVries 1990) lead to an increase in glider diversity. A positive correlation between increased canopy free space and the number of gliders has also been suggested (Dial et al. 2004). Free space in the canopy both reduces the number of substrates connecting adjacent trees and allows for longer glides without interruption, as gliders must climb high into the canopy to gain the potential energy to glide long distances. Furthermore, due to the biomechanical constraints of wing loading, larger animals must climb to greater heights to attain similar distance as smaller gliders. As a result, it might be expected that larger gliders would live higher in the canopy than smaller ones (Inger 1983; Ando and Shiraishi 1993) and a taller forest would allow for a greater number of species to be stratified by body size. This rationale might help to explain the great diversity of gliders in southeast Asia, but many other tall forests have few, if any, gliding vertebrates, suggesting a more complex relationship between habitat structure and gliding behavior. A recent phylogenetic analysis demonstrates the plausibility of a forest-structure explanation for the high diversity of gliders in southeast Asia (Heinicke et al. 2012), but overall, little attention has been paid to this interesting ecophysiological issue.

Morphology

Despite having the common selective pressure of gliding, mammalian gliders exhibit a great diversity of form, including a 100-fold variation in body size among species. The smallest gliders, including

Fig. 7. Force production in mammalian gliders. (A) Measured forces on a colugo (Sunda flying lemur, *Galeopterus variegatus*) using two dual-axis MEMS accelerometers attached to the body, recorded under natural conditions. The red (X), purple (Y), and blue (Z) traces represent components of the total force (black) along the craniocaudal, lateral, and dorsoventral axes, respectively. The arrows represent the colugo in position on the tree just prior to takeoff and landing; the gray bands represent the takeoff and landing durations. The broken line indicates the force production required to support body weight in air, showing that this colugo produced a force surplus at some points in the trajectory. (From Byrnes et al. 2008; reproduced with permission of Proc. R. Soc. B Biol. Sci., vol. 275, issue 1638, ©2008 The Royal Society.) (B) A model of force production in the northern flying squirrel (*Glaucomys sabrinus*). The black arrow represents one body weight and other forces are scaled accordingly. Drag and lift are shown in blue and red, respectively, and their vector sum (the net aerodyamic force) is shown in purple. The net force on the animal is shown in orange. This summary is based on lift and drag coefficients calculated using three-dimensional position data. If the squirrel was in equilibrium, the net force and resultant aerodynamic force would be equal in magnitude and direction, which is not shown here. (From Bahlman et al. 2013; reproduced with permission of J. R. Soc. Interface, vol. 10, issue 80, ©2013 The Royal Society.)
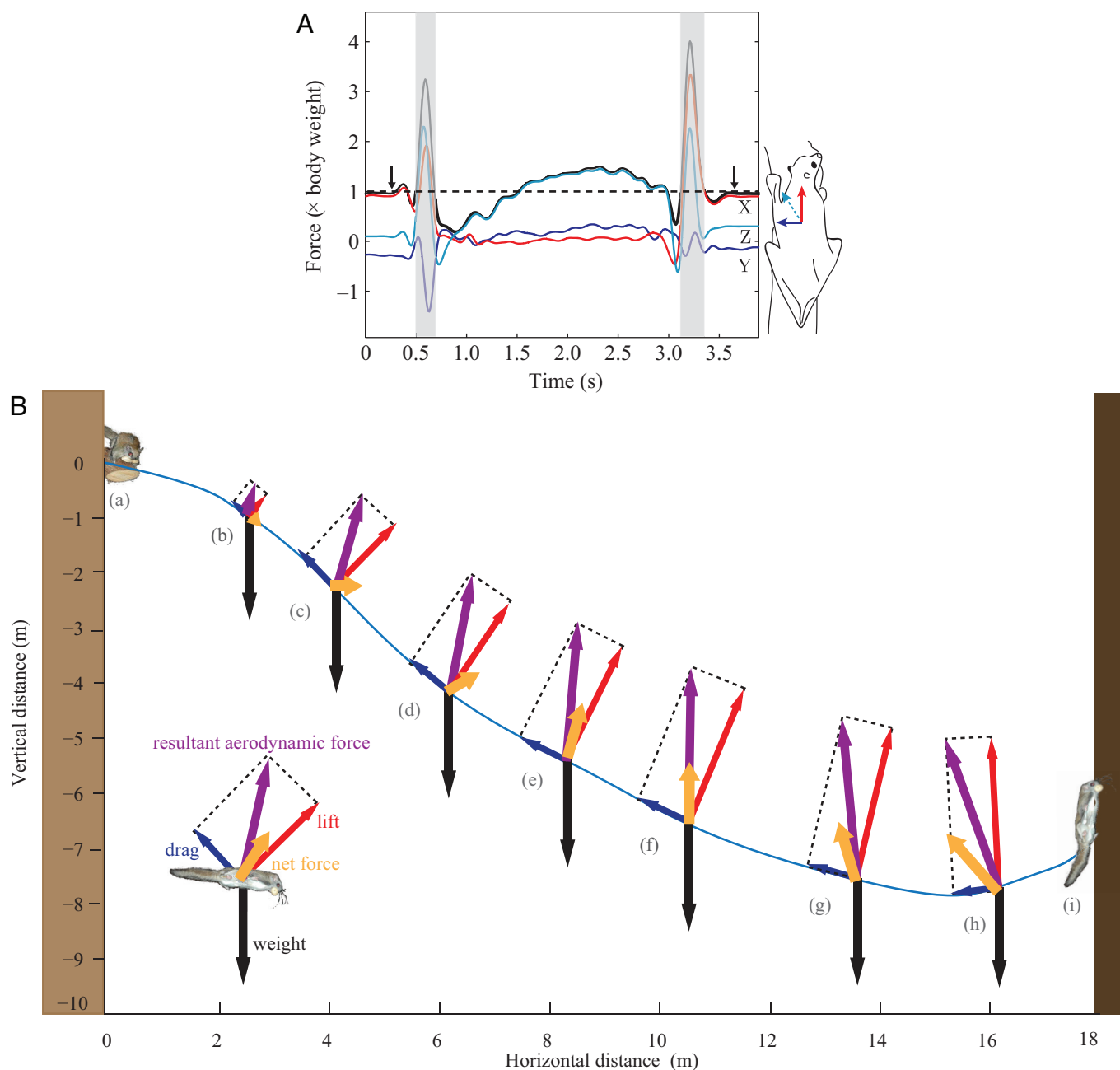

the marsupial feathertail glider and the pygmy flying squirrels, have masses of roughly 10 g, whereas the greater glider, colugos, and giant flying squirrels have body masses often exceeding 1.5 kg. The shape of the tail seems to vary with body size rather than with phylogenetic relatedness. Small gliders have relatively short, flattened, or dis- tichous (laterally bristled) tails, whereas gliders larger than roughly 500 g have extremely long and cylindrical tails (Thorington et al. 2002). These longer tails, which can reach lengths as great as 1.5 body lengths, have been hypothesized to serve for counter-balancing pur- poses (Dudley et al. 2007) or for maneuvering (Hayssen 2008).

Fig. 8. Examples of dynamic movements by gliders. For A and B, time progresses from left to right. (A) Side view of two species of flying snake (Paradise Tree Snake (*Chrysopelea paradisi*), top; Golden Tree Snake (*Chrysopelea ornata*), bottom) showing changes in relative positioning of the body during aerial undulation. The start of the tail is indicated for reference in the last panels. Segments of the body of *C. paradisi* appear to be more closely aligned in the vertical axis than seen in *C. ornata*, which shows more vertical staggering. Duration between frames is 1 s. Data from J. Socha; recorded with a high-speed video camera by John Benam, courtesy and reproduced with permission of ©2014 National Geographic Creative. (B) Top rear view of a southern flying squirrel (*Glaucomys volans*) approaching a landing, showing a prominent side-to-side oscillation of the tail. The tail is marked with three white points for tracking; duration between frames is 12 ms. Data from G. Byrnes, recorded with a high-speed video camera. (C) Takeoff of an unidentified flying fish showing the fish becoming airborne. The zig-zag wake behind the fish is a track that reflects the lateral oscillation of the tail used to gain speed. Photo courtesy and reproduced with permission of Geoffrey Jones. Figure appears in color on the Web.
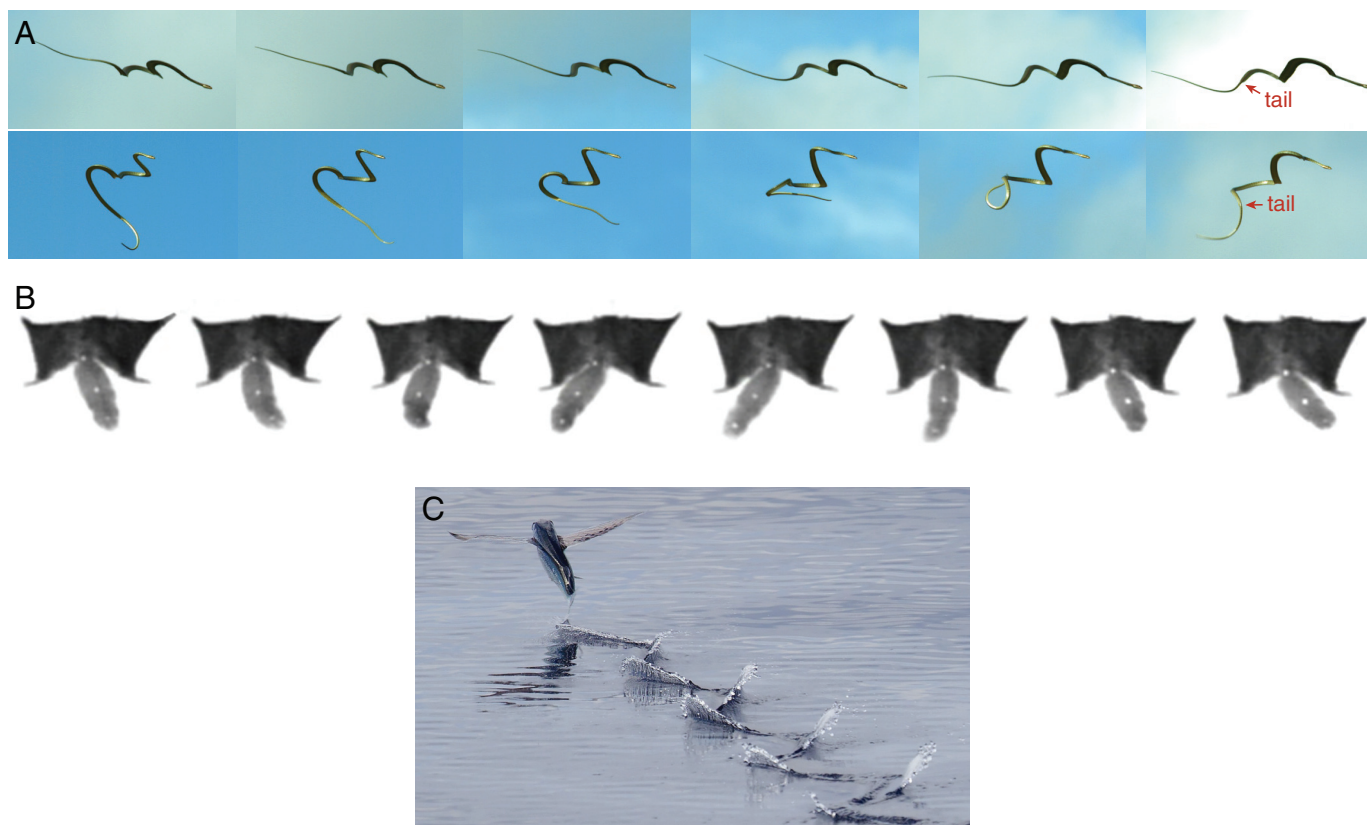
In addition to morphological differences related to body size, several differences in patagial form result from each lineage having independently acquired their gliding morphology. The patagium is formed of three major regions: (1) the plagiopatagium, which extends between the forelimbs and the hind limbs, (2) the propatagium, extending anterior to the forelimbs, and (3) the uropatagium, which extends posteriorly from the hind limbs and encompasses the tail to varying degrees in different groups. All gliding mammals have a well-developed plagiopatagium, but the presence and extent of the propatagium and uropatagium are variable by lineage (Johnson-Murray 1977, 1987; Thorington et al. 2002). For example, one clade of large flying squirrels have patagia that extend farther back along the tail than do smaller flying squirrels (Thorington et al. 2002).

