



SYMPOSIUM

Animal Aloft: The Origins of Aerial Behavior and Flight

Robert Dudley^{1,*†} and Stephen P. Yanoviak[‡]

*Department of Integrative Biology, University of California, Berkeley, CA 94720, USA; †Smithsonian Tropical Research Institute, P.O. Box 2072, Balboa, Republic of Panama ‡Department of Biology, University of Arkansas at Little Rock, 2801 S. University Ave., Little Rock, AR 72204, USA

From the symposium “The Biomechanics and Behavior of Gliding Flight” presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2011, at Salt Lake City, Utah.

¹E-mail: wings@berkeley.edu

Synopsis Diverse taxa of animals exhibit remarkable aerial capacities, including jumping, mid-air righting, parachuting, gliding, landing, controlled maneuvers, and flapping flight. The origin of flapping wings in hexapods and in 3 separate lineages of vertebrates (pterosaurs, bats, and birds) greatly facilitated subsequent diversification of lineages, but both the paleobiological context and the possible selective pressures for the evolution of wings remain contentious. Larvae of various arboreal hemimetabolous insects, as well as many adult canopy ants, demonstrate the capacity for directed aerial descent in the absence of wings. Aerial control in the ancestrally wingless archaeognathans suggests that flight behavior preceded the origins of wings in hexapods. In evolutionary terms, the use of winglets and partial wings to effect aerial righting and maneuvers could select for enhanced appendicular motions, and ultimately lead to powered flight. Flight behaviors that involve neither flapping nor wings are likely to be much more widespread than is currently recognized. Further characterization of the sensory and biomechanical mechanisms used by these aerially capable taxa can potentially assist in reconstruction of ancestral winged morphologies and facilitate our understanding of the origins of flight.

Introduction

Although many biologists view flight as a restricted or even rare form of locomotion characteristic only of birds, bats, the extinct pterosaurs, and pterygote insects, controlled aerial behaviors are much more widespread among animals. In addition to actively powered flapping flight, gliding with obvious wings or wing-like structures has evolved at least 30 times among diverse mammals, reptiles, and amphibians (Rayner 1988, Norberg 1990). In addition to such classically described gliders, directed aerial descent (*sensu* Yanoviak et al. 2005) can occur in the absence of obvious aerodynamic surfaces and is likely characteristic of many more taxa than currently recognized. Here, we survey a broad range of aerial behaviors, and suggest that the origins of animal flight derive primarily from either inadvertent or intentional descent within an arboreal context. Because of our interest in flapping flight, we exclude from consideration here lift-based aerial locomotion in certain marine taxa (e.g., flying fish and squid),

as well as the numerous botanical examples of lift-enhanced seed dispersal.

Definitionally, the word “flight” has been used in various ways in the biomechanics literature. We use the word here to indicate controlled aerial behavior either with or without obvious aerodynamic structures termed wings. Parachuting without regulation of the magnitude of the ensuing drag force can be truly passive, but all other aerial behaviors involve the generation and regulation of both lift and drag to reduce the rate of descent, to reorient the body, and to alter the flight trajectory. These behaviors could include such diverse phenomena as the aerial righting reflex, various maneuvers, and controlled landing (Table 1). Oliver (1951) distinguished between “gliding” and “parachuting”, with the former arbitrarily characterized by an angle of descent less than 45° relative to horizontal, and the latter with a descent angle greater than 45°. These definitions also assumed steady-state conditions of a constant translational velocity and equilibrium of forces. However, we suggest that such a discrete characterization of

Table 1 Generalized biomechanical scenario for the acquisition of aerial behaviors and flight

-
1. Arboreality; residence on elevated substrate
 2. Jumping (either volitional or via startle reflex); falling
 3. Aerial righting and landing reflexes
 4. Parachuting (drag-based descent)
 5. Directed aerial descent (lift-based and drag-based; steep glide angles)
 6. Gliding (predominantly lift-based; shallow glide angles)
 7. Elaboration of wings and maneuvers
 8. Flapping flight
-

what is a continuous variable is inappropriate. Many features of aerial behavior in gliding animals are unsteady, involving time-dependent changes in speed and orientation of the appendages and the body. Therefore, we use the term “gliding” as well as the phrase “directed aerial descent” to indicate controlled descent by an organism that converts gravitational potential energy to useful aerodynamic work. Dichotomous characterization of the instantaneous angle of descent (e.g., shallow vs. steep to characterize gliding and directed aerial descent, respectively) may nonetheless in some cases usefully distinguish what is clearly a continuum of descending flight (Dudley et al. 2007). In many cases, however, such descent is associated with volitional body displacements and rotations independent of the instantaneous trajectory angle relative to horizontal.

Indeed, Maynard Smith (1952) first suggested that control of the aerial trajectory when accelerating under gravity is essential to the evolution of both gliding and flapping flight. It is also important to distinguish between the origins of flight (i.e., of controlled aerial behavior) and the origins of wings as anatomical structures. For example, experimental studies of arboreal arthropods (Yanoviak et al. 2009) indicate that directed aerial descent and the capacity for maneuvers preceded phylogenetically the origin of wings in hexapods. Flight behaviors, therefore, do not necessarily involve those anatomical structures we term wings; aerodynamic control while falling and gliding can involve other axial and appendicular structures. This observation answers in part a classic question in evolutionary biology, namely why are there so few instances of wings “in their incipient and relatively imperfect functional condition”? (Mivart 1871); the potential uses of intermediate structures remain a topic of intense evolutionary scrutiny. Recognition of the diversity of controlled aerial behaviors seen in animal taxa is

thus an important step in addressing the nature of evolutionary transitions that ultimately may have led to fully powered flight in a small minority of lineages.

We propose a potential sequence (Table 1) for the acquisition of progressively more sophisticated aerial behaviors that may ultimately lead to either gliding or flapping flight. Millions of taxa (mostly arthropods) live in trees, shrubs, or herbaceous vegetation sufficiently tall as to permit gravitational acceleration to speeds that result in significant production of aerodynamic force on the body. Although less well documented, residence on elevated substrates such as cliffs or boulders would similarly provide opportunities for rapid downwards descent, particularly in arthropods (e.g., Fig. 1). Animals may become airborne either volitionally (e.g., by jumping) or unintentionally, as when chased by predators or displaced by winds and storms. Falling from trees, for example, is a commonplace occurrence in some frogs and lizards that otherwise exhibit no obvious aerial ability (Stewart 1985, Schlesinger et al. 1993). Wingless ant workers fall from trees with high frequency in the phenomenon known as “ant rain” (Haemig 1997, Longino and Colwell 1997), and some arboreal ants jump from branches and the phyllosphere more generally to escape disturbance (Weber 1957).

