Gliding and the Functional Origins of Flight: Biomechanical Novelty or Necessity?

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Abstract

A biomechanically parsimonious hypothesis for the evolution of flapping flight in terrestrial vertebrates suggests progression within an arboreal context from jumping to directed aerial descent, gliding with control via appendicular motions, and ultimately to powered flight. The more than 30 phylogenetically independent lineages of arboreal vertebrate gliders lend strong indirect support to the ecological feasibility of such a trajectory. Insect flight evolution likely followed a similar sequence, but is unresolved paleontologically. Recently described falling behaviors in arboreal ants provide the first evidence demonstrating the biomechanical capacity for directed aerial descent in the complete absence of wings. Intentional control of body trajectories as animals fall from heights (and usually from vegetation) likely characterizes many more taxa than is currently recognized. Understanding the sensory and biomechanical mechanisms used by extant gliding animals to control and orient their descent is central to deciphering pathways involved in flight evolution.

INTRODUCTION

The evolution of novel locomotor modes plays an important role in the invasion of new habitats, partitioning of resources within those habitats, and ultimately in the generation of organismal diversity. Extreme habitat transitions, such as those between aquatic and terrestrial environments or between land and air, represent major themes in the history of life and involve both the co-option of existing traits as well as genuine "key" innovations (Vermeij 2006, Vermeij & Dudley 2000). The origin of flight represents one such important transition and requires the integration of a suite of morphological, physiological, and behavioral features. Although many biologists view flight as a specialized or even rare form of locomotion characteristic of only one extinct lineage (the pterosaurs) and three extant clades (birds, bats, and the pterygote insects), controlled aerial behaviors are much more widespread among animals. In addition to powered flapping flight, gliders with obvious wings or wing-like structures have evolved at least thirty times among terrestrial vertebrates, including mammals, reptiles, and amphibians (Norberg 1990, Rayner 1988). In addition to more classically described gliding, directed aerial descent (Yanoviak et al. 2005) occurs in the absence of obvious aerodynamic surfaces and is likely characteristic of many more taxa, both vertebrate and invertebrate. Here, we examine the full continuum of such aerial behaviors and place the origin of flight within a specific functional context relating to arboreality and either inadvertent or intentional descent. In particular, we suggest that the numerous evolutionary experiments in gliding and controlled descent may be inevitable consequences of living within vegetational structures elevated above the ground.

Definitionally, it is important to specify what is meant by the word flight. The Oxford English Dictionary (second edition) defines flight as the "action or manner of flying or moving through the air with or as with wings." Biomechanically, we here use the term to indicate any locomotor behavior in the air that involves active control of aerodynamic forces. Parachuting with no regulation of the magnitude or orientation of the ensuing drag force can be truly passive, but all other aerial behaviors involve the generation and often intentional regulation of lift and drag to slow descent, reorient the body, and alter the flight trajectory. A conceptual distinction has been historically made between gliding and parachuting, with the former characterized arbitrarily by a descent angle less than 45° relative to horizontal, and the latter with a descent angle greater than 45° (Oliver 1951). These definitions assume steady-state conditions of a constant speed and orientation of the body in the air, as well as the equilibrium of forces. However, such a discrete characterization of what is a continuous variable, namely the glide angle, is clearly inappropriate. Individual flying lizards in the genus *Draco*, for example, may glide at relatively shallow angles, but can also plummet at angles steeper than 45° according to the behavioral context (McGuire & Dudley 2005). The mechanisms of aerodynamic control during descent are similar in these two cases, differing only in magnitude and not fundamentally in kind. Many features of aerial behavior in gliding animals are also unsteady, involving time-dependent changes in orientation and speed of appendages and of the body itself. Therefore, we use the term gliding interchangeably with the phrase directed aerial descent to mean
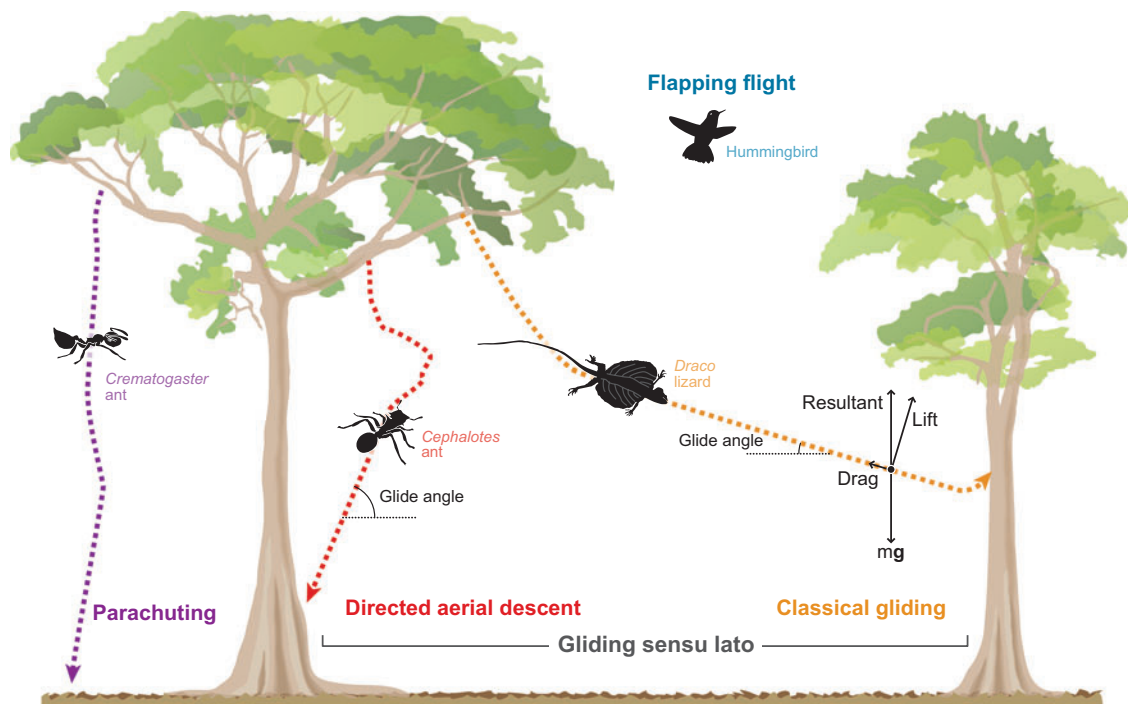
Figure 1