The structures supporting the gliding membrane also vary between groups. At one extreme, the plagiopatagium of the feather-tail glider extends only between the elbow and knee, with a negligible propatagium or uropatagium. At the other extreme, the colugo has the most extensive gliding surface of all the gliding taxa, with a large propatagium, a uropatagium that completely subtends the length of the tail, and fingers that are webbed, adding additional membrane area. Some gliders have evolved cartilaginous struts either at the wrist (styliform cartilage: Pteromyini; Thorington et al. 1998) or the elbow (olecranon cartilage: Anomaluridae, Pseudocheiridae; Johnson-Murray 1987). These protrusions

increase the area of the gliding membrane, which may increase force production and (or) change the wing shape for improved aerodynamics (Thorington et al. 1998; Bishop and Brim-DeForest 2008).

The patagial membrane includes muscular sheets associated with the neck, limbs, and tail (Peterka 1936; Gupta 1966; Johnson-Murray 1977, 1987; Endo et al. 1998). Similarly, rope-like muscles extend along the edges of the patagium in many gliding mammals. These include the musculus platysma II or the musculus sphincter colli profundus in the propatagium, the musculus tibiocarpalis in the plagiopatagium, and the musculus semitendinosus in the uropatagium (Johnson-Murray 1977, 1987; Thorington et al. 2002). This high level of muscular differentiation in the gliding membrane likely allows precise control over the gliding membrane during flight and is also used to hold the membranes against the body during quadrupedal locomotion.

These muscles allow the animal to control both the camber and the compliance of the wing membrane, and by doing so, to dynamically alter the aerodynamic properties of the patagium in flight. Much recent work has focused on the aeroelastic properties of flexible wings and their roles in aerodynamic performance (e.g., Shyy et al. 1999; Carruthers et al. 2007; Song et al. 2008; Mountcastle and Daniel 2009). For example, flexible wings have been shown to delay stall to higher angles of attack compared with rigid airfoils (Song et al. 2008; Rojratsirikul et al. 2010). In

addition, flexible wings show improved lift-to-drag ratios in both fixed and flapping wings (Song et al. 2008; Mountcastle and Daniel 2009; Zhao et al. 2011) or increased lift forces alone (Curet et al. 2013). It is thought that the improved aerodynamics result from modulation of the leading-edge vortex on the wing (Mountcastle and Daniel 2009; Rojratsirikul et al. 2010; Zhao et al. 2011; Curet et al. 2013), in part by altering the camber of the wing during flight, but leading-edge vortices are not known for any glider.

In addition to control by instrinsic muscles of the patagium, it is possible that changes in camber are the passive result of aeroelastic behavior of the flexible wing, similar to that in insects or some man-made flyers (Shyy et al. 1999; Combes and Daniel 2003; Mountcastle and Daniel 2009; Zhao et al. 2011). Unfortunately, work on the muscle activity of the patagial muscles during gliding is lacking. Gliding mammals could also control the camber of the wing by movement of the limbs, tail, or neck, which would alter the orientation of the propatagium and (or) uropatagium with respect to the plagiopatagium, as in bats (Gardiner et al. 2011). Despite the importance of wing camber for aerodynamic force production and flight control, relatively little work has been done to quantify the changes in camber during flight in gliding mammals (Nachtigall 1979; Bishop 2006, 2007). For both flying squirrels and sugar gliders, experimental studies of kinematics have shown that camber is variable during flight, influencing both the magnitude and the direction of aerodynamic forces on the body (Bishop 2006, 2007). These studies provide evidence that flying squirrels use both limb movements and active muscle contraction to control camber.

Limb position not only has an effect on camber, but can also be used to alter the shape and the position of the patagium with respect to the oncoming flow and the center of mass of the animal. For example, lowering or raising the limbs with respect to the body alters the dihedral or anhedral angle and thereby affects roll stability. Such postural adjustments allow for a stable configuration in straight glides, but a more unstable and thus maneuverable configuration to produce turns (Bishop and Brim-DeForest 2008). Altering limb position can also be used to change the angle of attack of the wing (Bishop 2006, 2007). By abducting or adducting the forelimbs, the center of pressure of the wing can be shifted anteriorly or posteriorly with respect to the center of mass of the animal as a means of controlling pitch angle during flight (Bishop 2006, 2007) or landing (G. Byrnes, unpublished data). In addition, any left–right asymmetries in the position of the limbs can result in turning moments about the roll or yaw axes that can be useful for flight maneuvers (Bishop and Brim-DeForest 2008). Anecdotally, gliding mammals are capable of complex maneuvers and tight turns (e.g., Dolan and Carter 1977; Ando and Shiraishi 1993; Jackson 2000), important for maneuvering flight in complex three-dimensional habitats, but only Bishop and Brim-Deforest (2008) have addressed the role of limb positions in turning behavior, with sequences recorded over a relatively short duration. However, from studies of other taxa, including gliding frogs, it is clear that limb position plays an important role in maneuvering flight and stability (McCay 2001). Recent work has shown the importance of wing morphing on the aerodynamic forces acting on the wings of birds (Lentink et al. 2007) and micro-air vehicles (e.g., Grant et al. 2010). Although it is unlikely that wing shape would be altered to such extremes by changes in limb position in gliding mammals, small changes in shape could have similar consequences on forces in both steady and maneuvering flights.

Gliding mammals exhibit a wide range of tail morphology including flattened tails in small flying squirrels, long and rounded tails with associated enlarged uropatagium in large flying squirrels, and tails completely enclosed in the uropatagium in colugos. The position and movement of these tails (e.g., Fig. 8B) likely have important consequences for aerodynamic control during glides. The inertia of moving tails has been shown to affect rotational accelerations both in the righting reflex of falling animals (Jusufi

et al. 2008, 2010) and in terrestrial animals climbing over obstacles (Libby et al. 2012), and may play a similar role during gliding. In addition, tails associated with an enlarged uropatagium could have aerodynamic and inertial effects. Movement of these tails could be used for control, because the tail's tensing effect on the patagium can affect the camber and angle of attack of the wing and thereby alter its aerodynamic characteristics. In bats, which have a uropatagium enclosing the tail, tail movement has been implicated in pitch control (Gardiner et al. 2011). Membrane wings have been shown to exhibit some aeroelastic instability (Song et al. 2008; Rojratsirikul et al. 2010; Curet et al. 2013), much like the fluttering of a flag associated with the shedding of bound vortices. Interestingly, this instability is associated with an increase in lift, which could have implications for the evolution of powered flight (Curet et al. 2013).

Reptiles and amphibians

Diversity

Numerous frog, lizard, and snake species exhibit some degree of gliding ability. Dudley et al. (2007) provide a detailed taxonomic account of frogs that are known or probable gliders, based on field and experimental data and observations of specific morphologies, and McGuire and Dudley (2011) provide a similar overview for lizards. A common characteristic of frog and lizard taxa is the presence of a few groups that are highly specialized for gliding, some groups with intermediate characteristics, and many taxa that are morphologically unspecialized but are able to glide under control at steep angles using posture alone. The wide range of unspecialized taxa that glide has led Dudley and colleagues to suggest that many other species with aerial capabilities are yet to be identified (Dudley et al. 2007; Dudley and Yanoviak 2011), particularly among arboreal lizards (McGuire and Dudley 2011). Snakes are less diverse than frogs and lizards and appear to include only one evolutionary origin of gliding (Socha 2011), although arboreal snakes in the New World have not been evaluated for gliding ability.

Gliding in frogs is most prominent in two unrelated families: the Old World Rhacophoridae and the New World Hylidae. Within Rhacophoridae, gliding is concentrated in the genera *Rhacophorus* Kuhl and van Hasselt, 1822 and *Polypedates* Tschudi, 1838 (Emerson and Koehl 1990; Emerson 1991; Dudley et al. 2007). *Rhacophorus* includes over 80 species that range from Africa to eastern Asia, with the highest diversity in southeast Asia. *Polypedates* is restricted to Asia and includes more than 20 species. Of the numerous hylid genera, the recently revised genus *Ecnomiohyla* Faivovich, Haddad, Garcia, Frost, Campbell and Wheeler, 2005 (Faivovich et al. 2005) may contain the greatest number of gliders (e.g., Mendelson et al. 2008). An additional family, Leptodactylidae, contains one species with aerial abilities; the Puerto Rican Coqui (*Eleutherodactylus coqui* Thomas, 1966) is a frog that is restricted to Puerto Rico and is capable of gliding at steep angles (>70°, estimated from experimental data from Stewart 1985) when it transits from trees at dawn. The lack of clarity on which species glide is likely a product of the frogs' arboreal habitats combined with the propensity for frogs to glide in hours of dim light or at night, making it difficult for researchers to recognize aerial behaviors in the wild.

Among lizards, the most specialized and best studied are the agamid lizards of the genus *Draco*, which comprises at least 45 species found in southeast Asia and southwest India (McGuire and Dudley 2011). All *Draco* glide, with flight being an integral aspect of their ecology. The family Gekkonidae contains the second largest diversity of gliding lizards, with representatives from *Ptychozoon* Kuhl and van Hasselt, 1822, *Hemidactylus* Gray, 1825 (formerly *Cosymbotus* Fitzinger, 1843), and *Luperosaurus* Gray, 1845, all of which are found primarily in southeast Asia (Brown et al. 2012a, 2012b; Heinicke et al. 2012). The seven species of *Ptychozoon* are the most specialized

gliding geckos. *Hemidactylus* contains almost 100 species, but only 2 species are confirmed gliders (Russell 1979; Honda et al. 1997; Jusufi et al. 2008, 2010). *Luperosaurus* includes at least 10 species, but its gliding is enigmatic, known only from anecdotal field observations (Dudley et al. 2007; J.A. McGuire, unpublished data). In the family Lacertidae, two species of the genus *Holaspis* Gray, 1863 are proficient gliders, with glide performance comparable with that of *Ptychozoon* (Schiøtz and Volsøe 1959; Vanhooydonck et al. 2009), and a range from western to southeast Africa. An additional number of species are capable of aerial behavior but are not gliding specialists, including members of the Asian genera *Calotes* Cuvier, 1817 and *Bronchocela* Kaup, 1827 and a few species of New World genus *Anolis* Daudin, 1802 (see McGuire and Dudley 2011 and references therein). Gliding has also been experimentally observed in the agamid *Leiolepis belliana* (Hardwicke and Gray, 1827) (Butterfly Lizard) (Losos et al. 1989), but this southeast Asian species is not arboreal and presumably does not glide in the wild.

Gliding in snakes appears to be restricted to one genus, *Chrysopelea* Boie, 1826, a colubrid taxa found in south and southeast Asia. Three of five species of *Chrysopelea* are confirmed gliders (Socha 2011), and based on phylogeny, it is likely that the other two species possess at least some components of the *Chrysopelea* gliding system. The sister taxon to *Chrysopelea* are the bronzebacks of the genus *Dendrelaphis* Boulenger, 1890, also an Asian group of arboreal snakes. One species of *Dendrelaphis* has the ability to jump from a perch using a behavioral sequence that appears to be similar to that in *Chrysopelea* (Socha 2011), but jumping in *Dendrelaphis* has not been studied in detail, and it is unclear to what degree its kinematics and motor control are shared with *Chrysopelea*. It is also unknown if *Dendrelaphis* can attain significant horizontal distance beyond the momentum provided from its jump, but gliding ability is unlikely because it does not appear to morph its body when becoming airborne, as does *Chrysopelea*.