Jumping via a startle response is in fact widespread among animals (Eaton 1984), including the diverse arboreal fauna of both arthropods and vertebrates. The evolution of flight as motivated by initial jumping and subsequent aerial escape may be a general selective force if it increases survivorship during evasion of predators. Suggestively, arboreality is associated with an increased lifespan, at least in mammals (Shattuck and Williams 2010). It is important to recognize here the anthropogenic bias toward horizontal substrates in studies of animal jumping; most animals do not necessarily jump upwards but rather laterally from vegetation, and in some cases jump downwards as well. All such jumps initiate aerial translation and can be viewed as potential precursors to flight. Energetic advantages may also ensue as gliders move more efficiently over longer distances relative to nongliders (Norberg 1983), and such advantages may be greater at smaller body size (Thorington and Heaney 1981; Scheibe and Robins 1998; Dial 2003; McGuire 2003).

Once falling, and if not oriented dorsoventrally, many animals exhibit an aerial righting reflex so as to reorient ventrally downwards (Magnus 1922, Jusufi et al. 2010, Jusufi et al., this volume). Righting responses in air may in fact derive from terrestrial righting reflexes, and the evolutionary



Fig. 1 General maritime habitat and close-up view (inset) of the shoreline bristletail *Petrobius brevistylus* (Machilidae) at Acadia National Park, Maine (photographs by Steve Yanoviak). Typical adult body length is approximately 2 cm. These bristletails jump upon disturbance and land in stable postures on variably-oriented rocky surfaces below the takeoff point.

origins of this behavior merit further attention, particularly given the intrigues of coordinated multiaxial bending (Edwards 1986, Dunbar 1988). After orienting properly, many otherwise seemingly nonaerial taxa exhibit behaviors that decrease their rate of descent during the subsequent fall (Oliver 1951; Dunbar 1988; Pellis et al. 1989). This drag-based method is termed parachuting, and implies (in contrast to some human parachuting devices) a slowing of descent but no active horizontal orientation in the air. Landing reflexes, although less well studied, may similarly characterize the advent of controlled aerial behaviors given the need to lower speed and reduce damage caused by impact upon the substrate.

If lateral force (i.e., lift) is generated while parachuting, deviation from a vertical trajectory ensues. At steep angles, this outcome is termed directed aerial descent (Yanoviak et al. 2005), whereas shallower trajectory angles have classically been termed gliding. Although relevant data are difficult to obtain in the field, it is clear that most such glides are not necessarily characterized by a constant angle and speed of descent. For example, an equilibrium phase is uncommon in *Draco* (i.e., only about 50% of studied glides; McGuire and Dudley 2005), in the gliding snake *Chrysopelea* (Socha and LaBarbera

2005; Socha et al. 2005), and in the southern flying squirrel (Bishop 2006), at least over the spatial scales under consideration. Both small-scale corrections and dramatic maneuvers are typical of animal gliders (Colbert 1967; Dolan and Carter 1977; Jackson 2000); gliding individuals can engage in large-scale directional changes, avoid obstacles, land lower down on the original takeoff tree, and make rapid last-second changes in landing sites. Air turbulence may similarly elicit dynamic corrections in course (McCay 2003).

Mechanistically, a diversity of studies indicates that gliding animals are able to use limb, tail, and whole-body movements to effect both axial and torsional maneuvers (Johnson-Murray 1987; Emerson and Koehl 1990; Emerson et al. 1990; McCay 2001; Socha and LaBarbera 2005; Socha et al. 2005; Wilkinson et al. 2006). The mechanical consequences of even small appendicular structures and augmented surface areas of the body may be substantial, given that aerodynamic torque and consequent rotations of the body are enhanced when forces act through points distant from rotational axes (Dudley 2002). The use of bilaterally asymmetric motions of the limbs or wings in maneuvers (and perhaps initiated with the aerial righting reflex) is not far removed

from symmetric motions and ultimately repetitive flapping. In turn, we examine the cases of winged hexapods and of volant vertebrates to evaluate the plausibility of the scenario outlined in Table 1 for the evolution of flapping flight.

The origins of insect flight

Knowledge of the origins and early evolution of winged insects is based on limited paleontological evidence. An approximately 65 million year (My) gap separates the occurrence of the earliest known winged insects (325 My) from fossils of their apterygote ancestors (395–390 My; Whalley and Jarzembowski 1981; Labandeira et al. 1988; Grimaldi and Engel 2005). The report of a dicondylic jawed hexapod from approximately 400 My may indicate contemporaneous wing origins (Engel and Grimaldi 2004), although thoracic structures were not found with the aforementioned specimen. Because pterygote insects appear abruptly in the fossil record with no obvious transitional forms, both the anatomical precursors to wings as well as the selective forces promoting their initial evolution remain unresolved. Nonetheless, paleobiological reconstruction and genetic studies can at least delineate possible scenarios of pterygote evolution.

Diverse molecular evidence now indicates that the hexapods derive from terrestrial crustaceans (Regier et al. 2005; Gao et al. 2008; Telford et al. 2008; Grimaldi 2010; Meusemann et al. 2010). Apteriygote insects are almost exclusively terrestrial with the exception of some derived collembolans (D'Haese 2002); the possession of a tracheal system by all hexapods clearly predisposes these animals to life in air. The hypothesis that insect wings evolved in freshwaters, being derived from gills or gill plates of primitively aquatic forms, thus appears unlikely for phylogenetic reasons (Messner 1988; Pritchard et al. 1993; Dudley 2000; Grimaldi and Engel 2005). Furthermore, the earliest fossilized aquatic insects are only known from deposits approximately 100 My after the first (and diversified) appearance of winged insects, although taphonomic considerations would suggest an enhanced likelihood of preservation for freshwater forms (Grimaldi and Engel 2005). The occurrence of hemocyanins in a stonefly species has also been adduced to support aquatic origins of hexapods (Hagner-Holler et al. 2004), but subsequent analysis has shown that these molecules are found in both apterygote and pterygote lineages, and that their presence is accordingly not informative relative to the origins of wings (Burmester and Hankeln 2007; Pick et al. 2009).