Diversity of aerial behaviors and a diagrammatic scenario for the evolution of flight.
Parachuting (*left*), directed aerial descent at steep angles (*center*), and classical gliding at
shallow angles (*right*) represent different stages of aerodynamic control and force production
that characterize a broad diversity of arboreal taxa. Flapping flight (*top*) is hypothesized to
derive from controlled aerial behaviors that phylogenetically precede fully articulated wings.
m**g**, force of gravity.

any controlled descent by an organism that converts gravitational potential energy to
useful aerodynamic work (**Figure 1**). In many if not all cases, such gliding is associated
with volitional horizontal, lateral, and rotational motions independent of particular
values of the instantaneous descent angle relative to horizontal. Following Maynard
Smith (1952), we suggest that the control of aerial trajectory when accelerating under
gravity is essential to the evolution of both gliding and flapping flight. Controlled
aerial behavior may accordingly precede the origin of wings per se. Here, we review a
variety of evidence for both arthropods and terrestrial vertebrates in support of these
possibilities.

MORPHOLOGICAL ADAPTATIONS FOR FLIGHT

The diversity of anatomical structures used aerodynamically by flying animals is im-
pressive. The fluid-dynamic features of such biological airfoils have been discussed
extensively elsewhere (Dudley 2000, Norberg 1990, Vogel 1994). True flapping wings

are easily recognizable as such; in the flying vertebrates they are modified limbs. The wing structures of bats, birds, and pterosaurs all involve the forelimb, and in bats also attach to the hindlimb. Insect wings are homologous neither with limbs nor with any other extant arthropod structure. Instead, these wings comprise thin cuticular membranes supported by venation extending from the thorax and are moved by muscles inserting at the wing base. In addition to the use of flapping wings, or such rudimentary wings as the feathered forelimbs of avian precursors, additional anatomical structures are employed for aerodynamic purpose. In mammals and reptiles, a patagial membrane is stretched laterally from the body, and is suspended between either bones or cartilaginous structures. Patagial membranes are strikingly variable. In mammals, the minimally nine independent origins of gliding flight are accompanied by substantial anatomical differences in the gliding membrane (Jackson 2000, Thorington 1984). Flying lizards of the genus *Draco* suspend the patagial membrane between elongated ribs (Colbert 1967, Russell & Dijkstra 2001); the extinct reptile *Sharovipteryx* sported a patagial membrane held only between the hindlimbs and tail (Dyke et al. 2006, Gans et al. 1987). The Permian reptile *Coelurosaurus* was characterized by a patagial membrane supported by a series of rod-like bones apparently not found in any other gliding animal (Frey et al. 1997). In the absence of a patagial membrane, flattening of the body (Arnold 2002, Losos et al. 1989, Socha 2002), use of lateral skin flaps (as in the gliding lizard *Ptychozoon*; Russell et al. 2001), flattened or relatively long tails (Thorington & Heaney 1981, Thorington et al. 2002), and the spreading of finger and toe webbing (as in hylid and rhacophorid gliding frogs, and in the lizard *Ptychozoon*) all serve to increase effective aerodynamic surface area and to improve lift:drag performance of the body as a whole.

In equilibrium gliding (i.e., moving at constant airspeed and glide angle), airspeed varies in proportion to the square root of the morphological parameter termed wing loading, the ratio of body weight to sustaining aerodynamic area (Norberg 1990). Therefore, species with higher wing loading glide faster when in equilibrium, independent of the lift:drag ratio of the animal. To reach these higher velocities, larger animals must fall vertically under gravity both a greater distance and over a longer time period to attain an equilibrium glide. Consistent with this expectation, gliding *Draco* lizards exhibit a significant correlation between wing loading and height lost over a standardized glide distance, with no evidence of physiological or behavioral compensation for increased body mass (McGuire 2003, McGuire & Dudley 2005). Given this general relationship between wing loading and glide performance, it is important to consider the allometry of aerodynamic surfaces (i.e., change in shape of the force-producing structures relative to change in body size). Relevant morphologies have not been studied in gliding arthropods (see below), but investigations of wing allometries in terrestrial vertebrate gliders have found isometric scaling (i.e., wing area increases in proportion to mass raised to the 2/3rds power) for the two cases of flying squirrels (Thorington & Heaney 1981) and *Draco* lizards (McGuire 2003). By contrast, flying fish exhibit a negative allometry in wing area because of functional constraints on pectoral fin retraction relative to tail beating in water (Davenport 2003). Selection toward smaller body size might thus be expected for terrestrial gliders if only equilibrium flight performance is of concern. Suggestively, large body size

only evolves in *Draco* lizards in the context of multispecies sympatry, an outcome that may derive from interspecific competition (McGuire & Dudley 2005). Increased wing loading also limits some aspects of flight maneuverability (Pennycuick 1975), further hindering aerial performance in larger gliders. Conversely, the biomechanical advantages of augmented surface area may be substantial, particularly as even small surfaces can nonetheless generate substantial aerodynamic torque and body rotations if positioned sufficiently far from rotational axes (Dudley 2002).