Morphology

Frogs display a limited suite of morphological adaptations for gliding, including enlarged feet and webbing between the toes, small skin flaps on the legs, and a relatively small waist. The effect of these features on glide performance interacts with posture in a complex fashion (Emerson and Koehl 1990; Emerson et al. 1990). Larger feet and greater webbing reduce glide speed and enhance lift-to-drag ratios (Emerson and Koehl 1990), but degree of webbing is not a reliable indicator of which taxa are proficient gliders. The Misfit Leaf Frog (*Agalychnis saltator*), for instance, appears to be capable of glide angles ~45° and uses gliding regularly for transit to breeding sites, but it possesses the least webbing (less than half of the foot) of any species within its genus (Roberts 1994). A recent survey within *Rhacophorus* shows that only a small number of species exhibit extensive webbing of the feet (4 of 24 species; Rowley et al. 2010), but it is unclear if this excludes gliding within these taxa.

All gliding frogs take on a bent-leg posture (Emerson and Koehl 1990; McCay 2001; Wang et al. 2014), which places the force-producing feet at an intermediate position away from the center of mass of the body. Each foot produces a net aerodynamic force with a moment arm away from the center of mass, which can be used for control of rotation about the yaw, roll, and pitch axes. Emerson and Koehl (1990) used models in a wind tunnel to show that posture can exert as large an effect on glide performance as morphology and the body itself is integral to glide performance. This study also concluded that maneuverability, rather than horizontal distance, may be the most ecologically relevant metric of performance for gliding by frogs.

McCay (2001) investigated the basis of this maneuverability in one species of frog, *Rhacophorus dennysi* Blanford, 1881 (Chinese Flying Frog; previously known as *Polypedates dennysi*), using live animals in a wind tunnel followed with physical model testing. Measurements of torque on the models showed that the airborne frog is statically stable about the pitch and roll axes, but is unstable about the yaw axis. However, the small magnitude of stability coefficients about these axes (<0.2/rad) indicates that the frog operates in a range where movements of the limbs and feet can easily produce rotations for control and maneuvering. This species can take advantage of these stability characteristics to produce two forms of turning: a familiar banked turn induced by roll rotation (likely shared by all gliding frogs; Emerson and Koehl 1990) and a unique "crabbed" turn induced by yaw rotation. The crabbed turn is produced when the frog holds one rear foot higher than the other, thereby inducing a force to the side, with turns directed in the opposite direction of the higher foot. The specific aerodynamics that produce the force asymmetries necessary for turning are not known, but it is clear that such control is relevant for staying on course and for maneuvering, as well as for dealing with perturbations such as wind gusts. Measured wind speeds in a forest inhabited by three species of flying frog were lower at night than during the day, but these gusts are capable of causing perturbations that affect glide paths or require control corrections (McCay 2003).

Draco lizards actively deploy two aerodynamic force-producing structures in flight: rib-supported patagial "wings", which likely provide the main source of lift, and small lappets on the sides of the head, which have been hypothesized to function as canards, providing pitch control (Stein et al. 2008; McGuire and Dudley 2011). It is also likely that the legs contribute to lift production (McGuire 2003; McGuire and Dudley 2011). The wings are additionally used as display structures in nonflight-related behaviors, but are otherwise folded back longitudinally along the body.

The wing of *Draco* is biomechanically unique among animals (McGuire and Dudley 2011), with a number of specializations that contribute to its role as a force-producing structure (Colbert 1967; John 1970; Russell and Dijkstra 2001). The major passive mechanical components that form the wing include 5–7 elongated ribs, ligaments, bands of collagen, integument, and raised scale rows. The main muscles that erect the wing are the iliocostalis and the intercostals, which primarily act on the first two ribs. The iliocostalis is long, originating in the neck, and when activated it rotates the first rib anteriorly; the second rib is close to the first rib and interconnected by muscle. As the first two ribs rotate, multiple ligaments that connect the remaining ribs pull taut, inducing rib rotation throughout the wing. The bands of elastin and collagen are also put in tension, tensing the membrane. The collagenous bands exhibit pre-tension, which apparently provides a continuous and unbuckled edge at any point during unfurling. Most of the ribs are connected distally to these bands via a costal cartilage intermediate; the tensing of the bands thereby induces posterior bending in the ends of some ribs, contributing to wing shape. Overall, this process of unfurling creates a wing that could be described as a curved flat plate, with camber produced by anterior–posterior curvature and potentially some mediolateral curvature. Colbert (1967) hypothesized that active flight control could be effected through muscle contraction that changes the wing curvature, suggesting that a dynamic analysis of aerial wing shape would be informative. Upon landing, the muscles apparently relax and the wings fold passively by elastic recoil.

Scales on the wing of *Draco* add textural features to its surface, but their functional effects are unknown. These features include a raised rim along the lateral edge of the wing and raised lines of scales on both the dorsal and ventral surfaces. Such surface roughnesses must have an influence on the formation of the boundary layer of the wing (Vogel 1994), potentially affecting its aerodynamics. Interestingly, mechanoreceptors can be found within the scale rows of the ventral surface. These receptors play an unknown role in flight, but they may serve to sense air pressure for flight control, akin to the function of sensory hairs recently found on bat wings (Sterbing-D'Angelo et al. 2011).

Multiple *Draco*-like reptiles have been found in the fossil record, demonstrating convergent evolution of bone-supported patagial wings. In general, their wings were relatively larger than those in *Draco*, but a scaling analysis indicates greater wing loadings and likely poorer glide performance for these extinct taxa (McGuire and Dudley 2011). One species (*Icarosaurus siefkeri* Colbert, 1966) possessed relatively large wings and small body size, and has been suggested to be the premiere terrestrial vertebrate glider among all extinct or extant groups (McGuire and Dudley 2011). Aerodynamic models are useful for understanding how these fossil taxa might have glided in the past (e.g., Stein et al. 2008), but leg and tail posture, as well as wing camber, can be difficult to infer and may greatly affect interpretation of performance (e.g., Chatterjee and Templin 2007; Alexander et al. 2010; Koehl et al. 2011; Evangelista et al. 2014).

At least two other species have been thought to use their ribs to increase surface area during gliding. Rather than forming wings, the ribs rotate to flatten the body, a mechanism used for basking (Arnold 2002) or wedging into small crevices (Revell et al. 2007). Experimental tests show that airborne Butterfly Lizard (*Leiolepis belliana*) increase surface area by 9% via dorsoventral flattening, resulting in a small (5%) change in descent speed (Losos et al. 1989). But this slight effect, in combination with the lack of ecological relevance of flight for this beach dweller, lead Losos et al. (1989) to conclude that flattening is not an adaptation for gliding and that *L. belliani* does not employ gliding in the wild. In contrast, the Sawtail Lizard (*Holaspis guentheri* Gray, 1863) is capable of flattening, but flattening appears to play little role in its glide performance. Instead, *H. guentheri* takes advantage of low wing loadings via reduced skeletal density to produce their steep descent trajectories (Vanhooydonck et al. 2009). Its lack of body morphing for flight is perhaps surprising given its elongated ribs and ability to flatten dorsoventrally to a substantial degree (described "as flat and round as a coin"; Arnold 2002).

Among geckos, the gliders of the genera *Ptychozoon*, *Hemidactylus*, and *Luperosaurus* exhibit cutaneous flaps on the body and tail and webbing between the toes (Honda et al. 1997; Heinicke et al. 2012). Postural adjustments of the limbs and tail are the primary mechanisms of flight control (Young et al. 2002; Jusufi et al. 2008, 2010, 2011), suggesting that the increased surface area resulting from webbing is used for more than just weight support per se. The cutaneous flaps are not muscularized (Russell 1979; Russell et al. 2001) and so their aerodynamic effects result from their passive morphological characteristics. *Ptychozoon* geckos exhibit the greatest degree of aerodynamically relevant excess integument. The two large cutaneous flaps on the lateral body between the front and rear legs are normally curled against the body wall and are unfurled passively by the air. In the feet, the interdigital webbing appears to be actively deployed by spreading of the toes (Young et al. 2002). Experimental manipulation of the large lateral flaps and the limbs or feet has shown that both are critical for aspects of glide performance (Marcellini and Keefer 1976; Young et al. 2002); for example, specimens of Kuhl's Flying Gecko (*Ptychozoon kuhli* Stejneger, 1902) were unable to maneuver when their feet were bound together. New aerodynamic studies are needed to determine the mechanistic effects of features of morphology and posture, as well as their interaction. Some caution is warranted for using specimens of *P. kuhli* from the pet trade to infer ecologically relevant metrics of glide performance. A recent study has found that these specimens are genetically and morphologically distinct from their conspecifics in the wild, which exhibit less exaggerated cutaneous flaps and webbing (Brown et al. 2012*b*).

The gliding system of snakes is composed of a specialized body shape and aerial undulation. The shape change is a dorsoventral flattening of the body from head to vent that occurs during take-off, with flattening effected via an anterodorsal rotation of the ribs (Socha 2011). The mechanism of flattening has been hypothesized by Socha (2011) to involve the same suite of muscles as used

for hooding in cobras (Young and Kardong 2010), but an anatomical study is needed. In the snake *Chrysopelea paradisi*, the aerial cross section at mid-body can be considered to be a rounded triangle, with two ventrally projecting lips at the lateral edges. Recent physical and computational modeling has shown that the snake's unusual cross-sectional shape is a surprisingly good airfoil in the Reynolds number regime of the gliding snake (Holden et al. 2014; Krishnan et al. 2014). Within angles of attack of 25° to 60°, lift coefficients range roughly between 1.0 and 1.5, reaching a peak of 1.9 at $\alpha = 35°$. Lift-to-drag ratios are positive from 10° to at least 60°, which helps to explain how gliding forces begin to be produced as the snake progresses from the ballistic dive into the shallowing glide (Fig. 5D). However, the exact orientation of the snake relative to the glide path is not known, so it is unclear if the snake makes postural adjustments to optimize force production throughout the glide.

The snake's aerial undulation has at least two major effects that could influence glide performance. First, undulation continuously repositions portions of the body relative to one another, which alters the patterns of airflow over the body. Preliminary data from a simple two-airfoil model show that there may be certain configurations that enhance force production for the snake (Miklasz et al. 2010), but a more anatomically-accurate approach is needed to address this issue. Furthermore, the dynamic movement of the snake itself may influence its aerodynamics. Differences in kinematics of undulation including relative body positioning (Fig. 8A) may help to explain observed differences in performance between species (Socha and LaBarbera 2005). Second, aerial undulation must shift the centers of mass and pressure (the location of the net aerodynamic force), creating a continuously changing force couple that will tend to rotate the snake. Theoretical modeling of the dynamics of undulation with the snake considered to be a three-bar or two-bar system suggest that the snake likely requires active control for stable gliding (Jafari et al. 2014). Further work that incorporates the full three-dimensional shape of the snake and its movements are needed to better understand how the snake produces forward gliding and maneuvering.

Terrestrial invertebrates

Despite a rich theoretical literature predicting that some wingless terrestrial invertebrates should be capable of gliding (e.g., Flower 1964; Ellington 1991; Kingsolver and Koehl 1985; Hasenfuss 2002), gliding in an extant terrestrial invertebrate has only recently been observed. Following the discovery of gliding in wingless workers of the neotropical arboreal ant *Cephalotes atratus* (Yanoviak et al. 2005), further work has focused on exploring the diversity of insect gliders, as well as attempting to understand the mechanisms that these gliders use to control their aerial behavior in the absence of any obvious morphological adaptations for aerodynamic performance.

