

THE EVOLUTIONARY PHYSIOLOGY OF ANIMAL FLIGHT: Paleobiological and Present Perspectives

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■ **Abstract** Recent geophysical analyses suggest the presence of a late Paleozoic oxygen pulse beginning in the late Devonian and continuing through to the late Carboniferous. During this period, plant terrestrialization and global carbon deposition resulted in a dramatic increase in atmospheric oxygen levels, ultimately yielding concentrations potentially as high as 35% relative to the contemporary value of 21%. Such hyperoxia of the late Paleozoic atmosphere may have physiologically facilitated the initial evolution of insect flight metabolism. Widespread gigantism in late Paleozoic insects and other arthropods is also consistent with enhanced oxygen flux within diffusion-limited tracheal systems. Because total atmospheric pressure increases with increased oxygen partial pressure, concurrently hyperdense conditions would have augmented aerodynamic force production in early forms of flying insects. By the late Permian, evolution of decompositional microbial and fungal communities, together with disequilibrium in rates of carbon deposition, gradually reduced oxygen concentrations to values possibly as low as 15%. The disappearance of giant insects by the end of the Permian is consistent with extinction of these taxa for reasons of asphyxiation on a geological time scale. As with winged insects, the multiple historical origins of vertebrate flight in the late Jurassic and Cretaceous correlate temporally with periods of elevated atmospheric oxygen. Much discussion of flight performance in *Archaeopteryx* assumes a contemporary atmospheric composition. Elevated oxygen levels in the mid- to late Mesozoic would, however, have facilitated aerodynamic force production and enhanced muscle power output for ancestral birds, as well as for precursors to bats and pterosaurs.

INTRODUCTION

Today's oxidizing atmosphere, with an oxygen concentration of about 21%, derives in part from the metabolic activity of photosynthetic organisms. Starting with the anoxic conditions and reducing atmosphere of the Archean and early Proterozoic eons, evolution of cyanobacteria, sulfide-oxidizing bacteria, and algae contributed to buildup of oxygen partial pressures by the beginning of the Cam-

brian (570 MYa) to values likely comparable to those of the present day (1–6). Increased atmospheric oxygen, in turn, may have been an important factor underlying radiations of metazoan taxa in the late Proterozoic and at the base of the Cambrian (7–14). The paleobiological significance of Proterozoic oxygen levels for animal evolution in aquatic habitats has long been recognized, as has been the role of gradual oxygen buildup for subsequent evolution of plant and animal terrestrial communities (6, 8, 9). Less well-studied, however, are potential fluctuations in atmospheric constituents through the course of the Phanerozoic.

In particular, variation in oxygen partial pressure and concomitant variation in air density potentially influence the physiology and biomechanics, respectively, of animal flight performance. Geophysical analyses suggest the presence of a late Paleozoic oxygen pulse beginning in the late Devonian and continuing through to the late Carboniferous. Oxygen concentrations ranged possibly as high as 35% during the initial period of insect flight evolution (late Devonian or early Carboniferous). Atmospheric hyperoxia may thus have physiologically facilitated the initial evolution of insect flight metabolism. Because total atmospheric pressure increases with an increased oxygen partial pressure, concurrently hyperdense conditions would have augmented aerodynamic force production in ancestral winged insects. The multiple historical origins of vertebrate flight similarly appear to correlate temporally with periods of hyperoxia. In particular, elevated oxygen levels in the mid- to late Mesozoic may have facilitated aerodynamic force production and enhanced muscle metabolism for ancestral birds, as well as for precursors to bats and pterosaurs. Because of such implications for the evolution of animal flight performance, discussion of the mechanisms underlying substantial variation in composition of the earth's atmosphere is warranted.