COMPONENTS OF AERIAL BEHAVIOR

Flight in animals involves a diversity of behaviors, including falls, startle jumps, volitional takeoff, accelerations, moving at constant airspeed, maneuvers, and landing. Many otherwise seemingly nonaerial taxa exhibit behavioral adaptations to allow them to decrease their rate of descent when falling (Dunbar 1988, Oliver 1951, Pellis et al. 1989). In order to initiate a glide, organisms must become airborne by either leaping or falling from structural or habitat heterogeneities. In the cypselurid flying fish, gliding is initiated by breaking through the air-water interface at a shallow angle, unfurling the large lateral fins, and rapidly beating the tail in the water prior to actual liftoff (Davenport 1994). Gliding squid similarly eject from the ocean's surface (Azuma 1992), but no analogous behavior (i.e., horizontal running to effect takeoff) has been identified in terrestrial gliders. All extant gliders are exclusively arboreal and use gravitational potential energy to accelerate downward, albeit initiating the behavior with a jump or fall. However, in many species, an active leap is involved. In the gliding snake, *Chrysopelea paradisi*, the body forms a "J"-shaped loop, hanging beneath the branch to initiate a glide. The anterior body is then accelerated upward and forward to leave the substrate at a horizontal speed of nearly 2 ms^{-1} (Socha 2002, 2006). More conventional gliders, including flying squirrels, typically leap from perches to initiate glides. The flying squirrel *Glaucomys volans*, for example, takes off at a mean speed of 2.5 ms^{-1} (Essner 2002). Furthermore, leaping motions in this flying squirrel closely resemble those of the nongliding tree squirrels and chipmunks. Takeoff of other gliding mammals has been described more qualitatively. For example, dermopterans hang vertically in a head-up position on the boles of trees before launching into a glide (R. Brown & G. Byrnes, personal observation). During this launch, hindlimbs are extended to effect takeoff while the body rolls through 180° (Mendoza & Custodio 2000). Flying lizards of the genus *Draco* employ the same mechanism when initiating a glide from a head-up, vertically perched position, whereas launching from near-horizontal surfaces (e.g., tree limbs) involves an initial leap (R. Brown, J. McGuire, & R. Dudley, personal observation).

Despite large morphological differences among extant gliders, aerodynamic commonalities pertain. Many gliders outstretch their limbs and spread their toes (e.g., aerial mammals and frogs), maximizing the area of gliding and control surfaces (Brown et al. 1997, Heyer & Pongsapipatana 1970). By contrast, nonarboreal taxa never maintain a stable posture when falling (Heyer & Pongsapipatana 1970, Oliver 1951). When their feet are bound, gliding geckos in the genus *Ptychozoon* fall like nongliders (Young et al. 2002). Impairment of body flaps hinders aerodynamic performance in

other lizards (Losos et al. 1989, Marcellini & Keefer 1976). Glide trajectories are highly dynamic, but can be broken down into distinct phases: accelerating descent, equilibrium gliding, and landing. Recent research conflates these features by considering only locomotor performance as averaged over the entire trajectory, typically by measuring the vertical height lost and total horizontal distance traveled during a gliding episode (e.g., Ando & Shiraishi 1993, Jackson 2000, Scholey 1986). However, each phase of the glide trajectory has distinctive biomechanical features that influence overall performance. Whereas either time-averaged or instantaneous glide angles are the most commonly reported performance measures, many other characteristics of aerial behavior may be equally relevant according to context, including takeoff speed, glide duration, and capacity to maneuver. Once in the air, gliding animals typically accelerate until the resultant of lift and drag forces acting on the organism equals the weight of the animal, producing a constant airspeed and glide angle (see **Figure 1**). Recent studies, however, have found that an equilibrium phase is uncommon in *Draco* (i.e., only about 50% of studied glides; McGuire & Dudley 2005), in the gliding snake *Chrysopelea* (Socha & LaBarbera 2005, Socha et al. 2005), and in the southern flying squirrel (Bishop 2006), at least over the spatial scales under consideration.

The capacity of gliding animals to maneuver once airborne has often been noted anecdotally (e.g., Colbert 1967, Dolan & Carter 1977, Jackson 2000). The complex structure of the forested habitat characteristic of most gliders sometimes requires alteration in the speed and direction of aerial trajectories. Air turbulence may similarly require dynamic course correction (McCay 2003). Aerial maneuverability and the negotiation of structurally complex environments require components of both axial and torsional agility (Dudley 2002). Axial agility describes the ability to accelerate along any of the three body axes, whereas torsional agility relates to the ability to rotate about these three axes. Patagial and propatagial membranes are under muscular control in many gliders (Colbert 1970, Johnson-Murray 1987, Wilkinson et al. 2006), allowing rapid adjustment of membrane configuration and camber either symmetrically or asymmetrically relative to the animal's longitudinal axis. Furthermore, gliding animals are able to use limb and whole-body movements to effect axial or torsional maneuvers. Adjusting the orientation of the propatagium (i.e., the membrane between the forelimbs and neck in gliding mammals) might also influence aerodynamic force production. Studies of gliding frogs (Emerson & Koehl 1990, Emerson et al. 1990, McCay 2001) illustrate just how complex such maneuvers can be, and furthermore illustrate the importance of the interactions between morphological structures and their displacement to effect whole-body directional change. Only recently, however, has three-dimensional analysis of a free-flying glider undertaking maneuvers been implemented (Socha & LaBarbera 2005, Socha et al. 2005). Many gliding animals exhibit distinct landing maneuvers to reduce flight speed and to increase control while landing. Qualitative descriptions of the landing maneuver exist for gliding marsupials (Jackson 2000, McKay 1983), anomalurids (Kingdon 1974), and flying squirrels (Nowak 1991, Scholey 1986). In all cases, both fore- and hindlimbs are moved forward and downward, increasing patagial billowing. The body pitches nose-upward, orientation of the flight membrane relative to oncoming flow increases, and lift production by the wing/body structure (i.e., aerodynamic stall) decreases rapidly as the animal