Diversity

Since the recent discovery of gliding in ants, gliding behaviors have been found in at least eight extant hexapod orders, including Hymenoptera, Homoptera, Hemiptera, various polyneopteran orders, and the ancestrally wingless order Archaeognatha (Dudley and Yanoviak 2011). The distinguishing feature of these disparate taxa is that gliding insects share no common glide-specific morphologies; instead, behavioral postures represent the main adaptations for gliding (Figs. 9A–9C). The range of postures used during gliding varies substantially across taxa, and it appears unlikely that these gliders derive from a single gliding common ancestor. Within ants, most myrmicine (including the genus *Cephalotes* Latreille, 1802) and pseudomyrmecine ants counter-intuitively glide backwards, with the abdomen and hind legs leading. But formicine ants (currently, only certain species within the genus *Camponotus* Mayr, 1861) and the Old World myrmicine genus *Nesomyrmex* Wheeler, 1910 glide head first, indicating that gliding may have

Fig. 9. Gliding postures adopted by three representative gliding arthropods. The left and right images depict front and side views, respectively. (A) *Cephalotes atratus*, a backward-gliding myrmicine ant. (B) *Camponotus sericeiventris* (Guérin-Méneville, 1838), a forward-gliding formicine ant. (C) Meinertellid bristletail, an ancestrally wingless gliding insect. Sketches were produced from video sequences of insects gliding in a vertical wind tunnel (data from Y. Munk).

A

B

C
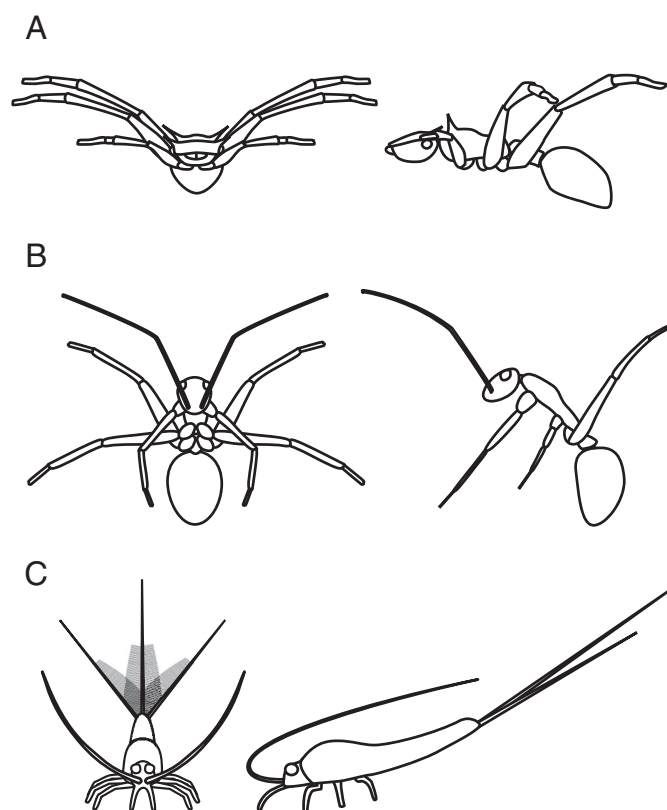
evolved independently within ants at least eight separate times (Flower 1964; Kingsolver and Koehl 1985; Ellington 1991; Hasenfuss 2002).

Gliding in bristletails (Archaeognatha) is especially interesting because this order is ancestrally wingless, which suggests that the use of controlled aerial behaviors for gliding may pre-date the origin of wings in insects. While all other known hexapod gliders are wingless juveniles that have winged adult forms, or secondarily wingless adults that derive from a winged ancestor, arboreal jumping bristletails belong to a lineage that has never evolved the capability for powered flight (Yanoviak et al. 2009). This line of evidence lends support to the hypothesis that gliding was an intermediate step in the evolution of wings and flapping flight in insects (Dudley and Yanoviak 2011).

Ecological context

As with terrestrial vertebrate gliders, all known invertebrates that glide occupy an arboreal ecological niche. However, there are several key distinctions between the two groups in terms of how gliding behavior integrates into their broader natural history.

All gliding invertebrates are sufficiently small that the damage suffered from an impact following a fall is nonlethal and essentially negligible. There are many species of arthropod that forage in both canopy and within the leaf litter of the tropical forest environment, but do not perform any kind of horizontally-directed descent when dropped from the canopy (Yanoviak et al. 2011). Many of these species stabilize their descent quite ably (Yanoviak et al. 2011), and as with gliders, these nongliders are unharmed upon impact

with the forest floor. Furthermore, their morphology is sufficiently similar to some gliding species to suggest that these nongliding species should be capable of gliding and yet do not (see Hasenfuss 2002). What factors, then, drive selection for gliding in arboreal invertebrates? Current evidence suggests that, at least in ants, gliding behavior is only found in species that forage almost exclusively in canopy environments, rarely visiting the forest floor. When one of these canopy ants is removed from the canopy environment and placed on the forest floor, it will stereotypically start to climb nearby woody plant stems in an apparent attempt to reach the canopy. However, in neotropical forest environments, only 10% of stems found close to the forest floor (<0.5 m) are connected to the canopy, in contrast to 85% of stems found at an elevation of >2 m (Yanoviak et al. 2011). Thus, if a canopy arthropod is able to land on a stem before hitting the forest floor, its return to the canopy is substantially more likely. However, there is more to consider than efficiency: while the damage incurred from impact may be negligible for arthropods that fall from the canopy, the forest floor presents additional secondary risks to displaced canopy taxa. The ant *Cephalotes atratus* is widespread in regions of the Neotropical rainforest subject to seasonal flooding, and ants that fall into the water are unable to swim and are quickly attacked by fish and consumed in less than a minute (Yanoviak et al. 2011). Ants that fall onto dry forest floor suffer lower mortality rates than those that fall into water, but are still exposed to attack from resident arthropod species that may respond aggressively to the fallen intruder. In an experimental study of *C. atratus*, ants released on the forest floor suffered attacks from other ants, beetles, and spiders as they attempted to climb stems and regain the canopy (Yanoviak et al. 2011). Thus, it is likely that the selective pressures that maintain gliding performance in arboreal invertebrate taxa are related to the indirect consequences of a fall to the forest floor, as opposed to the direct consequences of impact following a fall.

In contrast to vertebrate gliders, there are no known examples of canopy arthropods using gliding behavior to intentionally move between physically disconnected canopy environments. Gliding ants do not glide from one tree to the next, but rather target the closest highly reflectant columnar object in their field of view (Yanoviak and Dudley 2006). This supports the role of gliding as a recovery mechanism following a jumping escape response or following accidental dislodgement from the canopy due to, for example, wind gusts. Furthermore, gliding invertebrate taxa are not disproportionately represented within the tall, sparsely connected southeast Asian rainforests, as are gliding vertebrates (Emmons and Gentry 1983; Dudley and DeVries 1990; Dial et al. 2004), and are widespread in the cluttered Neotropical rainforests, where fewer gliding vertebrates are found. This distribution is consistent with the ecological context within which gliding is employed by canopy arthropods. Whereas forest "clutter" is an impediment for vertebrate gliders attempting to translate large distances between trees, for canopy arthropods merely trying to avoid falling to the forest floor, that same clutter becomes an abundance of potential glide targets that are likely connected to the canopy.

Morphology

To date, the use of morphology and posture in gliding by canopy arthropods has been most closely studied in the neotropical canopy ant *Cephalotes atratus* (Yanoviak et al. 2010) and various jumping bristletails (Yanoviak et al. 2009). Ablation experiments conducted using *C. atratus* ants showed that gliding performance, as measured by successfully landing upon a target column, is remarkably robust to the loss of large morphological structures such as legs and abdomen (Yanoviak et al. 2010). In all ablation cases, the glide ratio was negatively impacted, leading to trajectories that were up to twice as steep as those observed in nonablated individuals (Yanoviak et al. 2010). However, even with these steeper trajectories, ablated ants often successfully landed upon a target. Removal

of the gaster (the bulbous terminal abdominal segments, comprising 25% of the total animal mass) did not significantly change the rate of landing success, which for nonablated individuals was typically >90%. The hind limbs seem to matter most for gliding *Cephalotes*, as the removal of both hind legs reduced the success rate for individuals to below 50%. Although the mass of *C. atratus* hind legs are less than 6% of the total body mass, they are quite long: on average, hind-leg length in *C. atratus* is >90% of the total body length from head to the end of the abdomen (Yanoviak et al. 2010). These long cylinders likely produce substantial drag whose direction and magnitude can be modulated by re-orienting the limbs, a mechanism of control made possible because drag can vary substantially with orientation at low Reynolds numbers (Vogel 1994). The first tarsal segments of the legs are dorsoventrally flattened (Yanoviak et al. 2005) and may also serve an aerodynamic function; their position far from the trunk of the body means that they could produce relatively large stabilizing moments, aiding aerial control.

Although long legs are common in gliding invertebrates, a notable exception is the jumping bristletails, which have comparatively short legs and a long abdomen with three trailing caudal filaments (Fig. 9C). These caudal filaments contribute little to the total mass of the animal, but account for a significant fraction of its surface area. The role of the caudal filaments in gliding was investigated by ablating some or all of the filaments and comparing glide performance in ablated vs. nonablated individuals. Gliding success rates dropped from 90% in nonablated animals to below 50% with the caudal filaments removed (Yanoviak et al. 2009), roughly paralleling the reduction in performance observed by removing the hind legs in *C. atratus*. Thus, the long filaments of bristletails may serve similar functional roles as the hind legs do for *Cephalotes* ants.

Posture, stability, and control

Following a fall, many animals will perform an aerial righting response in which the animal rotates its ventral side downwards. The maneuver associated with the response is an active inertial twisting in large animals (e.g., geckos, cats) and a passive aerodynamic effect in smaller animals like stick insects and aphids (Jusufi et al. 2011; Ribak et al. 2013). For these smaller animals, dorsoventral righting could be achieved by shifting the center of aerodynamic pressure dorsally with respect to the center of mass. To achieve this, an animal may dorsally elevate its appendages, which have high surface area to mass ratio, while keeping its body parts with relatively higher mass and lower surface area oriented ventrally. In the ant *Cephalotes atratus*, the stereotypical gliding posture is one in which the legs are held elevated above the body axis, with the gaster held slightly flexed underneath the body (Yanoviak et al. 2011; Fig. 9A). However, successfully executing a dorsoventral righting response does not guarantee that an animal will be able to glide. Postures used by *C. atratus* and pea aphids (Ribak et al. 2013) are superficially similar, but pea aphids do not perform any directed horizontal motion over the course of their descent. To glide, the animal must be able to achieve a stable falling posture where the net aerodynamic force acting on the falling body has some horizontal component in addition to the vertical component aligned with gravity (Flower 1964; Ellington 1991), and must be able to exert some degree of control over this horizontal component to effectively steer towards targets. In *C. atratus*, high-speed video analysis has shown that these ants appear to use asymmetric motions of their hind legs to effect turns, suggesting that the dorsal elevation of the legs allows the ants to stabilize, and that asymmetric anteroposterior motions of these elevated legs permit steering (Yanoviak et al. 2010).

Gliding bristletails are, once again, a different story. These animals do not elevate their legs dorsally to achieve stability, but rather flex their abdomen and extend the caudal filaments dorsally as they fall (Fig. 9C). This posture produces a similar stabiliz-

ing effect to leg elevation in other insects, by vertically separating the parts of the body with high surface area and low mass from the parts with comparatively low surface area and high mass. Furthermore, the stable posture achieved by these animals involves the body being held at an inclined angle to the incident air flow, which according to the quasisteady analysis of Flower (1964), should be sufficient to generate the horizontal component of the aerodynamic force necessary for gliding. It is not currently known how bristletails perform turning maneuvers, although wind-tunnel data suggest that turns are modulated by lateral flexions of the abdomen (Y. Munk, unpublished data).

Future directions

In this review, we have summarized the physical characteristics of glide trajectories and the morphological structures used to produce force across the diversity of vertebrate and invertebrate gliders. In the future, we see great potential for advancement in our understanding of gliding behavior made possible by emerging technologies and computational techniques. As it becomes increasingly clear that gliding is a more dynamic behavior than previously thought, new questions are raised regarding the motor mechanisms governing active gliding control and the sensory modalities implicated in providing feedback to the animal. A more complete understanding of these phenomena will come from a mixture of improving sensing hardware, new computational methods, and new field techniques.