PHANEROZOIC VARIATION IN THE EARTH'S ATMOSPHERE

The physical properties of the earth's atmosphere are determined almost exclusively by two major constituents, namely diatomic oxygen and diatomic nitrogen. Nitrogen content of the atmosphere is thought to have been approximately constant through geological time (15–17), although some variation in this constituent may derive through biotic linkages with the atmospheric pool (CD Nevison, unpublished data). Various models for oxygen content of the atmosphere in Phanerozoic times have suggested major fluctuations that are driven biotically (6, 8, 13, 16, 19, 20). In particular, geochemical modeling (21, 22) suggests a late Paleozoic disequilibrium between the rate of carbon fixation by terrestrial plants and the rate at which this fixed material was decomposed and recycled. Through the mid- to end-Devonian (390–362 MYa), this disequilibrium led to a moderate increase in oxygen concentration from 18 to 20%, followed by a more substantial

rise by the end of the Carboniferous (290 MYa) to remarkable values as high as 35% (see Figure 1). Thereafter, an equally pronounced decline resulted in end-Permian and early Triassic values as low as 15%. Relative to the present atmospheric level of 21% (PAL), such hyperoxic and subsequently hypoxic conditions must have had major biological effects during the Paleozoic (23–26). Moreover, atmospheric hyperoxia may also have characterized portions of the Mesozoic. According to the aforementioned geochemical model (21), a secondary rise in oxygen levels characterized the the mid-Jurassic and the Cretaceous (170–65 MYa), with oxygen concentration increasing to 25 to 30% and then declining to PAL only by the end-Tertiary (Figure 1). Such postulated changes in oxygen concentration are at sharp odds with any uniformitarian perspective of atmospheric composition.

The various assumptions underlying reconstruction of ancient atmospheric composition obviously require examination. Current models for Phanerozoic oxygen and carbon dioxide concentrations (21, 27–29) are based on estimates of the exchange rates of fixed and reduced carbon among atmospheric, oceanic, and sedimentary reservoirs. Variation in rates of carbon exchange is driven primarily by the effects of plant terrestrialization, variable rates of organic carbon deposition and decomposition, and changes in continental weathering (20, 22, 30–32). An additional feedback loop potentially influencing atmospheric oxygen levels involves marine phosphorus (33, 34). Because the relative importance of these different mechanisms can be, in many cases, only broadly constrained, considerable uncertainty must be associated with such efforts that model global geochemical cycles. Of particular relevance to the late Paleozoic atmosphere,

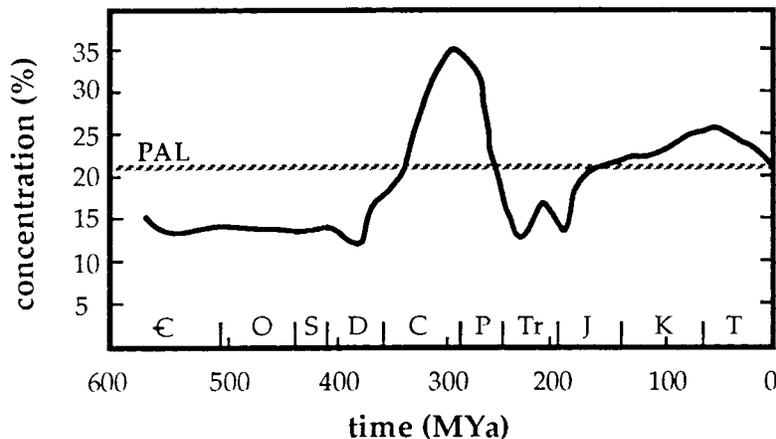


Figure 1 Estimate of atmospheric oxygen concentrations through the Phanerozoic (21). PAL: present atmospheric level (20.95%).

however, are the changes necessarily associated with the global phenomenon of terrestrialization by plants. During this process, photosynthetic production of oxygen became decoupled from breakdown of fixed carbon. An ensuing compositional bottleneck, due apparently to the absence of biotic processes leading to rapid breakdown, resulted in extensive deposition of coal and other carbonates. Subsequent evolution by the mid-Permian of microbial decomposers, in particular fungi, then depleted atmospheric oxygen via decay processes and inhibited further carbon accumulation (20, 31, 35). Biological underpinnings to a late Paleozoic oxygen pulse are thus well-grounded, although more precise estimates of excursions in atmospheric carbon dioxide and oxygen await further investigation.