approaches the landing site (Nachtigall 1979), with a substantial reduction in speed prior to impact (G. Byrnes, unpublished observations). Quantitative descriptions of landing behavior in gliding taxa are otherwise not available.

THE ARBOREAL CONTEXT OF GLIDING FLIGHT

The evolutionary impetus and selective advantages of gliding and powered flight are associated with diverse and sometimes taxon-specific adaptive explanations (e.g., Beard 1990; Dudley 2000; Kingsolver & Koehl 1994; Norberg 1985, 1990; Padian & Chiappe 1998; Scholey 1986; Videler 2005). The frequency with which controlled aerial descent and gliding have evolved suggests that the requisite morphological and behavioral modifications are not necessarily difficult to implement. A variety of advantages may accrue to those animals capable of flight. Aerial behavior may have initially evolved to aid in pursuit of other organisms, or may have served as a means to escape predation, as described below. Powered flight in particular allows organisms to extend dramatically either foraging or breeding territories, to migrate seasonally between divergent habitats, and even to inhabit unpredictable environments or environments with highly dispersed resources (Norberg 1985). For organisms living within a vegetational canopy, gliding or controlled falling may offer an efficient mechanism for travel from branch to branch or from tree to tree. The instantaneous energetic cost of gliding is likely very low relative to active wing flapping given that only minor postural adjustments are required once the animal is airborne. Gliders may thus move more efficiently over longer distances relative to nongliders. For example, Norberg (1983) showed it was more efficient for birds to climb upward and then to glide between trees than to fly directly if the distance between successive trees exceeded about one-half the maximum glide distance. Similar biomechanical and energetic arguments have been advanced for the selective advantages of smaller body size in other gliders (Dial 2003, McGuire 2003, Scheibe & Robins 1998, Thorington & Heaney 1981).

All extant vertebrate gliders are exclusively arboreal and initiate their flights with a jump. Moreover, jumping via a startle response is widespread among animals (Eaton 1984), and one potential commonality among both flying vertebrates and insects may have been the initial acquisition of flight via the pathway of jumping and subsequent aerial trajectories to escape predation. Jump-initiated glides that increased survivorship during predation attempts would then potentially select for greater aerodynamic performance. The increased longevity of flying animals relative to their nonflying counterparts has been adduced as support for the hypothesis that predation avoidance is a major factor underlying the evolution of aerial locomotion (Holmes & Austad 1994, Pomeroy 1990). Arboreality obviously enhances the efficacy of jumping escapes given gravitationally accelerated body motion and access to a three-dimensional physical environment. Greater takeoff heights should facilitate such escapes and promote the evolution of aerial behaviors. For example, the canopy of lowland Indo-Malayan rainforests is typically tens of meters higher than that of African or New World counterparts, and residence at such heights may have structurally facilitated the multiple independent evolution of dedicated vertebrate gliders in this region relative to other tropical areas (de Gouvenain & Silander

2003, Dudley & DeVries 1990). Moreover, even arboreal taxa that are not gliders become inadvertently airborne from time to time. Falling from trees, for example, is a commonplace occurrence in certain frogs and lizards that otherwise exhibit no aerial abilities (Schlesinger et al. 1993, Stewart 1985).

Potential arboreal origins for winged vertebrates have been discussed at length elsewhere (e.g., Padian & Chiappe 1998, Rayner 1988, Zhou 2004). Here, we focus on aerial behavior in arboreal but wingless arthropods that are both common and diverse in forest canopies. Prominent examples include ant and termite workers, isopods, mites, spiders, and thysanurans, as well as the immature stages of many insect orders, especially the Orthoptera, Mantodea, Blattaria, Phasmida, Homoptera, and Hemiptera (Stork et al. 1997). Falling out of or being knocked down from tree crowns is a significant hazard for these and other wingless arboreal arthropods. The branching structure of forest canopies confines walking or running to a limited number of high-traffic routes. As a result, walking or running individuals face an enhanced probability of attracting predators and of becoming dislodged by physical disturbances (e.g., wind, rain), which potentially leads either to escape jumps or to accidental falls.

Falling wingless animals are inevitably displaced to lower vegetational levels or to the understory for all but the smallest forms. Whereas landing on midstory branches, saplings, or shrubs may be inconsequential to small arboreal taxa, landing on the forest floor presents new problems, including structurally complex terrain (e.g., leaf litter) and an unfamiliar suite of predators. One important example concerns the flood plains of large tropical rivers (e.g., varzéa). Landing in the understory of such flooded forests reveals the greatest hazard, namely the abundance of surface-feeding carnivorous fish in this aquatic setting (de Mérona & Rankin-de-Mérona 2004, Saint-Paul et al. 2000). A small fallen animal will be maimed or consumed within seconds of hitting the water. Thus, in both upland and inundated forests, selection should favor traits that either prevent a fall (e.g., modified adhesive appendages; Beutel & Gorb 2001), or that allow the animal to influence how and where it lands (e.g., controlled descent and gliding). Controlled gliding in wingless arthropods has been postulated as now extinct intermediate behavior in the acquisition of flapping wings and powered flight (Dudley 2000, Hasenfuss 2002, Maynard Smith 1952). The recent discovery of directed aerial descent in ants (Yanoviak et al. 2005), an evolutionarily derived lineage, suggests that the behavior may be widespread among extant arboreal arthropods.