The use by certain extant Plecoptera of wings to drift passively, to row, or to skim actively along water surfaces has been proposed as a transitional behavior to flight for ancestrally aquatic pterygotes (Marden and Kramer 1994; Marden and Kramer 1995; see also Lang 1891, p. 457). Such behaviors are, however, derived rather than retained ancestral traits of winged insects given their rare occurrence and derived condition within the Paleoptera (Samways 1996; Ruffieux et al. 1998; Marden et al. 2000). Surface-skimming has also evolved independently multiple times within the Neoptera, including taxa in such varied orders as the Plecoptera, Diptera, and Trichoptera (Will 1995; Dudley 2000). Moreover, surface rowing by some plecopteran taxa, which represents a putatively ancestral biomechanical condition relative to the flapping of wings in air, occurs in a highly derived group of stoneflies (Thomas et al. 2000; Marden and Thomas 2003). These considerations lend further indirect support to the robust phylogenetic conclusion that pterygotes were ancestrally terrestrial.

Independent of their associations with particular habitats, however, both larvae and adults of ancestral winged insects probably expressed lateral lobed structures on the abdominal as well as on the thoracic segments (Kukalová-Peck 1987; Carroll et al. 1995). If winglets or wings derived initially from fixed paranotal lobes or from modified leg styli, flapping motions might have emerged indirectly through action of dorsoventral leg muscles that insert on the thorax, as characterizes so-called bifunctional muscles in many extant insects (Wilson 1962; Fournier and Randall 1982). A general question relating to the origins of wings concerns the possible evolution of novel winglike structures, as opposed to modification of pre-existing morphological features. Derivation of flapping wings from ancestrally mobile structures (Wigglesworth 1973; Kukalová-Peck 1983) might seem more parsimonious than from stationary paranotal lobes (Rasnitsyn 1981; Bitsch 1994), although the neontological and paleontological data available at present do not unequivocally distinguish between these 2 hypotheses (Dudley 2000; Grimaldi and Engel 2005; Béthoux and Briggs 2008). However, a recent developmental study of 3 regulatory genes in bristletails and ephemeropterans strongly indicates paranotal origins for wings (Niwa et al. 2010), in contrast to earlier studies of gene expression that suggested their homology with crustacean gills (Averof and Cohen 1997; Damen et al. 2002), but that also failed to include apterygote taxa in the comparative analyses.

Primary among hypotheses for flight evolution in terrestrial hexapods has been the proposed use of jumping for aerial escape from land predators. Neurobiological studies support the ancestral presence of dedicated sensorimotor pathways underlying escape behavior in both apterygotes and pterygotes (Ritzmann 1984; Edwards and Reddy 1986). 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 (Libersat 1994; Edwards 1997; Hasenfuss 2002, 2008). 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 (Rolfe 1985; Shear and Kukalová-Peck 1990; Behrensmeier et al. 1992). The earliest spider fossil is from the Middle Devonian (Shear et al. 1984), suggesting coevolutionary interactions between spiders and pterygote insects close to the origins of the latter group (Penney 2004). Furthermore, the increasing arborescence and geometrical complexity of terrestrial vegetation through the Devonian and into the Carboniferous (Kenrick and Crane 1997; Dilcher et al. 2004) would have provided abundant three-dimensional substrate suitable for aerial escape and maneuvers. Foraging on reproductive structures of the diversifying flora would also have been enhanced by greater gliding abilities. In addition to such potential aerodynamic uses, winglets on hexapods may also have served in a variety of other roles, including epigamic display during courtship and thermoregulation (Douglas 1981; Kingsolver and Koehl 1985; Ellington 1991; Kingsolver and Koehl 1994).

Importantly, recent work demonstrates that controlled aerial behavior phylogenetically precedes the origin of wings in hexapods (Yanoviak et al. 2009). Arboreal bristletails use an aerial righting reflex when falling to reorient from a vertical tumble to a stable dorsoventral and headfirst posture, and then to glide with nontrivial lift:drag ratios and targeted maneuvers toward a nearby tree trunk. Aerial control is presumably mediated visually, as in gliding ants (Yanoviak and Dudley 2006). Dorsoventral and lateral ruddering of the abdominal filaments, with their substantial moment arm relative to the body center of mass, is used to continuously steer and to effect targeting. These results suggest that the sensory and biomechanical capacities to orient during free fall and to effect controlled gliding may have preceded the appearance of wings proper. The typical body

sizes of extant archaeognathans, moreover, match well the inferred ancestral body lengths of pterygotes (2–4 cm; Flower 1964; Wootton 1976; Labandeira et al. 1988; see also Fig. 1). Enhanced force production on protowings (as well as gigantism evident in the late Paleozoic arthropod fauna) would also have been facilitated by the contemporaneous hyperoxic atmosphere and an increased total atmospheric pressure (Dudley 1998). The existence of aerial control in the ancestrally wingless bristletails, and its association with an arboreal lifestyle, are consistent with the hypothesis of a terrestrial origin for winged flight in insects.

Vegetational canopies, moreover, present both opportunity and danger to wingless arthropods. Diverse invertebrate and vertebrate taxa (e.g., spiders, ants, insectivorous birds, marmosets) either dislodge or prey upon wingless invertebrates. Thunderstorms of the metonymous rainforest and other forest canopies may also knock arthropods out of trees. The selective benefits of the aerial behaviors delineated in Table 1 may accordingly be substantial, particularly given major ecological differences between the arboreal habitat and a potentially hostile ground fauna. Although never systematically surveyed, aerial righting as well as landing reflexes (Table 1) likely characterize most arboreal animals, be they invertebrate or vertebrate. The phenomenon of directed aerial descent is now known to characterize either larval or wingless adult insects from at least 8 different hexapod orders (Fig. 2). What is not present among modern insects, however, is an ancestrally flightless taxon that expresses partial wings or winglets (nymphal hemimetabolous insects can possess large wingbuds in the final instar, but these are not articulated). However, the study of secondarily flightless phasmids with varying degrees of wing reduction and flight capacity can assess biomechanical functionality of such morphological intermediates (Y. Zeng, personal communication).