Constraints on fire processes can be used to evaluate the validity of geophysical reconstructions of ancient atmospheres. The models of atmospheric oxygen considered here suggest concentrations approaching but not exceeding 35%, a value that represents an approximate threshold for sustained combustion of the terrestrial biosphere (36, 37). Proliferation of terrestrial ecosystems would clearly be precluded under such circumstances, and analysis of charcoal deposits and of the vegetational fossil record demonstrates that atmospheric oxygen concentrations have not exceeded this upper bound (38). At the lower extreme, the minimum oxygen concentration required for contemporary natural fuels to ignite is about 13% (36, 39); the regular presence of charcoal in the fossil record suggests that atmospheric oxygen never fell below this level (40–42). Methodologically, it is important to realize that ignition of homogeneous woody or paper materials in modern laboratory contexts is not functionally equivalent to the propagation of fire in natural ecosystems. Extrapolation of experimental results with contemporary fuels to the prediction of fire regimes in Paleozoic vegetation is necessarily imprecise, although some inference is possible (34). In sum, these considerations suggest that atmospheric oxygen levels have been historically constrained between 13 and 35%; the best estimate derived from atmospheric modeling (15–35%; Reference 21) is nominally congruent with this range.

No direct indicator is available to test empirically these predictions for ancient levels of atmospheric oxygen. However, diverse geochemical and isotopic evidence is consistent with substantial late Permian declines in both marine and atmospheric oxygen concentrations, declines that likely contributed to the end-Permian extinction event (43–51). Furthermore, atmospheric models incorporating effects of plant terrestrialization suggest substantial changes in the concentration of carbon dioxide. Both modeling and empirical observations demonstrate an approximate 10-fold reduction in carbon dioxide from the mid- to late Paleozoic (22, 27–29, 53–56). For plants, the physiological effects of this draw-down in carbon dioxide are evident in paleontological analyses of stomatal density and other proxies of photosynthetic activity (56–58). Shortcomings of atmospheric modeling notwithstanding, a diversity of empirical evidence is consistent both with carbon dioxide drawdown and with an oxygen pulse in the mid- to late Paleozoic, and with enhanced levels of oxygen in the mid- to late Mesozoic and in much of the Cenozoic.

THE ORIGINS OF ANIMAL FLIGHT

Powered flapping flight evolved independently four times during the Phanerozoic, once in the insects and three times among vertebrates. Evolutionary origins of all volant taxa remain controversial, but both insects and the three taxa of flying vertebrates may have originated during periods of atmospheric hyperoxia. Flight is both biomechanically and physiologically demanding, and the evolution of flight requires dramatic up-regulation of metabolic capacity in addition to the expression of flapping structures that generate useful aerodynamic forces. Although wings are not homologous between insects and volant vertebrates, common physical mechanisms of flight suggest that historically elevated concentrations of atmospheric oxygen have yielded similar aerodynamic consequences during flight evolution.

Wings and Aerodynamic Force Production

Fundamental to force generation by flapping animal wings is the physical nature of the medium to which the wings transfer momentum (59). Air density, the mass of air per unit volume, is a principal determinant of force production by airfoils, biological and otherwise; aerodynamic forces on structures tend to increase linearly with air density. Also, air responds to applied forces by resisting not deformation but rather the rate of deformation, as determined by the viscosity or the internal resistance to flow. For an object such as a wing moving in a fluid, the ensuing reaction force acting parallel to the direction of movement is termed drag. Presence of the wing removes momentum and thus kinetic energy from the moving fluid system, and acts to slow the wing relative to flow. This pressure drag, also known as inertial drag, derives from disruption of the inertial characteristics of the moving flow field and varies with fluid density, relative fluid velocity, and the wing's shape.

Viscous drag, by contrast, emerges from boundary interactions between the wing and the surrounding fluid. Viscosity ensures resistance to flow between adjacent layers of fluid, engendering shear forces within the boundary layer over the wing and imposing a reaction force throughout the fluid that terminates at the wing's surface. Viscous drag thus varies not with density but with fluid viscosity, the relative fluid velocity, and the total wetted surface area of the wing. Pressure and viscous drag have in common a dependence on relative fluid velocity and on object dimensions, but differ fundamentally in their dependence on fluid density and viscosity, respectively. The ratio of inertial to viscous forces on an object moving within a fluid will therefore vary with the ratio of density and viscosity, and must additionally change with object dimensions and its relative velocity. The simplest dimensionless formulation of these four parameters is the Reynolds number (Re), which is proportional to the ratio of inertial to viscous forces that act on objects moving within fluids. Different situations of fluid flow are physically equivalent if the corresponding Re s are approximately the same. In contrast,

variation in either the density or viscosity of a fluid alters the relative magnitude of inertial and viscous forces.

