Convergent pathways in the evolution of animal flight: from gliding to powered wings

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Abstract. The evolution of flight represents one of the most remarkable and recurrent innovations in the animal kingdom, emerging independently in insects, pterosaurs, birds, and bats, while gliding behaviors evolved in multiple reptiles and mammals. Despite profound anatomical differences, these lineages display convergent patterns in the incremental acquisition of aerial behaviors, morphological transformation of forelimbs into airfoils, musculoskeletal and metabolic adaptations for high power output, and repeated shifts between flight-capable and flightless forms. Comparative studies in biomechanics, development, genomics, and paleontology reveal shared trajectories from controlled descent to fully powered flight, highlighting the importance of pre-existing behaviors, unsteady aerodynamics, and repurposed developmental modules. Flight acquisition profoundly shapes ecological and macroevolutionary outcomes, enhancing dispersal, diversification, and migration, yet it can be secondarily lost under ecological constraints. This mini-review synthesizes current evidence for these convergent evolutionary solutions, providing a unified perspective on the repeated conquest of the air across animal clades.

Key Words: aerodynamics, animal flight, convergence, developmental genetics, evolutionary biomechanics, flight loss, gliding, macroevolution, musculoskeletal adaptation, powered flight.

Introduction. The conquest of the air ranks among the most transformative innovations in animal evolution. Powered or controlled aerial locomotion evolved independently in insects, pterosaurs, birds and bats, and gliding or parachuting has arisen repeatedly in diverse reptiles and mammals. Despite profound anatomical differences, these lineages exhibit common evolutionary patterns: incremental acquisition of aerial behaviors, progressive transformation of anterior appendages into airfoils, reconfiguration of musculoskeletal and metabolic systems for high power output, and repeated shifts between flight-capable and flightless forms. Comparative work in biomechanics, development, genomics and paleontology now allows a synthetic view of these shared trajectories across insects, reptiles, birds and mammals (Dudley & Yanoviak 2011; Chin & Lentink 2016; Almudi et al 2020; Anderson & Ruxton 2020; Cao & Jin 2020; Treidel et al 2024).

This review aims to synthesize comparative evidence across insects, reptiles, birds, and mammals to identify shared behavioral, morphological, physiological, and genomic pathways underlying the independent evolution of aerial locomotion.

From aerial behavior to powered flight: **a shared behavioral continuum**. Across clades, flight appears not as a sudden leap but as the endpoint of a continuum of aerial behaviors. Many arboreal insects, including wingless forms, show controlled aerial descent, mid-air righting and gliding, demonstrating that sophisticated control can precede the evolution of wings (Dudley & Yanoviak 2011). Similar non-flapping aerial behaviors characterize gliding lizards, flying squirrels, colugos and other species, in which extended limbs and membranes generate lift and control without powered downstrokes (Figure 1). Dudley & Yanoviak (2011) argued that in insects, controlled descent and use of incipient winglets for righting and maneuvering could have been incrementally elaborated into flapping flight; they proposed that analogous behavioral sequences - jumping, parachuting, gliding, then flapping - likely structured the origins of vertebrate flight as well.