Gliding vertebrates and flapping flight

As with winged insects, the historical origins of flying vertebrates remain indeterminate. The most recent volant vertebrates are the bats, with a modern morphology apparent in a microchiropteran fossil from 50 My. Given this dating, chiropteran origins appear to lie within the early Paleocene or late Cretaceous (Gunnell and Simmons 2005). Birds first appeared in the mid-Jurassic to late Jurassic (Prum 2002; Zhou 2004; Norell and Xu 2005). The timing of pterosaur origination and early diversification is unknown but possibly lies within the Permian given well-developed

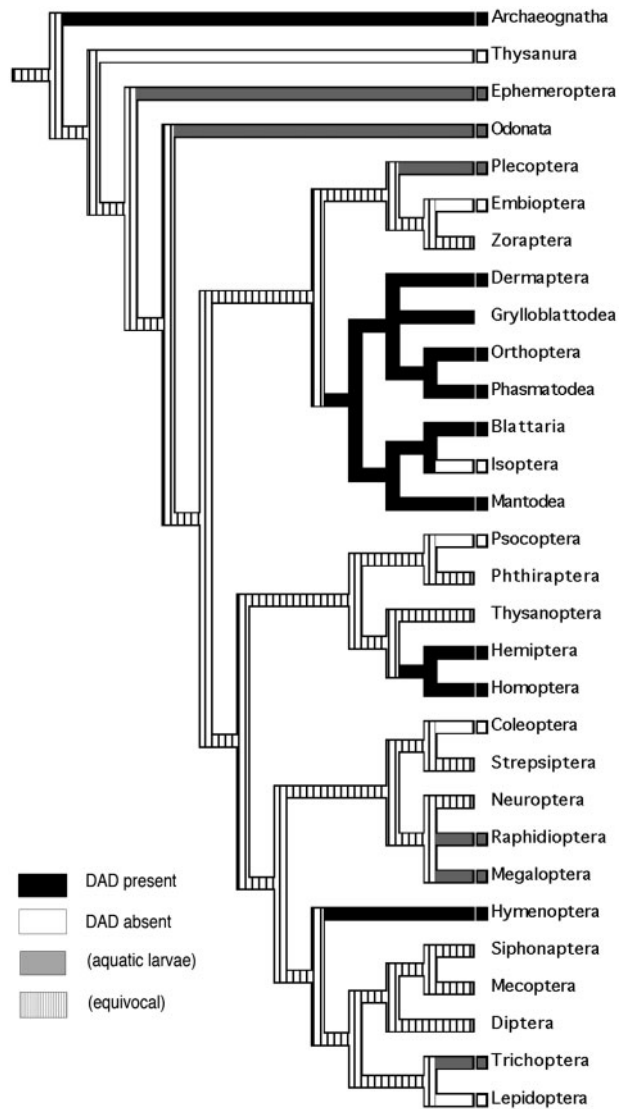


Fig. 2 Phylogenetic distribution of directed aerial descent (DAD) among orders of Hexapoda (topology following Grimaldi and Engel 2005). Occurrence of DAD in one or more larval representative of a particular lineage is indicated in black; presence of obligately aquatic larvae for which DAD is precluded ecologically is indicated in gray. A missing terminal square at an ordinal branch tip indicates absence of data for the lineage in question.

pterosaur morphologies by the mid-Triassic to late Triassic (Buffetaut and Mazin 2003; Unwin 2006). The wing structures of bats, birds, and pterosaurs all involve the forelimb, and in bats also attach to the hind limb. Numerous vertebrate gliders (characterized by obvious aerodynamic surfaces and shallow equilibrium glide angles) are also found among the extant fauna, including at least 9 independent origins in mammals (Thorington 1984; Jackson 2000), and an abundant and certainly undercounted diversity of gliders among both extinct and extant reptiles and

amphibians (Dudley et al. 2007). These latter groups utilize a variety of dermal flaps, interdigital webbing, tail crenulation, and body flattening to increase their aerodynamic surface area during flight.

All extant vertebrate gliders are arboreal, whereas many nongliding arboreal taxa also exhibit aerial righting reflexes and parachuting behavior (Dudley et al. 2007; Jusufi et al. 2010). Moreover, some reptiles with no obvious morphological specialization for flight glide with shallow descent trajectories (Oliver 1951; Schiøtz and Volsøe 1959; Arnold 2002). These observations suggest that the number of arboreal taxa capable of either gliding or directed aerial descent may be dramatically underestimated, and that dynamic positioning of the body and limbs may be the initial innovation in aerial behavior, starting with the righting reflex. For example, both righting responses and sky-diving postures with extended limbs and an arched back have been reported in a diversity of nonvolant amphibians and reptiles exposed to microgravity (Wassersug et al. 2005). Unfortunately, the ecological context of gliding flight is known only for the lizard genus *Draco*, for which this behavior is the primary means of movement within a home range that typically encompasses multiple trees (Alcala 1967; Mori and Hikida 1993; Mori and Hikida 1994). Other aerial reptiles are known to use gliding in escape (Honda et al. 1997). In general, only limited data are available on the specific contexts of flight for gliding reptiles and amphibians, in part because of the difficulties of observing individuals high up in the tree canopy. Mammalian gliders, all of which are herbivorous, often use this locomotor behavior as a feature of their nocturnal foraging routine.

A functional transition from gliding to flapping flight with the production of forward thrust in addition to gravitational offset is known to be theoretically feasible (Norberg 1985; Nudds and Dyke 2009). The limited paleontological evidence currently available precludes assessment of this possibility for early pterosaurs (Buffetaut and Mazin 2003). It is nonetheless suggestive that the basal lineages were primarily long-tailed and thus more passively stable in gliding, with more derived forms exhibiting progressive diminution of the tail (Lu et al. 2009). Similarly, the morphologies of aerodynamically transitional early bats are unknown, although their arboreal origins are not disputed, particularly given the number of extant gliding mammalian taxa that serve well as functional exemplars of this lifestyle (Gunnell and Simmons 2005; Bishop 2008). Most disputed among potential evolutionary transitions to flight is the origin of birds. However, a diversity of recent

studies support an arboreal context and gliding intermediates for flight in this group (Geist and Feduccia 2000; Long et al. 2003; Zhou 2004; Longrich 2006; Chatterjee and Templin 2007). In contrast, theoretical modeling of *Archaeopteryx* flapping suggests a running takeoff speed that is sufficient for generation of aerodynamic force to yield upwards flight (Burgers and Chiappe 1999). However, this model assumed an unreasonably high mean lift coefficient for the wings (i.e., a value of 2.0), and also ignored drag forces on both the wings and body which would act to substantially reduce horizontal thrust. Moreover, ongoing paleontological discoveries indicate that avian morphologies passed initially through a long-tailed, 4-winged stage suggestive of gliding prior to locomotor dedication of the forelimbs as flapping structures (Xu and Zhang 2005; Hu et al. 2009; Alexander et al. 2010; Hone et al. 2010; Ruben 2010; see also Beebe 1915).