Ants compose a substantial fraction of insect abundance and biomass in tropical forests (Davidson et al. 2003, Fittkau & Klinge 1973, Stork et al. 1997, Tobin 1995), and are the most conspicuous arthropods in the crowns of tropical trees. Arboreal ant workers, which are wingless, fall from trees with high frequency in the phenomenon known as "ant rain" (Haemig 1997, Longino & Colwell 1997). Fallen workers that become lost or depredated are costly to the colony, and selection has favored multiple behavioral and morphological traits in arboreal ants to preclude falling. Nonetheless, ants frequently fall from tree crowns (Haemig 1997, Longino & Colwell 1997), and some jump from branch surfaces to escape disturbance (Weber 1957). Whereas many ants simply free-fall once airborne, workers of numerous species can direct their aerial descent to return to their home tree trunk (Yanoviak et al. 2005). Whether initiated by

a jump or involuntarily, the subsequent directed descent leading back to the tree trunk is "J"-shaped and can be described as a three-part process: (*a*) an initial uncontrolled vertical drop with appendages extended (i.e., parachuting), (*b*) a rapid turn that results in alignment of the abdomen toward the tree trunk, and (*c*) a steep backward glide to the trunk (Yanoviak & Dudley 2006, Yanoviak et al. 2005; see **Figure 1**). Gliding behavior is now known to occur in at least seven arboreal ant genera (some of which are not closely related), demonstrating ample need for effective aerial performance in diverse taxa. More generally, these studies suggest that the occurrence of controlled gliding in arthropods and possible diversity of underlying aerodynamic mechanisms are substantially underestimated.

EVOLUTIONARY EXPERIMENTS IN VERTEBRATE GLIDING

In contrast to aforementioned findings with gliding ants, the diversity of terrestrial vertebrate gliders has long been appreciated. The 60 extant species of gliding mammals are a remarkably diverse group deriving from minimally nine independent evolutionary origins (Jackson 2000, Mein & Romaggi 1991, Meng et al. 2006, Scheibe & Robins 1998, Storch et al. 1996). Furthermore, this group exhibits tremendous size variation, ranging over two orders of magnitude in body mass (Nowak 1991). The rodent family Sciuridae includes no fewer than 44 species of flying squirrels for which a high degree of maneuverability is typically noted. It has been hypothesized that larger gliding squirrels have relatively longer tails to aid in steering (Thorington & Heaney 1981, Thorington et al. 2002). However, using independent contrasts analysis (as implemented in CAIC; Purvis & Rambaut 1995) and recent sciurid phylogenies (Mercer & Roth 2003, Thorington et al. 2002), we find no support for a positively allometric relationship in tail length within either gliding or nongliding squirrels. All large arboreal squirrels, gliders or otherwise, use their large round tail as a counterweight for balance along narrow branches. By contrast, small gliding squirrels, and the smallest mammalian glider of all, the marsupial feathertail glider, have distichous (i.e., flattened) tails that may serve an important aerodynamic function in the absence of selection pressure for a large counterbalancing tail. Dermopterans, by contrast, are the only large mammalian gliders with a tail that is completely subtended by the patagial membrane; not surprisingly, they are exclusively suspensory but are nonetheless aerially maneuverable.

In contrast to the mammalian gliders, other gliding vertebrates are not well known. Here we review the fascinating taxonomic and morphological diversity of gliding in reptiles and amphibians. Aerial descent has been reported for many anuran taxa in the context of breeding aggregations. Gliding descent at angles less than 45° has been observed in at least two anuran families, the Rhacophoridae and Hylidae, whereas steeper trajectories have been observed in both of these families as well as in the Leptodactylidae. Controlled aerial behaviors are well documented in numerous New World species of the family Hylidae, including *Ecnomiohyla miliaria*, *Phyllomedusa callidryas*, *Pachymedusa dacnicolor*, *Agalychnis spurrelli*, *A. saltator*, and *Scinax ruber* (Duellman 2001, Faivovich et al. 2005, Pauly et al. 2005, Pyburn 1970, Roberts 1994, Scott & Starrett 1974). Some of these species possess minimal aerodynamic surfaces in the

form of webbed hands and feet and/or the presence of supplementary integumentary folds bordering the limbs (e.g., *P. callidryas*, *A. saltator*), but nonetheless are sufficiently aerial as to regularly use gliding locomotion. Intermediate degrees of webbing are exhibited by several documented gliders (*P. dacnicolor*, *Cruziohyla calcarifer*) and extensive webbing characterizes *Hyla miliaria* and *A. spurrelli*. Additional species with morphologies similar to those of well-documented gliders can be assumed to carry out some form of controlled aerial descent. These include various taxa with intermediate degrees of hand and feet webbing (e.g., *Smilisca sordida*, *S. sila*, *Hypsiboas rufitelus*, *H. salvaje*, *Ptychohyla dendrophasma*, *Ecnomiohyla valancifer*, *E. minera*, *Agalychnis annae*, and *A. calcarifer*), as well as species with full or nearly complete webbing of hands and feet (e.g., *Hypsiboas boans*, *Ecnomiohyla thysanota*, and *Agalychnis litodryas*).