Modern sensing technologies provide opportunities to measure aerial performance of gliders in the wild using small, wireless sensor "backpacks". These on-board attached devices have been used for over a decade on freely flying birds (Weimerskirch et al. 2005; Sato et al. 2008; Taylor et al. 2008; Halsey et al. 2009; Shamoun-Baranes et al. 2012; Amélineau et al. 2014; Lopes et al. 2014), but have only been used to study one species of gliding mammal (Byrnes et al. 2008, 2011a, 2011b). Lightweight inertial measurement units (known as "IMUs") allow for measurement of heading, translational and rotational velocities, and acceleration, each with three degrees of freedom, and these can be combined with GPS instrumentation to provide an unprecedented window into the local dynamics of gliding animals in a minimally obtrusive package. These units can also be designed to measure heart rate (Ropert-Coudert et al. 2006), neural and electromyographic signals (Harrison et al. 2011; Thomas et al. 2012), and environmental temperature and pressure (Bouten et al. 2013). Data collection can occur via flash memory or be telemetered by radio-frequency signals, and power can come from batteries or solar cells; all combinations are possible (Bouten et al. 2013). Miniature video cameras can also be attached to the animal, which can be used for viewing the local environment and for making spatial measurements (Taylor et al. 2008; Kane and Zamani 2014). For birds, the use of these devices can be more challenging in the context of flapping flight, as heaving dynamics from flapping can interfere with the readings from the device (Taylor et al. 2008), but in gliding animals this problem may be negligible or nonexistent. Furthermore, some gliding mammals glide with attached offspring (Byrnes et al. 2008), potentially making these animals less sensitive to attached additional weight. However, weights of devices as small as 38 mg have been achieved (Thomas et al. 2012), demonstrating the potential utility for a broad range of gliding taxa.

Obtaining access to direct measurements of body dynamics for a gliding animal would furthermore improve our ability to develop computational models of gliding behavior. Current models of gliding behavior (Willis et al. 2011) suggest that gliders may be able to significantly improve glide performance by taking advantage of unsteady aerodynamic effects, and a logical progression would be to compare the predictions of these computational models with direct measurements of glide dynamics obtained from sensor backpacks. Although acceleration data may be inferred

from multiple-camera videography (Socha 2002, 2006; Socha and LaBarbera 2005; Socha et al. 2005, 2010; Bahlman et al. 2013), measuring acceleration data directly from a backpack unit would eliminate the need to estimate accelerations from noisy position data, as has been shown in colugo studies (Byrnes et al. 2008, 2011a, 2011b). Furthermore, most models of gliding treat gliding animals as static airframes (but see Jafari et al. 2014), and we have a limited understanding of how gliders actively manipulate their aerodynamic control surfaces during gliding flight (McCay 2001; Bishop 2006, 2007; Bishop and Brim-DeForest 2008). With better measurements of gliding dynamics, future refinements of our computational gliding models will help us understand how gliders achieve and modulate both stability and control. Overall, the new research needed to address these physical issues of gliding will greatly benefit from ongoing and new collaborations with engineers, mathematicians, and physicists.

Finally, we currently do not understand how gliding animals integrate sensory modalities to measure their environment and provide feedback to the motor processes used to control their trajectories. Many gliders perform their glides under low-light conditions within densely cluttered environments, and while vision seems likely to be the primary sensory modality involved in flight control, it seems likely that these animals are able to use mechano-sensing to provide feedback from aerodynamic forces acting upon them during flight. The sensory gains associated with these modalities during typical gliding flight are unknown, but might conceivably be inferred by providing controlled perturbations to these inputs under experimental conditions (using, for example, a virtual reality flight chamber for visual perturbations, a prepared wind tunnel for mechanical perturbations, or controlled gusts of air in open flight). Current explorations of integrative sensorimotor control of flight behavior are dominated by experimental subjects capable of powered flapping flight. We humbly suggest, in light of the relative simplicity of gliding flight (McGuire 2003) and its more extensive phylogenetic representation (Dudley et al. 2007), that gliding animals deserve a closer look.

Acknowledgements

References

Adams, L.E. 1906. The flight of flying fish. Zoologist, **4**: 145–148.

Alexander, D.E., Gong, E., Martin, L.D., Burnham, D.A., and Falk, A.R. 2010. Model tests of gliding with different hindwing configurations in the four-winged dromaeosaurid *Microraptor gui*. Proc. Nat. Acad. Sci. **107**(7): 2972–2976. doi:10.1073/pnas.0911852107. PMID:20133792.

Amélineau, F., Péron, C., Lescroël, A., Authier, M., Provost, P., and Grémillet, D. 2014. Windscape and tortuosity shape the flight costs of northern gannets. J. Exp. Biol. **217**(6): 876–885. doi:10.1242/jeb.097915. PMID:24622894.

Andersen, A., Pesavento, U., and Wang, Z. 2005. Unsteady aerodynamics of fluttering and tumbling plates. J. Fluid Mech. **541**: 65–90. doi:10.1017/S0022112005000594X.

Ando, M., and Shiraishi, S. 1993. Gliding flight in the Japanese giant flying squirrel *Petaurista leucogenys*. J. Mamm. Soc. Jpn. **18**(1): 19–32.

Arnold, E. 2002. *Holaspis*, a lizard that glided by accident: mosaics of cooption and adaptation in a tropical forest lacertid (Reptilia, Lacertidae). Bull. Nat. Hist. Mus. Zool. Ser. **68**(2): 155–163. doi:10.1017/S0968047002000171.

Bahlman, J.W., Swartz, S.M., Riskin, D.K., and Breuer, K.S. 2013. Glide performance and aerodynamics of non-equilibrium glides in northern flying squirrels (*Glaucomys sabrinus*). J. R. Soc. Interface, **10**(80): 20120794. doi:10.1098/rsif.2012.0794.

Baird, G.W. 1886. The flight of the flying-fish. Science, **8**(178): 10–12.

Barrows, W.B. 1883. Flight of the flying-fish. Science, **1**(21): 603. doi:10.1126/science.ns-1.21.603.

Bishop, K.L. 2006. The relationship between 3-D kinematics and gliding performance in the southern flying squirrel, *Glaucomys volans*. J. Exp. Biol. **209**(4): 689–701. doi:10.1242/jeb.02062. PMID:16449563.

Bishop, K.L. 2007. Aerodynamic force generation, performance and control of body orientation during gliding in sugar gliders (*Petaurus breviceps*). J. Exp. Biol. **210**(15): 2593–2606. doi:10.1242/jeb.002071. PMID:17644674.

Bishop, K.L. 2008. The evolution of flight in bats: narrowing the field of plausible hypotheses. Q. Rev. Biol. **83**(2): 153–169. doi:10.1086/587825. PMID:18605533.

Bishop, K.L., and Brim-DeForest, W. 2008. Kinematics of turning maneuvers in the southern flying squirrel, *Glaucomys volans*. J. Exp. Zool. A Ecol. Gen. Physiol. **309**(5): 225–242. doi:10.1002/jez.447.

Boistel, R., Herrel, A., Lebrun, R., Daghfous, G., Tafforeau, P., Losos, J.B., and Vanhooydonck, B. 2011. Shake rattle and roll: the bony labyrinth and aerial descent in squamates. Integr. Comp. Biol. **51**(6): 957–968. doi:10.1093/icb/icr034. PMID:21700578.

Bonser, R., and Rayner, J. 1996. Measuring leg thrust forces in the common starling. J. Exp. Biol. **199**(2): 435–439. PMID:9318079.

Bouten, W., Baaij, E.W., Shamoun-Baranes, J., and Camphuysen, K.C. 2013. A flexible GPS tracking system for studying bird behaviour at multiple scales. J. Ornithol. **154**(2): 571–580. doi:10.1007/s10336-012-0908-1.

Breder, C.M. 1929. Field observations on flying fishes; a suggestion of methods. Zoologica, **9**: 295–312.

Brown, R.M., Siler, C.D., Das, I., and Min, Y. 2012a. Testing the phylogenetic affinities of Southeast Asia's rarest geckos: Flap-legged geckos (*Luperosaurus*), Flying geckos (*Ptychozoon*) and their relationship to the pan-Asian genus *Gekko*. Mol. Phylogenet. Evol. **63**(3): 915–921. doi:10.1016/j.ympev.2012.02.019. PMID:22425705.

Brown, R.M., Siler, C.D., Grismer, L.L., Das, I., and McGuire, J.A. 2012b. Phylogeny and cryptic diversification in Southeast Asian flying geckos. Mol. Phylogenet. Evol. **65**(2): 351–361. doi:10.1016/j.ympev.2012.06.009. PMID:22750115.

Byrnes, G., and Spence, A.J. 2011. Ecological and biomechanical insights into the evolution of gliding in mammals. Integr. Comp. Biol. **51**(6): 991–1001. doi:10.1093/icb/icr069. PMID:21719434.

Byrnes, G., Lim, N.T.-L., and Spence, A.J. 2008. Take-off and landing kinetics of a free-ranging gliding mammal, the Malayan colugo (*Galeopterus variegatus*). Proc. R. Soc. B Biol. Sci. **275**(1638): 1007–1013. doi:10.1098/rspb.2007.1684.

Byrnes, G., Libby, T., Lim, N.T.-L., and Spence, A.J. 2011a. Gliding saves time but not energy in Malayan colugos. J. Exp. Biol. **214**(16): 2690–2696. doi:10.1242/jeb.052993. PMID:21795564.

Byrnes, G., Lim, N.T.-L., Yeong, C., and Spence, A.J. 2011b. Sex differences in the locomotor ecology of a gliding mammal, the Malayan colugo (*Galeopterus variegatus*). J. Mammal. **92**(2): 444–451. doi:10.1644/10-MAMM-A-048.1.

Carruthers, A.C., Thomas, A.L.R., and Taylor, G.K. 2007. Automatic aeroelastic devices in the wings of a steppe eagle *Aquila nipalensis*. J. Exp. Biol. **210**(23): 4136–4149. doi:10.1242/jeb.011197. PMID:18025013.

Chatterjee, S., and Templin, R.J. 2007. Biplane wing planform and flight performance of the feathered dinosaur *Microraptor gui*. Proc. Natl. Acad. Sci. **104**(5): 1576–1580. doi:10.1073/pnas.0609975104. PMID:17242354.

Colbert, E.H. 1967. Adaptations for gliding in the lizard *Draco*. Am. Mus. Novit. **2283**: 1–20.

Cole, K.S., and Gilbert, D.L. 1970. Jet propulsion of squid. Biol. Bull. **138**(3): 245–246. doi:10.2307/1540209.

Combes, S.A., and Daniel, T.L. 2003. Into thin air: contributions of aerodynamic and inertial–elastic forces to wing bending in the hawkmoth *Manduca sexta*. J. Exp. Biol. **206**(17): 2999–3006. doi:10.1242/jeb.00502. PMID:12878668.

Corbin, C.E., and Cordeiro, N.J. 2006. Gliding characteristics of Lord Derby's anomalure (*Anomalurus derbianus*) in Tanzania. Afr. J. Ecol. **44**(1): 106–108. doi:10.1111/j.1365-2028.2006.00600.x.

Crawford, R.L., and Baker, W.W. 1981. Bats killed at a north Florida television tower: a 25-year record. J. Mammal. **62**(3): 651–652. doi:10.2307/1380421.

Curet, O.M., Swartz, S.M., and Breuer, K.S. 2013. An aeroelastic instability provides a possible basis for the transition from gliding to flapping flight. J. R. Soc. Interface, **10**(80): 20120940. doi:10.1098/rsif.2012.0940.

Davenport, J. 1994. How and why do flying fish fly? Rev. Fish Biol. Fish. **4**(2): 184–214. doi:10.1007/BF00044128.

Davenport, J. 2003. Allometric constraints on stability and maximum size in flying fishes: implications for their evolution. J. Fish Biol. **62**(2): 455–463. doi:10.1046/j.1095-8649.2003.00041.x.

Dial, R., Bloodworth, B., Lee, A., Boyne, P., and Heys, J. 2004. The distribution of free space and its relation to canopy composition at six forest sites. For. Sci. **50**(3): 312–325.