Alternatively, recent studies have proposed that bird wings evolved as flapping structures that facilitated running ascent on either inclined or vertical surfaces (i.e., wing-assisted incline running, or WAIR; Dial 2003; Dial et al. 2006). Whereas the mechanics of this behavior are well-documented in some extant birds (Bundle and Dial 2003), and are particularly important for juveniles with reduced wing area relative to adults (Jackson et al. 2009), the phylogenetic distribution of this trait has not yet been assessed. The behavior of WAIR may be derived relative to ancestral traits in birds, although knowledge of its distribution among contemporary avian taxa may also be evolutionarily noninformative given that the most basal extant palaeognaths are flightless ratites such as ostriches and rheas (Harshman et al. 2008). This outcome clearly illustrates the limits of studying modern birds to infer evolutionary origins of avian flight; as pointed out by Nudds and Dyke (2009), the elevated wingbeat frequencies (>12 Hz) used in WAIR by extant birds are unlikely to have occurred in avian precursors. Anatomy of the flight feathers in *Archaeopteryx* and *Confuciusornis* (a later bird from the Early Cretaceous) is also mechanically inconsistent with use in wing flapping, but would have been sufficient to support gliding flight (Nudds and Dyke 2010). These observations thus indirectly support aerial as opposed to cursorial hypotheses for the origins of avian flight.

The ontogenetic timing of both WAIR and its counterpart, wing-assisted descent, is also informative relative to understanding the potentially multiple functions of wing flapping. When falling, juvenile chukar only one day old can flap their rudimentary wings and reduce gravitational acceleration by about

10% (see Fig. 2 in Jackson et al. 2009). Deceleration of this magnitude through flapping continues through Day 5, and then increases substantially to yield a >50% reduction in gravitational acceleration by Day 20. Wing flapping in descent may also advantageously reorient the body to effect landing (see Fig. 1 in Jackson et al. 2009). In contrast, aerodynamic use of WAIR (as distinct from asymmetric contact with the substrate by the wings) becomes effective only at day 8 following hatching. Wing-assisted descent thus ontogenetically precedes by 1 week the use of wing flapping in air to enable incline running. These differences in timing further illustrate the complexities of interpreting incipient flight behavior in modern birds relative to their historical origins. For juvenile birds today, wing-assisted descent could potentially serve in inadvertent falls, escape from predation while in the nest, and the ontogenetic acquisition of large-amplitude flapping flight. Because neither WAIR nor wing-assisted descent has been characterized biomechanically under natural conditions, the potential selective advantages associated with these behaviors remain unknown.

Conclusions and future directions

Numerous evolutionary experiments in controlled aerial behavior, all of which can semantically be characterized as incipient flight, are inextricably linked with gravitational acceleration while falling. Both lift and drag are concomitantly generated on diverse anatomical structures during such falls. We are now only beginning to characterize broadly the ubiquity of such behaviors, including aerial righting and maneuvers, and to understand their potential implications for the evolution of wings proper and of powered flapping flight. Nonetheless, it is clear that there are numerous morphological and behavioral variants of flight, broadly construed. We look forward to many more studies of diverse arboreal taxa as they fall, orient, maneuver, and potentially delineate those historical pathways involved in the acquisition of wings.

Acknowledgments

We thank the SICB Divisions of Animal Behavior, Comparative Biomechanics, and Vertebrate Morphology for funding this symposium. Marc Badger, Sofia Chang, Dennis Evangelista, Erica Kim, Mimi Koehl, Jim McGuire, Yonatan Munk, Victor Ortega, Kevin Peterson, Nir Sapir, Marta Wolf, and Yu Zeng kindly provided comments on the manuscript. We also thank two anonymous reviewers for additional suggestions.

Funding

National Science Foundation (IOS-0837866 to R.D. and IOS-0843120 to S.P.Y.).