Additional predictions may be made from the wide range of morphological variation exhibited by hylid frogs (Cott 1926, Duellman 2001). Nearly all species for which aerial descent has been documented are relatively slender forms with dorsoventrally flattened bodies. It is important to note that just because a species has moderate webbing and/or supplementary dermal flaps does not necessitate that it is a functional glider. Heavy-bodied species that are not capable of aerial descent may possess interdigital webbing and dermal ornamentation as a result of other adaptive contexts (e.g., crypsis). Some species that are endowed with relatively extensive webbing are nevertheless heavy-bodied and are not expected to be gliders (e.g., *Charadrahyla nephila*, *C. trux*, and members of the genus *Plectrohyla*). Slender-bodied forms such as *H. boans*, *H. rosenbergi*, *H. wavrini*, and *Osteopilus vastus* are morphologically likely candidates for gliding behavior, as is *Cruziohyla craspedopus*, a species with extensive cutaneous flaps and fringes on the outer edges of the fore- and hindlimbs. One New World anuran species in the family Leptodactylidae (*Eleutherodactylus coqui*) has been documented to parachute (Stewart 1985), but with little or no horizontal transit, this mode of aerial descent is far from specialized.

The Old World tree frogs (Family Rhacophoridae) have independently converged on gliding morphologies and behavior, with at least five species in the genus *Rhacophorus* documented to be aerially proficient (Boulenger 1912, Emerson & Koehl 1990, Inger 1966, Liem 1970, McCay 2001). Additional species that possess at best limited webbing of hands and feet (e.g., *Polypedates leucomystax*, *P. macrotis*, and *P. otilophus*) are nonetheless capable of substantial lift generation and controlled descent under experimental conditions (Emerson & Koehl 1990, Emerson et al. 1990). Extensive webbing of the hands and feet together with accessory flaps bordering the limbs suggest that additional rhacophorids may be proficient gliders, including *Rhacophorus harrissoni*, *R. dulitensis*, *R. georgii*, *R. prominanus*, *R. maximus*, *R. feae*, and *R. rufipes*. The numerous *Rhacophorus* species with more limited morphological specializations may well be capable of simple parachuting but have not been studied. An additional anuran glider is *Hyperolius castaneus* (Hyperoliidae) in Rwanda and the eastern Congo. Arboreal and semiarboreal habits are typical of these relatively unstudied anuran taxa.

Reptiles exhibit a diversity of aerial locomotor behaviors ranging from simple parachuting in many lizards and snakes to the powered flight of birds and pterosaurs. Here, we focus our attention on the nonpowered fliers, both among extant squamates and early diverging but now extinct reptilian lineages. As discussed above in the

context of arthropods, it seems likely that the number of arboreal species capable of either gliding or controlled aerial descent can be dramatically underestimated if we assume that gliding species will exhibit obvious morphological innovations. For example, two lizard species, the polychrotid green anole (*Anolis carolinensis*) and the lacertid *Holaspis guentheri*, can generate glides with less than 45°descent angles although neither species has a patagium, elaborated skin folds, or toe webbing that one might expect in a gliding lizard [Oliver 1951, Schiøtz & Volsøe 1959; note that *Holaspis* exhibits a number of less obvious modifications associated with gliding (Arnold 2002)]. This finding is not surprising given that aerodynamic lift is proportional to the square of speed—if a lizard falls rapidly enough and assumes a proper body orientation, it will be able to produce forward momentum. Thus, the first innovation in an incipiently gliding lineage is likely to be behavioral and to involve appropriate positioning of the body and limbs.

Numerous squamate lineages exhibit morphological and behavioral adaptations for flight. Several species of Southeast Asian geckos in the genera *Ptychozoon*, *Luperosaurus*, and *Cosymbotus* have fully webbed hands and feet, flaps or folds of skin along the lateral body wall, and dorsoventrally flattened tails with or without marginal crenulations that increase surface areas (Brown & Diesmos 2000; Brown et al. 1997, 2000, 2007; Russell 1979; Russell et al. 2001). Although only *Ptychozoon* among these genera has been studied in any detail with respect to gliding performance or body motions (Heyer & Pongsapipatana 1970, Marcellini & Keefer 1976, Young et al. 2002), all are likely capable of highly directed aerial descent. Several species of *Ptychozoon* and two species of *Cosymbotus* have been observed to jump from the trunk of a tree, glide some distance lower, and return to the same tree (Brown et al. 1997, Honda et al. 1997; J. McGuire, personal observations). The agamid flying lizards (genus *Draco*) of Southeast Asia and southern India are clearly the most accomplished squamate gliders. This genus comprises approximately 45 species (McGuire & Kiew 2001), all of which have similar glide membranes composed of a patagium supported by 5–6 elongated thoracic ribs, as well as laterally projectable throat lappets controlled by the hyoid apparatus (Colbert 1967, McGuire 2003, Russell & Dijkstra 2001) that possibly function as canards (i.e., an aerodynamic control surface mounted in front of an aircraft). A number of nonsquamate fossil lineages were putative gliders with morphologies analogous to that of *Draco* in that they had patagia supported by elongated ribs or bony rib-like structures. These lineages include the Late Triassic kuehneosaurids *Icarosaurus seifkeri* and *Kuehneosaurus*, the Late Permian *Coelurosauravus jaekeli*, and the Late Triassic *Sharovipteryx mirabilis*, each of which had its own peculiarities with respect to patagial morphology (Carroll 1978, Dyke et al. 2006, Evans 1982, Frey et al. 1997, Gans et al. 1987, Robinson 1962). The Southeast Asian flying snakes (genus *Chrysopelea*) are thought to lack morphological innovations related to gliding locomotion (Socha 2002, Socha & LaBarbera 2005). However, these snakes have hinged ventral scales (as do a number of other arboreal snake taxa in Southeast Asia such as *Dendrelaphis* and *Ahaetulla*) that could contribute to the concave body form exhibited by gliding *Chrysopelea*.