Dolan, P.G., and Carter, D.C. 1977. *Glaucomys volans*. Mamm. Species, **78**: 1–6.

Dudley, R., and DeVries, P. 1990. Tropical rain forest structure and the geographical distribution of gliding vertebrates. Biotropica, **22**(4): 432–434. doi:10.2307/2388564.

Dudley, R., and Yanoviak, S.P. 2011. Animal aloft: the origins of aerial behavior and flight. Integr. Comp. Biol. **51**(6): 926–936. doi:10.1093/icb/icr002. PMID:21558180.

Dudley, R., Byrnes, G., Yanoviak, S.P., Borrell, B., Brown, R.M., and McGuire, J.A. 2007. Gliding and the functional origins of flight: biomechanical novelty or

necessity? Annu. Rev. Ecol. Evol. Syst. **38**(1): 179–201. doi:10.1146/annurev.ecolsys.37.091305.110014.

Dunbar, R.I. 1992. Time: a hidden constraint on the behavioural ecology of baboons. Behav. Ecol. Sociobiol. **31**(1): 35–49. doi:10.1007/BF00167814.

Edgerton, H., and Breder, C. 1941. High speed photographs of flying fishes in flight. Zoologica, **26**: 311–314.

Ellington, C.P. 1991. Aerodynamics and the origin of insect flight. Adv. Insect Physiol. **23**: 171–210. doi:10.1016/S0065-2806(08)60094-6.

Emerson, S.B. 1991. The ecomorphology of Bornean tree frogs (family Rhacophoridae). Zool. J. Linn. Soc. **101**: 337–357. doi:10.1111/j.1096-3642.1991.tb00656.x.

Emerson, S.B., and Koehl, M.A.R. 1990. The interaction of behavioral and morphological change in the evolution of a novel locomotor type: "flying" frogs. Evolution, **44**(8): 1931–1946. doi:10.2307/2409604.

Emerson, S.B., Travis, J., and Koehl, M.A.R. 1990. Functional complexes and additivity in performance: a test case with flying frogs. Evolution, **44**(8): 2153–2157. doi:10.2307/2409624.

Emmons, L.H., and Gentry, A.H. 1983. Tropical forest structure and the distribution of gliding and prehensile-tailed vertebrates. Am. Nat. **121**(4): 513–524. doi:10.1086/284079.

Endo, H., Yokokawa, K., Kurohmaru, M., and Hayashi, Y. 1998. Functional anatomy of gliding membrane muscles in the sugar glider (*Petaurus breviceps*). Ann. Anat. **180**(1): 93–96. doi:10.1016/S0940-9602(98)80149-0. PMID:9488912.

Ern, P., Risso, F., Fabre, D., and Magnaudet, J. 2012. Wake-induced oscillatory paths of bodies freely rising or falling in fluids. Annu. Rev. Fluid Mech. **44**: 97–121. doi:10.1146/annurev-fluid-120710-101250.

Essner, R.L. 2002. Three-dimensional launch kinematics in leaping, parachuting and gliding squirrels. J. Exp. Biol. **205**: 2469–2477. PMID:12124370.

Evangelista, D., Cardona, G., Guenther-Gleason, E., Huynh, T., Kwong, A., Marks, D., Ray, N., Tisbe, A., Tse, K., and Koehl, M. 2014. Aerodynamic characteristics of a feathered dinosaur measured using physical models. Effects of form on static stability and control effectiveness. PLoS ONE, **9**(1): e85203. doi:10.1371/journal.pone.0085203.

Faivovich, J., Haddad, C.F.B., Garcia, P.C.A., Frost, D.R., Campbell, J.A., and Wheeler, W.C. 2005. Systematic review of the frog family Hylidae, with special reference to Hylinae: phylogenetic analysis and taxonomic revision. Bull. Am. Mus. Nat. Hist. **1**: 1–240. doi:10.1206/0003-0090(2005)294%5B0001:SROTFF%5D2.0.CO;2.

Fish, F.E. 1990. Wing design and scaling of flying fish with regard to flight performance. J. Zool. (Lond.), **221**: 391–403. doi:10.1111/j.1469-7998.1990.tb04009.x.

Flaherty, E.A., Scheibe, J.S., and Goldingay, R. 2008. Locomotor performance in the squirrel glider, *Petaurus norfolcensis*, and the sugar glider, *Petaurus breviceps*. Aust. Mammal. **30**(1): 25–35.

Flaherty, E.A., Ben-David, M., and Smith, W.P. 2010. Quadrupedal locomotor performance in two species of arboreal squirrels: predicting energy savings of gliding. J. Comp. Physiol. B, **180**(7): 1067–1078. doi:10.1007/s00360-010-0470-1.

Flower, J.W. 1964. On the origin of flight in insects. J. Insect Physiol. **10**: 81–88. doi:10.1016/0022-1910(64)90096-4.

Gardiner, J.D., Dimitriadis, G., Codd, J.R., and Nudds, R.L. 2011. A potential role for bat tail membranes in flight control. PLoS ONE, **6**(3): e18214. doi:10.1371/journal.pone.0018214. PMID:21479137.

Grant, D.T., Abdulrahim, M., and Lind, R. 2010. Design and analysis of biomimetic joints for morphing of micro air vehicles. Bioinspir. Biomim. **5**(4): 045007. doi:10.1088/1748-3182/5/4/045007.

Gupta, B.B. 1966. Notes on the gliding mechanism in the flying squirrel. Occas. Pap. Mus. Zool. Univ. Mich. **645**: 1–7.

Halsey, L.G., Portugal, S.J., Smith, J.A., Murn, C.P., and Wilson, R.P. 2009. Recording raptor behavior on the wing via accelerometry. J. Field Ornithol. **80**(2): 171–177. doi:10.1111/j.1557-9263.2009.00219.x.

Harrison, R.R., Fotowat, H., Chan, R., Kier, R.J., Olberg, R., Leonardo, A., and Gabbiani, F. 2011. Wireless neural/EMG telemetry systems for small freely moving animals. IEEE Trans. Biomed. Circ. Syst. **5**(2): 103–111. doi:10.1109/TBCAS.2011.2131140.

Hasenfuss, I. 2002. A possible evolutionary pathway to insect flight starting from lepismatid organization. J. Zool. Syst. Evol. Res. **40**: 65–81. doi:10.1046/j.1439-0469.2002.00180.x.

Hayssen, V. 2008. Patterns of body and tail length and body mass in Sciuridae. J. Mammal. **89**(4): 852–873. doi:10.1644/07-MAMM-A-217.1.

Heinicke, M.P., Greenbaum, E., Jackman, T.R., and Bauer, A.M. 2012. Evolution of gliding in Southeast Asian geckos and other vertebrates is temporally congruent with dipterocarp forest development. Biol. Lett. **8**(6): 994–997. doi:10.1098/rsbl.2012.0648. PMID:22977067.

Hertel, H. 1966. Take-off and flight of the flying fish. *In* Structure–form–movement. Reinhold, New York. pp. 218–224.

Heyer, W.R., and Pongsapipatana, S. 1970. Gliding speeds of *Ptychozoon lionatum* (Reptilia: Gekkonidae) and *Chrysopelea ornata* (Reptilia: Colubridae). Herpetologica, **26**: 317–319.

Holden, D., Socha, J.J., Cardwell, N.D., and Vlachos, P.P. 2014. Aerodynamics of the flying snake *Chrysopelea paradisi*: how a bluff body cross-sectional shape contributes to gliding performance. J. Exp. Biol. **217**(3): 382–394. doi:10.1242/jeb.090902. PMID:24477611.

Honda, M., Hikida, T., Araya, K., Ota, H., Nabhitabhata, J., and Yong, H.S. 1997. *Cosymbotus craspedotus* (Frilly Gecko) and *C. platyurus* (Flat-tailed Gecko). Gliding behavior. Herpetol. Rev **28**(1): 42–43.

Howland, H.C. 1974. Optimal strategies for predator avoidance: the relative importance of speed and manoeuvrability. J. Theor. Biol. **47**(2): 333–350. doi:10.1016/0022-5193(74)90202-1. PMID:4437191.

Huang, W., Liu, H., Wang, F., Wu, J., and Zhang, H.P. 2013. Experimental study of a freely falling plate with an inhomogeneous mass distribution. Phys. Rev. E, **88**(5): 053008. doi:10.1103/PhysRevE.88.053008.

Hubbs, C.L. 1918. The flight of the California flying-fish (*Cypselurus californicus*). Copeia, **1918**(62): 85–88. doi:10.2307/1435974.

Hubbs, C.L. 1933. Observations on the flight of fishes, with a statistical study of the flight of the Cypselurinae and remarks on the evolution of the flight of fishes. Pap. Mich. Acad. Sci. Art. Lett. **17**: 575–611.

Hubbs, C.L. 1936. Further observations and statistics on the flight of fishes. Pap. Mich. Acad. Sci. Art. Lett. **22**: 641–660.

Inger, R.F. 1983. Morphological and ecological variation in the flying lizards (genus *Draco*). Fieldiana Zool. **18**: 1–35. doi:10.5962/bhl.title.3131.

Jackson, S.M. 2000. Glide angle in the genus *Petaurus* and a review of gliding in mammals. Mammal Rev. **30**(1): 9–30. doi:10.1046/j.1365-2907.2000.00056.x.

Jackson, S., and Schouten, P. 2012. Gliding mammals of the world. CSIRO Publishing, Collingwood, Victoria, Australia.

Jackson, S.M., and Thorington, R.W., Jr.. 2012. Gliding mammals: taxonomy of living and extinct species. Smithson. Contrib. Zool. **638**: 1–117. doi:10.5479/si.00810282.638.1.

Jafari, F., Ross, S.D., Vlachos, P.P., and Socha, J.J. 2014. A theoretical analysis of pitch stability during gliding in flying snakes. Bioinspir. Biomimet. **9**(2): 025014. doi:10.1088/1748-3182/9/2/025014.

John, K. 1970. Studies on the histophysiology of the muscles of the South Indian flying lizard, *Draco dussumieri* (Dum. & Bib.). J. Anim. Morphol. Physiol. **17**: 44–55.

Johnson-Murray, J.L. 1977. Myology of the gliding membranes of some petauristine rodents (genera: *Glaucomys*, *Pteromys*, *Petinomys*, and *Petaurista*). J. Mammal. **58**(3): 374–384. doi:10.2307/1379336.

Johnson-Murray, J.L. 1987. The comparative myology of the gliding membranes of *Acrobates*, *Petauroides* and *Petaurus* contrasted with the cutaneous myology of *Hemibelideus* and *Pseudocheirus* (Marsupialia: Phalangeridae) and with selected gliding Rodentia (Sciuridae and Anamoluridae). Aust. J. Zool. **35**: 101–113. doi:10.1071/ZO9870101.

Jusufi, A., Goldman, D.I., Revzen, S., and Full, R.J. 2008. Active tails enhance arboreal acrobatics in geckos. Proc. Natl. Acad. Sci. U.S.A. **105**(11): 4215–4219. doi:10.1073/pnas.0711944105. PMID:18347344.

Jusufi, A., Kawano, D.T., Libby, T., and Full, R.J. 2010. Righting and turning in mid-air using appendage inertia: reptile tails, analytical models and bioinspired robots. Bioinspir. Biomim. **5**(4): 045001. doi:10.1088/1748-3182/5/4/045001.

Jusufi, A., Zeng, Y., Full, R.J., and Dudley, R. 2011. Aerial righting reflexes in flightless animals. Integr. Comp. Biol. **51**(6): 937–943. doi:10.1093/icb/icr114. PMID:21930662.

Kane, S.A., and Zamani, M. 2014. Falcons pursue prey using visual motion cues: new perspectives from animal-borne cameras. J. Exp. Biol. **217**(2): 225–234. doi:10.1242/jeb.092403. PMID:24431144.

Kawachi, K., Inada, Y., and Azuma, A. 1993. Optimal flight path of flying fish. J. Theor. Biol. **163**(2): 145–159. doi:10.1006/jtbi.1993.1113.