References

- Alcala AC. 1967. Population biology of the “flying” lizard, *Draco volans*, on Negros Island, Philippines. *Natural Appl Sci Bull* 20:335–72.
- Alexander DE, Gong E, Martin LD, Burnham DA, Falk AR. 2010. Model tests of gliding with different hindwing configurations in the four-winged dromaeosaurid *Microraptor gui*. *Proc Natl Acad Sci USA* 107:2972–6.
- Arnold EN. 2002. *Holaspis*, a lizard that glided by accident: mosaics of cooption and adaptation in a tropical forest lacertid (Reptilia, Lacertidae). *Bull Nat Hist Mus Lond (Zool)* 68:155–63.
- Averof M, Cohen SM. 1997. Evolutionary origin of insect wings from ancestral gills. *Nature* 385:627–30.
- Beebe CW. 1915. A tetrapteryx stage in the ancestry of birds. *Zoologica II* 2:39–52.
- Behrensmeyer AK, Damuth JD, DiMichele WA, Sues H-D, Wing SL, editors. 1992. *Terrestrial ecosystems through time: evolutionary paleoecology of terrestrial plants and animals*. Chicago: University of Chicago Press.
- Béthoux O, Briggs DEG. 2008. How *Gerarus* lost its head: stem-group Orthoptera and Paraneoptera revisited. *Syst Ent* 33:529–47.
- Bishop KL. 2006. The relationship between 3D kinematics and gliding performance in the southern flying squirrel, *Glaucomys volans*. *J Exp Biol* 209:689–701.
- Bishop KL. 2008. The evolution of flight in bats: narrowing the field of plausible hypotheses. *Q Rev Biol* 83:153–69.
- Bitsch J. 1994. The morphological groundplan of Hexapoda: critical review of recent concepts. *Ann Soc Entomol Fr (N.S.)* 30:103–29.
- Buffetaut E, Mazin J-M, editors. 2003. *Evolution and palaeobiology of pterosaurs*. *Geol Soc Spec Publ* 217:1–347.
- Bundle MW, Dial KP. 2003. Mechanics of wing-assisted incline running (WAIR). *J Exp Biol* 206:4533–64.
- Burgers P, Chiappe LM. 1999. The wing of *Archaeopteryx* as a primary thrust generator. *Nature* 399:60–2.
- Burmester T, Hankeln T. 2007. The respiratory proteins of insects. *J Insect Physiol* 53:285–94.
- Carroll SB, Weatherbee SD, Langeland JA. 1995. Homeotic genes and the regulation and evolution of insect wing number. *Nature* 375:58–61.
- Chatterjee S, Templin RJ. 2007. Biplane wing planform and flight performance of the feathered dinosaur *Microraptor gui*. *Proc Natl Acad Sci USA* 104:1576–80.
- Colbert EH. 1967. Adaptations for gliding in the lizard *Draco*. *Am Mus Novitat* 2283:1–20.
- D’Haese CA. 2002. Were the first springtails semi-aquatic? A phylogenetic approach by means of 28S rDNA and optimization alignment. *Proc R Soc Lond B* 269:1143–51.
- Damen WG, Saridaki T, Averof M. 2002. Diverse adaptations of an ancestral gill: a common evolutionary origin for wings, breathing organs, and spinnerets. *Curr Biol* 12:1711–6.
- Dial KP. 2003. Wing-assisted incline running and the evolution of flight. *Science* 299:402–4.
- Dial KP, Randall RJ, Dial TR. 2006. What use is half a wing in the ecology and evolution of birds? *BioScience* 56:437–45.
- Dial R. 2003. Energetic savings and the body size distributions of gliding mammals. *Evol Ecol Res* 5:1151–62.
- Dilcher DL, Lott TA, Wang X, Wang Q. 2004. A history of tree canopies. In: Lowman MD, Rinker HB, editors. *Forest canopies*. 2nd edn Burlington, MA: Elsevier Academic Press. p. 118–37.
- Dolan PG, Carter DC. 1977. *Glaucomys volans*. *Mammal Species* 78:1–6.
- Douglas MM. 1981. Thermoregulatory significance of thoracic lobes in the evolution of insect wings. *Science* 211:84–6.
- Dudley R. 1998. Atmospheric oxygen, giant Paleozoic insects and the evolution of aerial locomotor performance. *J Exp Biol* 201:1043–50.
- Dudley R. 2000. *The biomechanics of insect flight: form, function, evolution*. Princeton: Princeton University Press.
- Dudley R. 2002. Mechanisms and implications of animal flight maneuverability. *Integr Comp Biol* 42:135–40.
- Dudley R, Byrnes G, Yanoviak SP, Borrell BJ, Brown R, McGuire JA. 2007. Gliding and the functional origins of flight: biomechanical novelty or necessity? *Ann Rev Ecol Evol Syst* 38:179–201.
- Dunbar DC. 1988. Aerial maneuvers of leaping lemurs: The physics of whole-body rotations while airborne. *Am J Primatol* 16:291–304.
- Eaton RC, editor. 1984. *Neural mechanisms of startle behavior*. New York: Plenum Press.
- Edwards JS. 1997. The evolution of insect flight: implications for the evolution of the nervous system. *Brain Behav Evol* 50:8–12.
- Edwards JS, Reddy GR. 1986. Mechanosensory appendages in the firebrat (*Thermobia domestica*, Thysanura): a prototype system for terrestrial predator evasion. *J Comp Neurol* 243:535–46.
- Edwards MH. 1986. Zero angular momentum turns. *Am J Phys* 54:846–7.
- Ellington CP. 1991. Aerodynamics and the origin of insect flight. *Adv Insect Physiol* 23:171–210.
- Emerson SB, Koehl MAR. 1990. The interaction of behavioral and morphological change in the evolution of a novel locomotor type: “flying” frogs. *Evolution* 44:1931–46.
- Emerson SB, Travis J, Koehl MAR. 1990. Functional complexes and additivity in performance: a test case with “flying” frogs. *Evolution* 44:2153–7.
- Engel MS, Grimaldi DA. 2004. New light shed on the oldest insect. *Nature* 427:627–30.
- Flower JW. 1964. On the origin of flight in insects. *J Insect Physiol* 10:81–8.