Among gliding reptiles, the ecological contexts of flight are only well-documented for the lizard genus *Draco*, for which gliding is the primary means of movement within

a home range that typically encompasses multiple trees (Alcala 1967; Mori & Hikida 1993, 1994). Flying lizards appear to avoid coming to the ground (except when females come to the ground to deposit eggs in the substrate) and thus movement from one tree to another usually involves gliding. *Draco* also will take to the air to avoid predators, chase conspecific males intruding on their territories, seek mating opportunities with females, and move between trees during foraging. For the lacertid *H. guentheri*, Schiøtz & Volsøe (1959) observed gliding behavior similar to that observed for *Draco*, with lizards initiating glides from one tree to another in several contexts. In one case, the lizard crossed a small river, and in other instances, the lizard immediately began foraging upon landing. Our knowledge of the ecological context of gliding in other reptiles is poorly known. It is clear that the geckos *Ptychozoon*, *Cosymbotus*, and *Luperosaurus*, and the flying snakes (*Chrysopelea*) utilize gliding for close-context escape (Honda et al. 1997; J. McGuire, personal observation). However, it is unclear if any of these taxa utilize gliding as a means of routine displacement (e.g., while foraging) within the forest canopy.

EVOLUTIONARY TRANSITIONS TO FLAPPING FLIGHT

Powered flapping flight has evolved independently four times in birds, bats, pterosaurs, and pterygote insects. The paleobiological context and biomechanical features of transitional forms are controversial in each case and have long been the subject of intense speculation. In general, the functional transition from gliding to flapping and associated production of thrust is biomechanically feasible (Norberg 1985). Recent findings on avian feathering and flight origins have been reviewed elsewhere (Norell & Xu 2005, Prum 2002), as has been pterosaur evolution (Buffetaut & Mazin 2003). No paleontological evidence is available for the morphologies of aerodynamically transitional bats, although their arboreal origins seem clear (Gunnell & Simmons 2005). For the evolution of bird flight, a recent hypothesis (Dial 2003a,b) suggests that forewing-generated aerodynamic forces facilitated hindlimb traction during running ascent on inclined or vertical surfaces (i.e., wing-assisted incline running); whereas the mechanics of this behavior are well documented in some extant birds (Bundle & Dial 2003) and are particularly important for juveniles with reduced wing area relative to adults (Dial et al. 2006), the phylogenetic distribution of this trait has not yet been assessed. The behavior may derive from ancestral use of wings in inadvertent falls, escape from nest predators, or during the ontogenetic acquisition of flapping (i.e., wing-assisted descent). In this vein, a diversity of recent biomechanical and paleontological studies support arboreal origins and gliding intermediates for flight in birds (Chatterjee & Templin 2007, Geist & Feduccia 2000, Long et al. 2003, Longrich 2006, Zhou 2004). Here, we review in detail the relevant literature pertaining to the origins of insect flight.

For the winged (i.e., pterygote) insects, historical origins are indeterminate but probably lie in the Upper Devonian or early Lower Carboniferous. Wingless hexapods are known from 395–390 Mya (Labandeira et al. 1988, Shear et al. 1984), whereas fossils of pterygote hexapods (i.e., winged insects) date from approximately 325 Mya (Nelson & Tidwell 1987). By the Upper Carboniferous, pterygotes are

impressively diversified into about fifteen orders (Grimaldi & Engel 2005, Labandeira & Sepkoski 1993). Although pterygote insects are likely monophyletic (Grimaldi & Engel 2005, Regier et al. 2005), the morphological origins of wings remain obscure. Wings have been proposed to derive either from fixed paranotal outgrowths of thoracic and abdominal segments in terrestrial taxa (Bitsch 1994, Rasnitsyn 1981) or from ancestrally mobile gills, gill covers, leg structures, or styli in aquatic forms (Averof & Akam 1995, Kukalová-Peck 1983, Wigglesworth 1973). An intermediate possibility involves a terrestrial origin of wings derived from pre-existing leg, thoracic, or abdominal structures.

Unfortunately, no transitional forms are known between the wingless apterygotes and the winged pterygote insects, and the biology of early winged forms remains speculative and contentious. Of particular interest to the origins of flight is ancestral habitat association of early winged insects—were these animals terrestrial or aquatic? Phylogenetically, the closest sister taxa to the pterygote insects, the apterygote insect orders Zygentoma and Archaeognatha (Thysanura sensu *lato*), are exclusively terrestrial. Deeper within the phylogeny, the sister group to the insectan hexapods is the entognathan hexapods, the Collembola and the Diplura. The few aquatic species of collembolans are clearly derived (D'Haese 2002), and the remainder of the Collembola and all of the Diplura are terrestrial taxa. All hexapods, in turn, derive from a terrestrial crustacean lineage (Regier et al. 2005). An abundance of phylogenetic evidence is now clear on these points: hexapods evolved terrestrially, and the extant lineages closest to the winged insects are exclusively terrestrial. Apterygote insects, and particularly the thysanurans, thus offer the closest similarities of all extant taxa to predecessors of the winged insects.