Just as drag is the force parallel to flow around an object, lift is defined as the component of force orthogonal to flow and thus perpendicular to drag in a two-dimensional perspective. For wings at low angles of attack, air flows smoothly over both dorsal and ventral wing surfaces. Because pressure drag of well-designed airfoils is low, momentum extraction from the flow field is minimized. The positive camber of the wing and the downward deflection of air near the trailing wing edge yield slightly different translational velocities for the dorsal and ventral airstreams—airflow is slightly faster above and slower beneath the airfoil. Bernoulli's Principle indicates that this difference in dorsal and ventral airstream velocities results in a pressure gradient; a net force (i.e. lift) acts dorsally upon the wing. In a cross-sectional perspective, air appears to move anteriorly from the ventral to dorsal wing surface and to yield a net rotational movement of air around the wing. This motion of air is equivalent to a rotating flow field or vortex that circulates around the wing and that is centered about the wing itself. For every bound wing vortex, a starting vortex of comparable magnitude but of opposite sense is shed into the wake, ensuring conservation of angular momentum in the fluid.

The physical origin of lift thus lies within the creation of net air circulation about a translating wing. As a wing translates in space, the pressure gradient underlying lift production yields airflow not only around spanwise wing sections (the bound circulation), but also around the wing tip, creating the so-called tip vortex. The tip vortex is linked to the starting and the bound wing vortices and creates a closed vortex loop that exerts a momentum flux on the surrounding air. The downward momentum induced by the presence of the vortex loop is accordingly proportional to the mass of the air moved ventrally (i.e. to the air density) and to the velocity at which the air moves (i.e. the circulation). Lift production thus increases with increased air density (59). The Re at which a wing is operating also exerts a strong influence on lift production. Under highly viscous circumstances, vortex generation becomes more difficult as intermolecular stickiness progressively impedes rotational motions of airflow. Circulatory lift becomes increasingly more difficult to maintain at low Re , whereas the effects of viscous drag also become more pronounced. The lift:drag ratio must then decrease at lower Re , as confirmed empirically for insect and vertebrate wings (60, 61).

Lifting characteristics of wings are thus strongly dependent on both air density and the Re at which they operate. Concomitant with large-scale changes in oxygen concentration during the Phanerozoic, numerous physical characteristics of air must vary if, as suggested previously, nitrogen content of the atmosphere remains constant (23). Parameters such as heat capacity of air, thermal conductivity, diffusivity, and the speed of sound would all have substantially changed under hyperoxic conditions. Of particular interest for the evolution of animal flight is the possibility of density-mediated increases in aerodynamic performance during initial periods of wing evolution (23, 25). The predicted value of air density at the

peak of the late Paleozoic oxygen pulse (285 MYa) is about 1.56 kg/m^3 , an increase of 29% relative to the present sea-level value of 1.21 kg/m^3 . The relative changes in the viscosity of air are, by contrast, much smaller (23). Winglets or proto-wings moving in hyperoxic atmospheres would thus experience a higher air density and would be moving at a comparably increased Re . Both conditions would have facilitated lift production in early flying forms, although the magnitude of these aerodynamic effects would have varied both with morphological features and with the particular wing and body motions of the taxon concerned. Because insect and vertebrate wings are so distinct both ontogenetically and anatomically, origins of flight in the two groups are considered separately.

Origins of Flight in Insects

The evolution of insect flight, a major event in biotic history, can be correlationally linked to atmospheric hyperoxia. The origins of winged (pterygote) insects are indeterminate but probably lie in the Upper Devonian or early Lower Carboniferous. Wingless hexapods are known from 395–390 MYa (62–65), whereas fossils of pterygote hexapods (i.e. winged insects) date from approximately 325 MYa (66, 67). By the Upper Carboniferous, pterygotes are impressively diversified into about fifteen orders (68–71). Although pterygote insects are likely monophyletic (72–78), 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 (79–86), or from ancestrally mobile gills, gill covers, leg structures, or styli in aquatic forms (87–95). Unfortunately, no transitional forms are known between the wingless apterygotes and the winged pterygote insects, and the biology of early protopterygote forms remains speculative and contentious. Of particular interest to the origins of flight is ancestral habitat association of protopterygotes—were these animals terrestrial or aquatic?