Keith, M.M., Scheibe, J.S., and Hendershott, A.J. 2000. Launch dynamics in *Glaucomys volans*. *In* Biology of gliding mammals. *Edited by* R.L. Goldingay and J.S. Scheibe. Filander Verlag, Fürth, Germany. pp. 185–198.

Kingsolver, J.G., and Koehl, M.A.R. 1985. Aerodynamics, thermoregulation, and the evolution of insect wings: differential scaling and evolutionary change. Evolution, **39**(3): 488–504. doi:10.2307/2408648.

Klem, D., Jr.. 1990. Bird injuries, cause of death, and recuperation from collisions with windows. J. Field Ornithol. **61**(1): 115–119.

Koehl, M.A.R., Evangelista, D., and Yang, K. 2011. Using physical models to study the gliding performance of extinct animals. Integr. Comp. Biol. **51**(6): 1002–1018. doi:10.1093/icb/icr112. PMID:21937667.

Krishnan, A., Socha, J.J., Vlachos, P.P., and Barba, L.A. 2014. Lift and wakes of flying snakes. Phys. Fluids, **26**(3): 031901. doi:10.1063/1.4866444.

Kutschera, U. 2005. Predator-driven macroevolution in flyingfishes inferred from behavioural studies: historical controversies and a hypothesis. Ann. Hist. Philos. Biol. **10**: 59–77.

Lee, P.-F., Lin, Y.-S., and Progulske, D.R. 1993. Reproductive biology of the red-giant flying squirrel, *Petaurista petaurista*, in Taiwan. J. Mammal. **74**: 982–989.

Lekagul, B., and McNeeley, J.A. 1977. Mammals of Thailand. Sahakarnbhat, Bangkok.

Lentink, D., Müller, U.K., Stamhuis, E.J., de Kat, R., van Gestel, W., Veldhuis, L.L.M., Henningsson, P., Hedenström, A., Videler, J.J., and van Leeuwen, J.L. 2007. How swifts control their glide performance with morphing wings. Nature, **446**(7139): 1082–1085. doi:10.1038/nature05733. PMID:17460673.

Libby, T., Moore, T.Y., Chang-Siu, E., Li, D., Cohen, D.J., Jusufi, A., and Full, R.J. 2012. Tail-assisted pitch control in lizards, robots and dinosaurs. Nature, **481**(7380): 181–184. doi:10.1038/nature10710. PMID:22217942.

Loeb, L.B. 1936. The "flight" of flying fish. Science, **83**(2150): 260–261. doi:10.1126/science.83.2150.260. PMID:17757099.

Lopes, P., Springthorpe, D., and Bentley, G. 2014. Increased activity correlates with reduced ability to mount immune defenses to endotoxin in zebra

finches. J. Exp. Zool. Part A Ecol. Genet. Physiol. **321**: 422–431. doi:10.1002/jez.1873.

Losos, J.B., Papenfuss, T.J., and Macey, J.R. 1989. Correlates of sprinting, jumping, and parachuting performance in the butterfly lizard, *Leiolepis belliani*. J. Zool. (Lond.), **217**: 559–568. doi:10.1111/j.1469-7998.1989.tb02511.x.

Macia, S., Robinson, M.P., Craze, P., Dalton, R., and Thomas, J.D. 2004. New observations on airborne jet propulsion (flight) in squid, with a review of previous reports. J. Mollusc. Stud. **70**(3): 297–299. doi:10.1093/mollus/70.3.297.

Marcellini, D.L., and Keefer, T.E. 1976. Analysis of the gliding behavior of *Ptychozoon lionatum* (Reptilia: Gekkonidae). Herpetologica, **32**: 362–366.

McCay, M.G. 2001. Aerodynamic stability and maneuverability of the gliding frog *Polypedates dennysi*. J. Exp. Biol. **204**(16): 2817–2826. PMID:11683437.

McCay, M.G. 2003. Winds under the rain forest canopy: the aerodynamic environment of gliding tree frogs. Biotropica, **35**(1): 94–102. doi:10.1111/j.1744-7429.2003.tb00266.x.

McGuire, J.A. 2003. Allometric prediction of locomotor performance: an example from southeast Asian flying lizards. Am. Nat. **161**(2): 337–349. doi:10.1086/346085. PMID:12675377.

McGuire, J.A., and Dudley, R. 2005. The cost of living large: comparative gliding performance in flying lizards (Agamidae: *Draco*). Am. Nat. **166**(1): 93–106. doi:10.1086/430725. PMID:15937792.

McGuire, J.A., and Dudley, R. 2011. The biology of gliding in flying lizards (genus *Draco*) and their fossil and extant analogs. Integr. Comp. Biol. **51**(6): 983–990. doi:10.1093/icb/icr090. PMID:21798987.

Mein, P., and Romaggi, J.-P. 1991. Un gliridé (Mammalia, Rodentia) planeur dans le Miocene supérieur de l'Ardeche : une adaptation non retrouvée dans la nature actuelle. Geobios M.S. **13**: 45–50.

Melville, W. 1996. The role of surface-wave breaking in air–sea interaction. Annu. Rev. Fluid Mech. **28**(1): 279–321. doi:10.1146/annurev.fl.28.010196.001431.

Mendelson, J.R., Savage, J.M., Griffith, E., Ross, H., Kubicki, B., and Gagliardo, R. 2008. Spectacular new gliding species of *Ecnomiohyla* (Anura: Hylidae) from central Panama. J. Herpetol. **42**(4): 750–759. doi:10.1670/08-025R1.1.

Meng, J., Hu, Y., Wang, Y., Wang, X., and Li, C. 2006. A Mesozoic gliding mammal from northeastern China. Nature, **444**(7121): 889–893. doi:10.1038/nature05234. PMID:17167478.

Meng, J., Hu, Y., Wang, Y., Wang, X., and Li, C. 2007. Corrigendum: A Mesozoic gliding mammal from northeastern China. Nature, **446**(7131): 102. doi:10.1038/nature05639.

Miklasz, K., LaBarbera, M., Chen, X., and Socha, J. 2010. Effects of body cross-sectional shape on flying snake aerodynamics. Exp. Mech. **50**(9): 1335–1348. doi:10.1007/s11340-010-9351-5.

Mills, C.A. 1936. Source of propulsive power used by flying fish. Science, **83**(2143): 80. doi:10.1126/science.83.2143.80-a. PMID:17756685.

Moffett, M.W. 2000. What's "up"? A critical look at the basic terms of canopy biology. Biotropica, **32**(4a): 569–596.

Mountcastle, A.M., and Daniel, T.L. 2009. Aerodynamic and functional consequences of wing compliance. Exp. Fluids, **46**(5): 873–882. doi:10.1007/s00348-008-0607-0.

Munk, Y., Yanoviak, S.P., and Dudley, R. 2011. Directed aerial descent in canopy ants. *In* The Biomechanics and Behavior of Gliding Flight Symposium at the Annual Meeting of The Society for Integrative and Comparative Biology, Salt Lake City, Utah, 3–7 January 2011. The Society for Integrative and Comparative Biology, McLean, Va.

Muramatsu, K., Yamamoto, J., Abe, T., Sekiguchi, K., Hoshi, N., and Sakurai, Y. 2013. Oceanic squid do fly. Mar. Biol. **160**(5): 1171–1175. doi:10.1007/s00227-013-2169-9.

Nachtigall, W. 1979. Gleitflug des Flugbeutlers *Petaurus breviceps papuanus* II. Filmanalysen zur Einstellung von Gleitbahn und Rumpf sowie zur Steuerung des Gleitflugs. J. Comp. Physiol. **133**: 89–95.

Nachtigall, W., Grosch, R., and Schultze-Westrum, T. 1974. Gleitflug des Flugbeutlers *Petaurs breviceps papuanus* (Thomas). J. Comp. Physiol. **92**: 105–115. doi:10.1007/BF00696530.

O'Dor, R.K. 2013. How squid swim and fly. Can. J. Zool. **91**(6): 413–419. doi:10.1139/cjz-2012-0273.

O'Dor, R., Stewart, J., Gilly, W., Payne, J., Borges, T.C., and Thys, T. 2013. Squid rocket science: how squid launch into air. Deep-Sea Res. Part II: Top. Stud. Oceanogr. **95**: 113–118. doi:10.1016/j.dsr2.2012.07.002.

Oliver, J.A. 1951. "Gliding" in amphibians and reptiles, with a remark on an arboreal adaptation in the lizard, *Anolis carolinensis carolinensis* Voigt. Am. Nat. **85**: 171–176. doi:10.1086/281666.

Paoletti, P., and Mahadevan, L. 2011. Planar controlled gliding, tumbling and descent. J. Fluid Mech. **689**: 489–516. doi:10.1017/jfm.2011.426.

Park, H., and Choi, H. 2010. Aerodynamic characteristics of flying fish in gliding flight. J. Exp. Biol. **213**(19): 3269–3279. doi:10.1242/jeb.046052. PMID:20833919.

Paskins, K.E., Bowyer, A., Megill, W.M., and Scheibe, J.S. 2007. Take-off and landing forces and the evolution of controlled gliding in northern flying squirrels *Glaucomys sabrinus*. J. Exp. Biol. **210**(8): 1413–1423. doi:10.1242/jeb.02747. PMID:17401124.

Pesavento, U., and Wang, Z.J. 2004. Falling paper: Navier-Stokes solutions, model of fluid forces, and center of mass elevation. Phys. Rev. Lett. **93**(14): 144501. doi:10.1103/PhysRevLett.93.144501. PMID:15524800.

Peterka, H.E. 1936. A study of the myology and osteology of tree sciurids with

regard to adaptation to arboreal, glissant, and fossorial habits. Trans. Kans. Acad. Sci. **39**: 313–332. doi:10.2307/3625186.

Rayner, J.M.V. 1986. Pleuston: animals which move in water and air. Endeavour, **10**(2): 58–64. doi:10.1016/0160-9327(86)90131-6.

Revell, L.J., Johnson, M.A., Schulte, J.A., Kolbe, J.J., and Losos, J.B. 2007. A phylogenetic test for adaptive convergence in rock-dwelling lizards. Evolution, **61**(12): 2898–2912. doi:10.1111/j.1558-5646.2007.00225.x. PMID:17894806.

Ribak, G., Gish, M., Weihs, D., and Inbar, M. 2013. Adaptive aerial righting during the escape dropping of wingless pea aphids. Curr. Biol. **23**(3): R102–R103. doi:10.1016/j.cub.2012.12.010. PMID:23391380.

Roberts, W.E. 1994. Explosive breeding aggregations and parachuting in a neotropical frog, *Agalychnis saltator* (Hylidae). J. Herpetol. **28**(2): 193–199. doi:10.2307/1564620.

Rojratsirikul, P., Wang, Z., and Gursul, I. 2010. Unsteady fluid–structure interactions of membrane airfoils at low Reynolds numbers. *In* Animal locomotion. *Edited by* G.K. Taylor, M.S. Triantafyllou, and C. Tropea. Springer-Verlag, Berlin. pp. 297–310.

Ropert-Coudert, Y., Wilson, R.P., Grémillet, D., Kato, A., Lewis, S., and Ryan, P.G. 2006. Electrocardiogram recordings in free-ranging gannets reveal minimum difference in heart rate during flapping versus gliding flight. Mar. Ecol. Prog. Ser. **328**: 275–284. doi:10.3354/meps328275.

Rowley, J.J.L., Le, D.T.T., Tran, D.T.A., Stuart, B.L., and Huy, H.D. 2010. A new tree frog of the genus *Rhacophorus* (Anura: Rhacophoridae) from southern Vietnam. Zootaxa, **2727**: 45–55.

Russell, A.P. 1979. The origin of parachuting locomotion in gekkonid lizards (Reptilia, Gekkonidae). Zool. J. Linn. Soc. **65**(3): 233–249. doi:10.1111/j.1096-3642.1979.tb01093.x.

Russell, A.P., and Dijkstra, L.D. 2001. Patagial morphology of *Draco volans* (Reptilia: Agamidae) and the origin of glissant locomotion in flying dragons. J. Zool. **253**: 457–471. doi:10.1017/S0952836901000425.