- Fourtner CR, Randall JB. 1982. Studies on cockroach flight: the role of continuous neural activation of non-flight muscles. *J Exp Zool* 221:143–54.
- Gao Y, Bu Y, Luan Y-X. 2008. Phylogenetic relationships of basal hexapods reconstructed from nearly complete 18S and 28S rRNA gene sequences. *Zool Sci* 25:1139–45.
- Geist NR, Feduccia A. 2000. Gravity-defying behaviors: identifying models for Protoaves. *Am Zool* 40:664–75.
- Grimaldi D, Engel MS. 2005. *Evolution of the insects*. New York: Cambridge University Press.
- Grimaldi DA. 2010. 400 million years on six legs: on the origin and early evolution of Hexapoda. *Arthropod Struct Dev* 39:191–203.
- Gunnell GF, Simmons NB. 2005. Fossil evidence and the origin of bats. *J Mammal Evol* 12:209–46.
- Haemig PD. 1997. Effects of birds on the intensity of ant rain: a terrestrial form of invertebrate drift. *Anim Behav* 54:89–97.
- Hagner-Holler S, Schoen A, Erker W, Marden JH, Rupperecht R, Decker H, Burmester T. 2004. A respiratory hemocyanin from an insect. *Proc Natl Acad Sci* 101:871–4.
- Harshman J, et al. 2008. Phylogenomic evidence for multiple losses of flight in ratite birds. *Proc Natl Acad Sci* 105:13462–7.
- Hasenfuss I. 2002. A possible evolutionary pathway to insect flight starting from lepismatid organization. *J Zool Syst Evol Res* 40:65–81.
- Hasenfuss I. 2008. The evolutionary pathway to insect flight: a tentative reconstruction. *Arthropod Syst Phylogeny* 66:19–35.
- Honda M, Hikida T, Araya K, Ota H, Nabjittabhata J, Hoi-Sen Y. 1997. *Cosymbotus craspedotus* (Frilly Gecko) and *C. platyurus* (Flat-tailed Gecko). *Gliding behavior*. *Herp Rev* 28:42–3.
- Hone DWE, Tischlinger H, Xu X, Zhang F. 2010. The extent of the preserved feathers on the four-winged dinosaur *Microraptor gui* under ultraviolet light. *PLoS ONE* 5:e9223.
- Hu D, Hou L, Zhang L, Xu X. 2009. A pre-*Archaeopteryx* troodontid theropod from China with long feathers on the metatarsus. *Nature* 461:640–3.
- Jackson BE, Segre P, Dial KP. 2009. Precocial development of locomotor performance in a ground-dwelling bird (*Alectoris chukar*): negotiating a three-dimensional terrestrial environment. *Proc R Soc Lond B* 276:3457–66.
- Jackson SM. 2000. Glide angle in the genus *Petaurus* and a review of gliding in mammals. *Mammal Rev* 30:9–30.
- Johnson-Murray JL. 1987. The comparative myology of the gliding membranes of *Acrobates*, *Petauroides* and *Petaurus* contrasted with the cutaneous myology of *Hemibelideus* and *Pseudocheirus* (Marsupalia: Phalangeridae) and with selected gliding Rodentia (Sciuridae and Anomaluridae). *Aust J Zool* 35:101–13.
- Jusufi A, Kawano DT, Libby T, Full RJ. 2010. Righting and turning in mid-air using appendage inertia: reptile tails, analytical models and bio-inspired robots. *Bioinspir Biomim* 5:1–12.
- Kenrick P, Crane PR. 1997. The origin and early evolution of plants on land. *Nature* 389:33–9.
- Kingsolver JG, Koehl MAR. 1985. Aerodynamics, thermoregulation, and the evolution of insect wings: differential scaling and evolutionary change. *Evolution* 39:488–504.
- Kingsolver JG, Koehl MAR. 1994. Selective factors in the evolution of insect wings. *Ann Rev Entomol* 39:425–51.
- Kukulová-Peck J. 1983. Origin of the insect wing and wing articulation from the arthropodan leg. *Can J Zool* 61:1618–69.
- Kukulová-Peck J. 1987. New Carboniferous Diplura, Monura, and Thysanura, the hexapod ground plan, and the role of thoracic lobes in the origin of wings (Insecta). *Can J Zool* 65:2327–45.
- Labandeira CC, Beall BS, Hueber FM. 1988. Early insect diversification: evidence from a Lower Devonian bristletail from Québec. *Science* 242:913–6.
- Lang A. 1891. *Text-book of comparative anatomy*. Part I. London: Macmillan and Co.
- Libersat F. 1994. The dorsal giant interneurons mediate evasive behavior in flying cockroaches. *J Exp Biol* 197:405–11.
- Long CA, Zhang GP, George TF, Long CF. 2003. Physical theory, origin of flight, and a synthesis proposed for birds. *J Theor Biol* 224:9–26.
- Longino JT, Colwell RK. 1997. Biodiversity assessment using structured inventory: capturing the ant fauna of a tropical rain forest. *Ecol Appl* 7:1263–77.
- Longrich N. 2006. Structure and function of hindlimb feathers in *Archaeopteryx lithographica*. *Paleobiology* 32:417–31.
- Lu J, Unwin DM, Jin X, Liu Y, Ji Q. 2009. Evidence for modular evolution in a long-tailed pterosaur with a pterodactyloid skull. *Proc R Soc Lond B* 277:383–9.
- Magnus R. 1922. Wie sich die fallende Katz in der Luft umdreht. *Arch Neerl Physiol* 7:218–22.
- Marden JH, Kramer MG. 1994. Surface-skimming stoneflies: a possible intermediate stage in insect flight evolution. *Science* 266:427–30.
- Marden JH, Kramer MG. 1995. Locomotor performance of insects with rudimentary wings. *Nature* 377:332–4.
- Marden JH, O'Donnell BC, Thomas MA, Bye JY. 2000. Surface-skimming stoneflies and mayflies: the taxonomic and mechanical diversity of two-dimensional aerodynamic locomotion. *Physiol Biochem Zool* 73:751–64.
- Marden JH, Thomas MA. 2003. Rowing locomotion by a stonefly that possesses the ancestral pterygote condition of co-occurring wings and abdominal gills. *Biol J Linn Soc* 79:341–9.
- Maynard Smith J. 1952. The importance of the nervous system in the evolution of animal flight. *Evolution* 6:127–9.
- McCay MG. 2001. Aerodynamic stability and maneuverability of the gliding frog *Polypedates dennysi*. *J Exp Biol* 204:2817–26.
- McCay MG. 2003. Winds under the rain forest canopy: the aerodynamic environment of gliding tree frogs. *Biotropica* 35:94–102.