Most evidence, particularly that relating to the physiology and origins of the insect tracheal system, indicates that winged insects are derived from terrestrial apterygote ancestors (61, 96–99). Aquatic larvae, particularly those of the extant and phylogenetically basal Odonata and Ephemeroptera, appear to be secondarily derived (73, 99, 100). 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 (68, 90, 101–103). If winglets or wings derived initially from fixed paranotal lobes, 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 (104–108). A general question relating to wing origins concerns the possible evolution of novel wing-like structures, as opposed to modification of pre-existing morphological features (85). 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 decide unequivocally between these two hypotheses (61).

A variety of possible functional roles have been attributed to winglets or wings of protopterygotes, including aerodynamic utility, epigamic display during courtship, and thermoregulation (109–115). Hydrodynamic use for what ultimately became aerodynamic structures has been proposed for ancestrally aquatic protopterygotes, as have been possibly amphibious lifestyles (116, 117). Protopterygotes could also have used wing-like structures in air either to drift passively or to skim actively along water surfaces, as do many extant insect taxa (118–122). This behavior is probably a derived rather than a retained ancestral trait of winged insects (61, 123, 124). Although improbable for reasons outlined above, biomechanical considerations suggest that aquatic protopterygotes 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 Re 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 (61). 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) likely characteristic of ancestral pterygotes (64, 125, 126).

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 are 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 (61). Neurobiological studies also support the ancestral presence of dedicated sensorimotor pathways underlying escape behavior in both apterygotes and pterygotes (127–129). 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 (130–137). 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 (138–142). Various morphological characteristics evident among the early Upper Carboniferous entomofauna are also consistent with the hypothesis of predatory defense (141, 143, 144).

Furthermore, the increasing arborescence and geometrical complexity of terrestrial vegetation through the Devonian and into the Carboniferous would have provided a three-dimensional substrate suitable for jumping escapes and ultimately the evolution of flight in protopterygotes (145). Terrestrial vegetation during the period of pterygote origins was composed of fern-like lycopsids and

psilopsids, together with arborescent lycopods, sphenopsids, and progymnosperms (146–150). Lateral jumps from branches or leaves, and particularly jumps directed downward, would have yielded the increased translational velocities necessary for substantial buildup of lift on both thoracic and abdominal projections. Access to nutritional resources, appropriate microhabitats, and suitable oviposition sites would have been facilitated by such an increased capacity for three-dimensional movements. Increased feeding on plants would have been one outcome of enhanced mobility. For example, non-insect hexapods (e.g. *Collembola*) that feed on living plant tissue are rare, whereas approximately 85% of extant insect species are phytophagous at some stage in their life cycle (151). Most tellingly, the fossil record confirms feeding on plants by insects in the Upper Carboniferous and early Permian (152–154).

Given this paleobiological background to wing evolution in insects, it is instructive to consider two distinct features of atmospheric hyperoxia that may have contributed to the evolution of flight. Biomechanically, the greater density of a hyperoxic atmosphere would yield enhanced aerodynamic characteristics of both winglets and the bodies of protopterygotes. Alternatively phrased, less winglet area would be necessary to generate comparable forces if air density were higher, although the magnitude of this effect is strongly dependent on the nature of vortex production around the body and winglets and on the relative air velocity and/or acceleration during takeoffs. Aerodynamic forces on both the body and winglets of protopterygotes would enhance aerial escape during either jumping or steady-state glides (115, 125, 155). The de facto increase in Re associated with increased air density may furthermore have contributed to greater lift production by winglets, particularly for the low aspect ratio wings and Re relevant to pterygote evolution (61, 156). In contrast to theories of wing evolution that require aquatic protopterygotes and a discontinuous selection regime across the air-water interface, escape jumping in terrestrial protopterygotes would from the outset favor gradual and continuous improvement in lift generation. Winglet mobility would then enhance force production, and additionally could be used to control body orientation during flight and while landing (109, 125, 157, 158). Increased air density and higher Re would have been advantageous in any evolutionary scenario involving lift production by winglets or wings. Greater air densities may also have facilitated flight in progressively larger taxa, leading to the giant pterygotes of the late Paleozoic, as discussed below (61, 159).