Russell, A.P., Dijkstra, L.D., and Powell, G.L. 2001. Structural characteristics of the patagium of *Ptychozoon kuhli* (Reptilia: Gekkonidae) in relation to parachuting locomotion. J. Morphol. **247**(3): 252–263. doi:10.1002/1097-4687(200103)247:3<252::AID-JMOR1015>3.3.CO;2-Q. PMID:11223931.

Sato, K., Daunt, F., Watanuki, Y., Takahashi, A., and Wanless, S. 2008. A new method to quantify prey acquisition in diving seabirds using wing stroke frequency. J. Exp. Biol. **211**(1): 58–65. doi:10.1242/jeb.009811. PMID:18083733.

Scheibe, J.S., and Robins, J.H. 1998. Morphological and performance attributes of gliding mammals. *In* Ecology and evolutionary biology of tree squirrels. *Edited by* J.F. Merritt and D.A. Zegers. Virginia Museum of Natural History, Martinsville. pp. 131–144.

Scheibe, J.S., Smith, W.P., Bassham, J., and Magness, D. 2006. Locomotor performance and cost of transport in the northern flying squirrel *Glaucomys sabrinus*. Acta Theriol. **51**(2): 169–178. doi:10.1007/BF03192668.

Schiøtz, A., and Volsøe, H. 1959. The gliding flight of *Holaspis guentheri* Gray, a West-African lacertid. Copeia, **1959**(3): 259–260. doi:10.2307/1440407.

Schlesinger, W.H., Knops, J.M., and Nash, T.H. 1993. Arboreal sprint failure: lizardfall in a California oak woodland. Ecology, **74**: 2465–2467. doi:10.2307/1939598.

Scholey, K.D. 1986. The climbing and gliding locomotion of the giant red flying squirrel *Petaurista petaurista* (Sciuridae). *In* Biona Report 5, Bat flight – Fledermausflug. *Edited by* W. Nachtigall. Gustav Fischer, Stuttgart, Germany. pp. 187–204.

Schultz, A.H. 1939. Notes on the diseases and healed fractures of wild apes and their bearing on the antiquity of pathological conditions in man. Bull. Hist. Med. **7**: 571–582.

Shamoun-Baranes, J., Bom, R., van Loon, E.E., Ens, B.J., Oosterbeek, K., and Bouten, W. 2012. From sensor data to animal behaviour: an oystercatcher example. PLoS ONE, **7**(5). doi:10.1371/journal.pone.0037997.

Shyy, W., Berg, M., and Ljungqvist, D. 1999. Flapping and flexible wings for biological and micro air vehicles. Prog. Aero. Sci. **35**(5): 455–505. doi:10.1016/S0376-0421(98)00016-5.

Socha, J.J. 2002. Gliding flight in the paradise tree snake. Nature, **418**: 603–604. doi:10.1038/418603a. PMID:12167849.

Socha, J.J. 2006. Becoming airborne without legs: the kinematics of take-off in a flying snake, *Chrysopelea paradisi*. J. Exp. Biol. **209**(17): 3358–3369. doi:10.1242/jeb.02381. PMID:16916972.

Socha, J.J. 2011. Gliding flight in *Chrysopelea*: turning a snake into a wing. Integr. Comp. Biol. **51**(6): 969–982. doi:10.1093/icb/icr092. PMID:21816808.

Socha, J.J., and LaBarbera, M. 2005. Effects of size and behavior on aerial performance of two species of flying snakes (*Chrysopelea*). J. Exp. Biol. **208**(10): 1835–1847. doi:10.1242/jeb.01580. PMID:15879064.

Socha, J.J., O'Dempsey, T., and LaBarbera, M. 2005. A 3-D kinematic analysis of gliding in a flying snake, *Chrysopelea paradisi*. J. Exp. Biol. **208**(10): 1817–1833. doi:10.1242/jeb.01579. PMID:15879063.

Socha, J.J., Miklasz, K., Jafari, F., and Vlachos, P.P. 2010. Non-equilibrium trajectory dynamics and the kinematics of gliding in a flying snake. Bioinspir. Biomim. **5**(4): 045002. doi:10.1088/1748-3182/5/4/045002.

Song, A., Tian, X., Israeli, E., Galvao, R., Bishop, K., Swartz, S., and Breuer, K. 2008. Aeromechanics of membrane wings with implications for animal flight. AIAA J. **46**(8): 2096–2106. doi:10.2514/1.36694.

Stafford, B.J., Thorington, R.W., Jr., and Kawamichi, T. 2002. Gliding behavior of

Japanese giant flying squirrels (*Petaurista leucogenys*). J. Mammal. **83**(2): 553–562. doi:10.1644/1545-1542(2002)083<0553:GBOJGF>2.0.CO;2.

Stein, K., Palmer, C., Gill, P.G., and Benton, M.J. 2008. The aerodynamics of the British late Triassic Kuehneosauridae. Palaeontology, **51**(4): 967–981. doi:10.1111/j.1475-4983.2008.00783.x.

Sterbing-D'Angelo, S., Chadha, M., Chiu, C., Falk, B., Xian, W., Barcelo, J., Zook, J.M., and Moss, C.F. 2011. Bat wing sensors support flight control. Proc. Natl. Acad. Sci. **108**(27): 11291–11296. doi:10.1073/pnas.1018740108. PMID:21690408.

Stewart, M.M. 1985. Arboreal habitat use and parachuting by a subtropical forest frog *Eleutherodactylus coqui*. J. Herpetol. **19**(3): 391–401. doi:10.2307/1564267.

Storch, G., Engesser, B., and Wuttke, M. 1996. Oldest fossil record of gliding in rodents. Nature, **379**(6564): 439–441. doi:10.1038/379439a0.

Suzuki, K., Asari, Y., and Yanagawa, H. 2012. Gliding locomotion of Siberian flying squirrels in low-canopy forests: the role of energy-inefficient short-distance glides. Acta Theriol. **57**(2): 131–135. doi:10.1007/s13364-011-0060-y.

Taylor, G.K., Bacic, M., Bomphrey, R.J., Carruthers, A.C., Gillies, J., Walker, S.M., and Thomas, A.L.R. 2008. New experimental approaches to the biology of flight control systems. J. Exp. Biol. **211**(2): 258–266. doi:10.1242/jeb.012625. PMID:18165253.

Thomas, S.J., Harrison, R.R., Leonardo, A., and Reynolds, M.S. 2012. A battery-free multi-channel digital neural/EMG telemetry system for flying insects. IEEE Trans. Biomed. Circ. Syst. **6**(5): 424–436. doi:10.1109/TBCAS.2012.2222881.

Thorington, R.W., Jr., Darrow, K., and Anderson, C.G. 1998. Wing tip anatomy and aerodynamics in flying squirrels. J. Mamm. **79**(1): 245–250. doi:10.2307/1382860.

Thorington, R.W., Jr., Pitassy, D., and Jansa, S.A. 2002. Phylogenies of flying squirrels (Pteromyinae). J. Mamm. Evol. **9**(1–2): 99–135. doi:10.1023/A:1021335912016.

Torres, G.E., and Mueller, T.J. 2001. Aerodynamic characteristics of low aspect ratio wings at low Reynolds numbers. *In* Fixed and flapping wing aerodynamics for micro air vehicle applications. AIAA, Reston, Va. pp. 115–141.

Vanhooydonck, B., Meulepas, G., Herrel, A., Boistel, R., Tafforeau, P., Fernandez, V., and Aerts, P. 2009. Ecomorphological analysis of aerial performance in a non-specialized lacertid lizard, *Holaspis guentheri*. J. Exp. Biol. **212**(15): 2475–2482. doi:10.1242/jeb.031856. PMID:19617441.

Varshney, K., Chang, S., and Wang, Z.J. 2012. The kinematics of falling maple seeds and the initial transition to a helical motion. Nonlinearity, **25**(1): C1. doi:10.1088/0951-7715/25/1/C1.

Varshney, K., Chang, S., and Wang, Z.J. 2013. Unsteady aerodynamic forces and torques on falling parallelograms in coupled tumbling–helical motions. Phys. Rev. E, **87**(5): 053021.

Vernes, K. 2001. Gliding performance of the northern flying squirrel (*Glaucomys*

sabrinus) in mature mixed forest of Eastern Canada. J. Mammal. **82**(4): 1026–1033. doi:10.1644/1545-1542(2001)082<1026:GPOTNF>2.0.CO;2.

Vogel, S. 1994. Life in moving fluids. Princeton University Press, Princeton, N.J.

Vogel, S. 2006. Living in a physical world VI. Gravity and life in the air. J. Biosci. **31**(1): 13–25. doi:10.1007/BF02705231.

Vogel, S. 2013. Comparative biomechanics: life's physical world. Princeton University Press, Princeton, N.J.

Wang, H., Wang, L., Shao, J., Liu, T., Tang, Y., and Dai, Z. 2014. The mechanism of air-righting performance in tree frogs. App. Mech. Mat. **461**(2014): 291–296. doi:10.4028/www.scientific.net/AMM.461.291.

Weimerskirch, H., Le Corre, M., Ropert-Coudert, Y., Kato, A., and Marsac, F. 2005. The three-dimensional flight of red-footed boobies: adaptations to foraging in a tropical environment? Proc. R. Soc. B Biol. Sci. **272**(1558): 53–61. doi:10.1098/rspb.2004.2918.

Willis, D., Bahlman, J., Breuer, K., and Swartz, S. 2011. Energetically optimal short-range gliding trajectories for gliding animals. AIAA J. **49**(12): 2650–2657. doi:10.2514/1.J051070.

Wilson, D.E., and Reeder, D.M. 1993. Mammal species of the world: a taxonomic and geographic reference. Smithsonian Institution Press, Washington, D.C.

Yanoviak, S.P., and Dudley, R. 2006. The role of visual cues in directed aerial descent of *Cephalotes atratus* workers (Hymenoptera: Formicidae). J. Exp. Biol. **209**(9): 1777–1783. doi:10.1242/jeb.02170. PMID:16621958.

Yanoviak, S.P., Dudley, R., and Kaspari, M. 2005. Directed aerial descent in canopy ants. Nature, **433**(7026): 624–626. doi:10.1038/nature03254. PMID:15703745.

Yanoviak, S., Fisher, B., and Alonso, A. 2008. Directed aerial descent behavior in African canopy ants (Hymenoptera: Formicidae). J. Insect Behav. **21**(3): 164–171. doi:10.1007/s10905-008-9116-5.

Yanoviak, S.P., Kaspari, M., and Dudley, R. 2009. Gliding hexapods and the origins of insect aerial behaviour. Biol. Lett. **5**(4): 510–512. doi:10.1098/rsbl.2009.0029. PMID:19324632.

Yanoviak, S.P., Munk, Y., Kaspari, M., and Dudley, R. 2010. Aerial manoeuvrability in wingless gliding ants (*Cephalotes atratus*). Proc. R. Soc. B Biol. Sci. **277**(1691): 2199–2204. doi:10.1098/rspb.2010.0170.

Yanoviak, S.P., Munk, Y., and Dudley, R. 2011. Evolution and ecology of directed aerial descent in arboreal ants. Integr. Comp. Biol. **51**(6): 944–956. doi:10.1093/icb/icr006. PMID:21562023.

Young, B.A., and Kardong, K.V. 2010. The functional morphology of hooding in cobras. J. Exp. Biol. **213**(9): 1521–1528. doi:10.1242/jeb.034447. PMID:20400637.

Young, B.A., Lee, C.E., and Daley, K.M. 2002. On a flap and a foot: aerial locomotion in the "flying" gecko, *Pychozoon kuhli*. J. Herpetol. **36**(3): 412–418. doi:10.2307/1566185.

Zhao, L., Deng, X., and Sane, S.P. 2011. Modulation of leading edge vorticity and aerodynamic forces in flexible flapping wings. Bioinspir. Biomim. **6**(3): 036007. doi:10.1088/1748-3182/6/3/036007. PMID:21852729.