Additional evidence, particularly that relating to the physiology and origins of the insect tracheal system, indicates that winged insects evolved from terrestrial apterygote ancestors (Dudley 2000, Grimaldi & Engel 2005, Messner 1988, Pritchard et al. 1993, Resh & Solem 1984). Aquatic larvae, particularly those of the extant and phylogenetically basal Odonata and Ephemeroptera, appear to be secondarily derived (Pritchard et al. 1993). Independent of habitat association, however, both larvae and adults of ancestral winged insects probably expressed lateral lobed structures on the abdominal as well as the thoracic segments (Carroll et al. 1995, Kukalová-Peck 1987). If winglets or wings derived initially from fixed paranotal lobes or from modified leg styli, flapping motions might have emerged indirectly through the action of dorsoventral leg muscles that insert on the thorax, as characterizes so-called bifunctional muscles in many extant insects (Fourtner & Randall 1982, Wilson 1962). A general question relating to wing origins concerns the possible evolution of novel winglike structures, as opposed to modification of pre-existing morphological features. Acquisition of wings from ancestrally mobile structures might seem more parsimonious than the derivation of flapping wings from stationary paranotal lobes, although the neontological and paleontological data available at present are insufficient to prove unequivocally either of these two hypotheses (Dudley 2000, Grimaldi & Engel 2005).

A variety of possible functional roles have been attributed to transitional winglets or early wings, including aerodynamic utility, epigamic display during courtship, and

thermoregulation (Douglas 1981; Ellington 1991; Kingsolver & Koehl 1985, 1994). Hydrodynamic use for features that ultimately became aerodynamic structures has been proposed for ancestrally aquatic forms. Hexapods could also have used winglike structures in air either to drift passively, row, or skim actively along water surfaces (i.e., an "airboat" hypothesis; Marden & Kramer 1994, 1995). These behaviors are clearly derived rather than retained ancestral traits of winged insects given their rare occurrence and derived condition in the Paleoptera (Ruffieux et al. 1998, Samways 1996), their multiple independent origins within the Neoptera—including plecopterans, several dipteran taxa, and some trichopterans (Dudley 2000, Will 1995)—and the phylogenetic improbability of ancestrally aquatic pterygotes (Grimaldi & Engel 2005).

Importantly, surface rowing by certain plecopteran taxa, which represents a putatively ancestral biomechanical condition relative to flapping of wings in air, occurs in a highly derived group of stoneflies (Marden & Thomas 2003, Thomas et al. 2000). Biomechanical considerations also suggest that postulated aquatic precursors would have been unlikely to evolve wings that served aerodynamic functions. Water and air differ by almost three orders of magnitude in density, with a corresponding difference in the Reynolds number and in the nature of forces generated by oscillating structures. The functionality of wing designs intermediate to either hydrodynamic or aerodynamic force generation is correspondingly unclear (Dudley 2000). Forces of surface tension would present a formidable physical barrier to partial body emergence as well as to projection and oscillation of flattened structures, particularly for the body sizes (2–4 cm) deduced as characteristic of ancestral pterygotes (Labandeira et al. 1988, Wootton 1976).

Given the assumption of terrestrial pterygote ancestors, a standard explanation for the evolution of wings has been that these structures aerodynamically facilitate jumping escapes from predators on land. Suggestively, a suite of morphological and behavioral protoadaptations for jump-mediated glides is evident among extant apterygote hexapods, the terrestrial sister taxon of the winged insects. Thoracic paranotal lobes as well as styli on the legs and abdominal segments of extant apterygotes could potentially have served in ancestral taxa to generate lift and to facilitate saltatorial escape. Neurobiological studies also support the ancestral presence of dedicated sensorimotor pathways underlying escape behavior in both apterygotes and pterygotes (Edwards & Reddy 1986, Ritzmann 1984). The startle response of ancestral apterygote insects was then apparently co-opted during pterygote evolution to stimulate jumping, wing flapping, and even evasive flight once airborne (Edwards 1997, Hasenfuss 2002, Libersat 1994). The historical context of early pterygote evolution was appropriate for imposition of intense predatory pressure by both invertebrates and vertebrates, with a diversity of insectivorous arthropods (particularly arachnids), amphibians, and reptiles found in Devonian and Carboniferous terrestrial ecosystems (Behrensmeyer et al. 1992, Rolfe 1985, Shear & Kukalová-Peck 1990). Furthermore, the increasing arborescence and geometrical complexity of terrestrial vegetation through the Devonian and into the Carboniferous (Dilcher et al. 2004, Kenrick & Crane 1997) would have provided suitable three-dimensional substrate suitable for aerial escape and maneuvers.

CONCLUSIONS

Locomotor evolution within an arboreal context has yielded diverse vertebrate and arthropod taxa capable of controlled falls, directed aerial descent, and sophisticated gliding. The regulation of aerodynamic forces produced while falling from trees can occur in the complete absence of wings and is enabled by movement of both axial and appendicular structures. Subsequent evolution of more dedicated aerodynamic surfaces such as patagial membranes and true wings likely follows the initial acquisition of aerial maneuverability. Morphological and behavioral intermediates to true flapping flight can accordingly exhibit progressive functionality as they become more elaborate. It may seem unnecessary to emphasize the origins of flight within an arboreal and thus aerial context. However, unlike competing running and even aquatic hypotheses for flight origins in certain groups, this scenario for the evolution of flight is not taxon-specific. Instead, we have emphasized here the relatively undocumented and understudied diversity of controlled aerial behaviors found across a broad range of arboreal taxa. As with other complex evolutionary outcomes (e.g., endothermy), flapping flight represents a specialization attained by only a minority of lineages. Nonetheless, the study of biomechanical and physiological intermediates can reveal both underlying functional demands and alternative strategies to problems imposed by common selective environments. Arboreality may be one such environment for which flight and its control are desirable outcomes.

DISCLOSURE STATEMENT

The authors are not aware of any biases that might be perceived as affecting the objectivity of this review.

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