Physiologically, an increased oxygen content of the late Paleozoic atmosphere would have favored higher and ever more sustained levels of the oxidative metabolism required for flight. As wing flapping became more rapid and of greater amplitude, the energetic costs of flight would have increased substantially; thoracic muscles of extant insects in flight exhibit the highest mass-specific rates of oxygen consumption known for any locomotor tissue (61, 160, 161). This demand for oxygen is met by the air-filled tracheal system, a branching network of cuticular tubes that functions primarily through gaseous diffusion rather than by convective air movement (162–165). Both diffusion and tracheal convection

represent potentially rate-limiting steps in insect respiration, although the much reduced thoracic diameters of small insects (e.g. *Drosophila*) probably alleviate any metabolically based need for active ventilation of the tracheal system. In larger insects, however, diffusional limits on oxygen supply likely constrain maximum body size. For example, flight metabolic rates in an extant dragonfly species vary directly with ambient oxygen concentration (166), a result consistent with diffusion-limited oxygen delivery by the tracheal system. In the late Paleozoic, diffusion of oxygen to the respiring flight muscles would obviously have been enhanced by greater partial pressures of this gas, as well as by the increased diffusion constants associated with an increased total pressure of the atmosphere (25).

Moreover, a spectacular bioindicator of atmospheric hyperoxia is provided by gigantism among late Paleozoic terrestrial arthropods (23, 25, 26). Gigantism in the Carboniferous and Permian was characteristic of many arthropod taxa, including a number of phylogenetically unrelated pterygote orders (141, 167, 168) as well as apterygote insects (169) and other arthropods, including diplopods, arthropleurids, and arachnids (138, 141, 170–172). Although a number of non-mutually exclusive selective forces may have contributed to the evolution of gigantism (90, 141, 173), relaxation of diffusional constraints on maximum body size through atmospheric hyperoxia seems to be the most parsimonious explanation for this phenomenon (19, 23, 25, 174, 175). Necessarily global effects of hyperoxia on animal physiology were thus manifested in the form of dramatically increased body size in diverse arthropod lineages. Furthermore, all giant arthropod taxa of the late Paleozoic went extinct by mid- to end-Permian (23, 25, 168), as would be predicted by the concomitant decline in atmospheric oxygen concentration. Also consistent with the hypothesis linking atmospheric oxygen and diffusional constraints on insect body size is a secondary peak of gigantism (e.g. among mayflies) in the Cretaceous at a time of elevated oxygen concentrations (25, 168). Systematic analysis of Paleozoic gigantism has been precluded to date because of generally poor fossil preservation and incomplete knowledge of interspecific body size distributions. However, detailed analysis of phyletic size change within diffusion-limited taxa does represent an important bioassay for possible effects of atmospheric hyperoxia in the late Paleozoic and the Cretaceous/Tertiary.

Origins of Vertebrate Flight

As with winged insects, the historical origins of flying vertebrates are known only imprecisely. Nonetheless, circumstantial evidence is at least consistent with origins of bats, birds, and pterosaurs during times of hyperdense and hyperoxic atmospheres. The most recent of volant vertebrates are the bats, with a modern morphology apparent in a microchiropteran fossil from 50 MYa. Given this date, chiropteran origins would appear to lie within the early Paleocene or late Cretaceous (176, 177). A similar appearance during hyperoxic times seems likely for birds in the mid- to late Jurassic (178–180). The timing of pterosaur origination

and early diversification is unknown but possibly lies within the Permian given well-developed pterosaur morphologies by the mid- to late Triassic (181, 182). Because a detailed fossil record is unavailable for any of these three taxa, biomechanical analysis of the transitional forms of flight is seriously constrained. Independent of the behavioral or ecological context of flight, however, greater atmospheric density would facilitate aerodynamic force production, whereas increased oxygen partial pressures would similarly enhance oxygen transport to and within the muscles powering flight. Aforementioned discussions of vertebrate flight origins generally assume atmospheric composition of the present day, although the implications of flight evolution in physically variable atmospheres clearly deserve further attention. In a similar vein, reconstructions of ancestral flight physiology that are based on comparisons with extant taxa (183–185) may not fully reflect aerial performance of now extinct taxa in hyperoxic and hyperdense atmospheres.