- McGuire JA. 2003. Allometric prediction of locomotor performance: an example from Southeast Asian flying lizards. *Am Nat* 161:337–49.
- McGuire JA, Dudley R. 2005. The cost of living large: comparative gliding performance in flying lizards (Agamidae: *Draco*). *Am Nat* 166:93–106.
- Messner B. 1988. Sind die Insekten primäre oder sekundäre Wasserbewohner? *Dtsch Ent Z, N.F.* 35:355–60.
- Meusemann K, et al. 2010. A phylogenomic approach to resolve the arthropod tree of life. *Mol Biol Evol* 27:2451–64.
- Mivart SGJ. 1871. On the genesis of species. New York: Appleton.
- Mori A, Hikida T. 1993. Natural history observations of the flying lizard, *Draco volans sumatranus* (Agamidae, Squamata) from Sarawak, Malaysia. *Raffles Bull Zool* 41:83–94.
- Mori A, Hikida T. 1994. Field observations on the social behavior of the flying lizard, *Draco volans sumatranus*, in Borneo. *Copeia* 1994:124–30.
- Niwa N, Akimoto-Kato A, Niimi T, Tojo K, Machida R, Hayashi S. 2010. Evolutionary origin of the insect wing via integration of two developmental modules. *Evol Dev* 12:168–76.
- Norberg RA. 1983. Optimal locomotion modes of foraging birds in trees. *Ibis* 125:172–80.
- Norberg UM. 1985. Evolution of vertebrate flight: an aerodynamic model for the transition from gliding to active flight. *Am Nat* 126:303–27.
- Norberg UM. 1990. Vertebrate flight. Berlin: Springer-Verlag.
- Norell MA, Xu X. 2005. Feathered dinosaurs. *Ann Rev Earth Planet Sci* 33:277–99.
- Nudds RL, Dyke GJ. 2009. Forelimb posture in dinosaurs and the evolution of the avian flapping flight-stroke. *Evolution* 63:994–1002.
- Nudds RL, Dyke GJ. 2010. Narrow primary feather rachises in *Confuciusornis* and *Archaeopteryx* suggest poor flight ability. *Science* 328:887–9.
- Oliver JA. 1951. “Gliding” in amphibians and reptiles, with a remark on an arboreal adaptation in the lizard, *Anolis carolinensis carolinensis* Voigt. *Am Nat* 85:171–6.
- Pellis SM, Pellis VC, Morrissey TK, Teitelbaum P. 1989. Visual modulation of vestibularly-triggered air-righting in the rat. *Behav Brain Res* 35:23–6.
- Penney D. 2004. Does the fossil record of spiders track that of their principal prey, the insects? *Trans R Soc Edin Earth Sci* 94:275–81.
- Pick C, Schneuer M, Burmester T. 2009. The occurrence of hemocyanin in Hexapoda. *FEBS J* 276:1930–41.
- Pritchard G, McKee MH, Pike EM, Scrimgeour GJ, Zloty J. 1993. Did the first insects live in water or in air? *Biol J Linn Soc* 49:31–44.
- Prum RO. 2002. Why ornithologists should care about the theropod origin of birds. *The Auk* 119:1–17.
- Rasnitsyn AP. 1981. A modified paranotal theory of insect wing origin. *J Morph* 168:331–8.
- Rayner JMV. 1988. The evolution of vertebrate flight. *Biol J Linn Soc* 34:269–87.
- Regier JC, Shultz, Kambic RE. 2005. Pancrustacean phylogeny: hexapods are terrestrial crustaceans and maxillopods are not monophyletic. *Proc R Soc Lond B* 272:395–401.
- Ritzmann RE. 1984. The cockroach escape response. In: Eaton RC, editor. *Neural mechanisms of startle behavior*. New York: Plenum Press. p. 93–131.
- Rolfé WD. 1985. Early terrestrial arthropods: a fragmentary record. *Phil Trans R Soc Lond B* 309:207–18.
- Ruben J. 2010. Paleobiology and the origins of avian flight. *Proc Natl Acad Sci* 107:2733–4.
- Ruffieux L, Elouard J-M, Sartori M. 1998. Flightlessness in mayflies and its relevance to hypotheses on the origin of insect flight. *Proc R Soc Lond B* 265:2135–40.
- Samways MJ. 1996. Skimming and insect evolution. *Trends Ecol Evol* 11:471.
- Scheibe JS, Robins JH. 1998. Morphological and performance attributes of gliding mammals. In: Steele MA, Merritt JF, Zegers DA, editors. *Ecology and evolutionary biology of tree squirrels*, Vol. 4. Richmond: Virginia Museum of Natural History Special Publication. p. 131–44.
- Schiøtz A, Volsøe H. 1959. The gliding flight of *Holaspis guentheri* Gray, a west-African lacertid. *Copeia* 1959: 259–60.
- Schlesinger WH, Knops JMH, Nash TH. 1993. Arboreal sprint failure: lizardfall in a California oak woodland. *Ecology* 74:2465–7.
- Shattuck MR, Williams SA. 2010. Arboreality has allowed for the evolution of increased longevity in mammals. *Proc Natl Acad Sci USA* 107:4635–9.
- Shear WA, Grierson JD, Rolfé WDI, Smith EL, Norton RA. 1984. Early land animals in North America: evidence from Devonian age arthropods from Gilboa, New York. *Science* 224:492–4.
- Shear WA, Kukalová-Peck J. 1990. The ecology of Paleozoic terrestrial arthropods: the fossil evidence. *Can J Zool* 68:1807–34.
- Socha JJ, LaBarbera M. 2005. Effects of size and behavior on the aerial performance of two species of flying snake (*Chrysopelea*). *J Exp Biol* 208:1835–47.
- Socha JJ, O’Dempsey TO, LaBarbera M. 2005. A 3-D kinematic analysis of gliding in a flying snake, *Chrysopelea paradisi*. *J Exp Biol* 208:1817–33.
- Stewart MM. 1985. Arboreal habitat use and parachuting by a subtropical forest frog. *J Herpetol* 19:391–401.
- Telford MJ, Bourlat SJ, Economou A, Papillon D, Rota-Stabelli O. 2008. The evolution of the Ecdysozoa. *Phil Trans R Soc B* 363:1529–37.
- Thomas MA, Wals KA, Wolf MR, McPheron BA, Marden JH. 2000. Molecular phylogenetic analysis of evolutionary trends in stonefly wing structure and locomotor behavior. *Proc Natl Acad Sci USA* 97:13178–83.
- Thorington RW. 1984. Flying squirrels are monophyletic. *Science* 225:1048–50.

- Thorington RW, Heaney LR. 1981. Body proportions and gliding adaptations of flying squirrels (Petauristinae). *J Mammal* 62:101–114.
- Unwin DW. 2006. Pterosaurs from deep time. New York: Pi Press.
- Wassersug RJ, et al. 2005. The behavioral responses of amphibians and reptiles to microgravity on parabolic flights. *Zoology* 108:107–20.
- Weber NA. 1957. The nest of an anomalous colony of the arboreal ant *Cephalotes atratus*. *Psyche* 64:60–9.
- Whalley P, Jarzembowski EA. 1981. A new assessment of *Rhyniella*, the earliest known insect, from the Devonian of Rhynie, Scotland. *Nature* 291:317.
- Wigglesworth VB. 1973. Evolution of insect wings and flight. *Nature* 246:127–9.
- Wilkinson MT, Unwin DM, Ellington CP. 2006. High lift function of the pteroid bone and forewing of pterosaurs. *Proc R Soc Lond B* 273:119–26.
- Will KW. 1995. Plecopteran surface-skimming and insect flight evolution. [Technical Comments]. *Science* 270:1684–5.
- Wilson DM. 1962. Bifunctional muscles in the thorax of grasshoppers. *J Exp Biol* 39:669–77.
- Wootton RJ. 1976. The fossil record and insect flight. In: Rainey RC, editor. *Insect flight*. Oxford: Blackwell Scientific Publications. p. 235–54.
- Xu X, Zhang F. 2005. A new maniraptoran dinosaur from China with long feathers on the metatarsus. *Naturwissenschaften* 92:173–7.
- Yanoviak SP, Dudley R. 2006. The role of visual cues in directed aerial descent of *Cephalotes atratus* workers (Hymenoptera: Formicidae). *J Exp Biol* 209:1777–83.
- Yanoviak SP, Dudley R, Kaspari M. 2005. Directed aerial descent in canopy ants. *Nature* 433:624–6.
- Yanoviak SP, Kaspari M, Dudley R. 2009. Gliding hexapods and the origins of insect aerial behaviour. *Biol Lett* 5:510–2.
- Zhou Z. 2004. The origin and early evolution of birds: discoveries, disputes, and perspectives from fossil evidence. *Naturwissenschaften* 91:455–71.