Most scenarios of vertebrate flight evolution presume jumping takeoffs (directed either with or against gravity), whereas jump-initiated gliding origins of flight are biomechanically more parsimonious than “ground-up” hypotheses for both volant vertebrates and insects (60, 61, 186–188). Jumping via a startle response is widespread among animals (189), and one potential commonality among volant vertebrates and pterygote insects is acquisition of active flight via the pathway of jumping and subsequent gliding to escape predation. Also, unsteady aerodynamic performance during the accelerating portion of a jump may be of greater relevance to escape success than steady-state glides (61). Jump-initiated glides that increased survivorship during predation attempts would potentially select for greater aerodynamic performance, an effect likely to be enhanced at the higher Re of hyperdense air. That predation is a major factor underlying the evolution of aerial locomotion is suggested by the increased longevity of flying animals relative to their non-volant counterparts. For example, volant endotherms have mortality rates significantly lower than those for non-volant endotherms of equivalent body mass (190–193). Paleophysiological simulations of jumping performance can be carried out in extant gliding and flying taxa using variable-density gas mixtures (194), and potentially can be used to investigate the ancestral role of jumping and takeoff aerodynamics in flight evolution.

CONCLUSIONS AND IMPLICATIONS

Modeling, isotopic and geochemical data, and indirect biological indicators suggest major historical changes in atmospheric composition, particularly during the late Paleozoic but also in the late Mesozoic and Tertiary. Periods of atmospheric hyperoxia can be correlationally linked with the late Paleozoic origin of flight in insects and with contemporaneous arthropod gigantism and can be more tentatively associated with the origin of flight in three vertebrate lineages. Causal

association between periods of hyperoxia and the appearance of flight resides at two levels: biomechanical enhancement of aerodynamic force production through increases in air density and the Re , and physiological facilitation of the oxygen flux required to sustain high rates of flight metabolism. In and of themselves, increased oxygen concentrations did not act directly on particular phenotypes or behaviors. Instead, a new selective background of slowly increasing oxygen concentrations provided the opportunity (but not necessity) for the evolution and progressive enhancement of a novel locomotor capacity (26).

Falsification of such historical hypotheses is necessarily challenging, but neontological investigations of animal flight performance provide a useful perspective on paleobiological reconstructions. Postulated air densities and oxygen concentrations of ancient atmospheres can be mimicked experimentally using different combinations of oxygen and nonreactive gases (194). Similar gas mixtures can be used to investigate the effects of atmospheric hyperoxia on the biomechanics and physiology of flight in extant volant forms. Phenotypic plasticity in the respiratory system of insects (195–197) and vertebrates (198–204) suggests widespread occurrence of ontogenetic as well as short-term and chronic physiological flexibility in response to variable oxygen availability. Over evolutionary time scales, artificial selection for enhanced flight performance in *Drosophila* (205) can be imposed in different gas mixtures that decouple the effects of hyperoxia from those associated with a hyperdense flight medium (25, 194).

In modern ecological contexts, variation in altitude provides the closest analogue to historic variation in atmospheric composition. Covariance in air density and oxygen partial pressure characterizes altitudinal gradients, as would similarly characterize atmospheres with varying oxygen content and a constant quantity of nitrogen. Modern volant taxa display remarkable flight abilities under both hypoxic and hypodense conditions (61, 206–209). In natural montane contexts, wing length of birds and insects varies directly with altitude, suggesting morphological compensation for the greater power expenditure during flight at lower air densities (194, 210–213). The wide range of extant adaptations to variation in air density and oxygen availability suggests substantial evolutionary capacity to respond to variable atmospheric composition. Although considerable uncertainty still surrounds paleoatmospheric reconstructions, further study of animal flight performance in simulated ancient atmospheres is likely to prove rewarding.

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