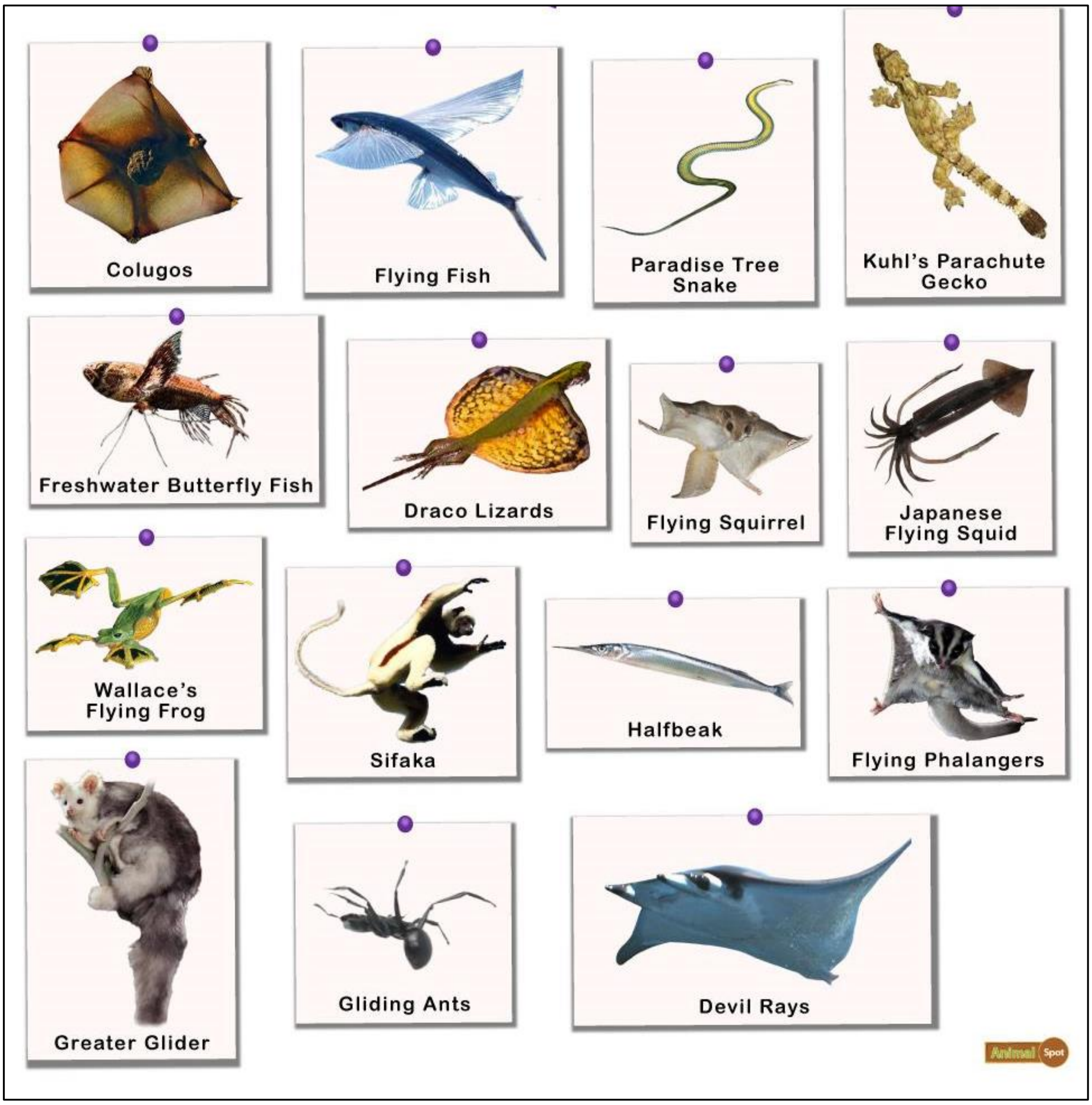

Figure 1. Animal taxa that are able to glide (Source: https://www.animalspot.net/wp-content/uploads/2023/01/Animals-That-Fly.jpg).

In all lineages, early aerial stages likely conferred advantages in predator escape, soft landing, gap crossing and access to new resources. These benefits would favor gradual increases in surface area, control authority and force production, setting the stage for the evolution of fully powered, flapping locomotion. Modern systems such as gliding lizards and flying mammals thus can be interpreted as snapshots along a broadly repeatable pathway toward air mastery.

Common morphological solutions: **turning forelimbs into airfoils**. A striking commonality across flying animals is the transformation of anterior appendages into wings that function as airfoils. Insects evolved articulated, membranous wings supported by veins, derived from dorsal body wall outgrowths genetically linked to leg and gill developmental programs (Almudi et al 2020; Moczek 2025). In vertebrates, the forelimb skeleton is reworked: in pterosaurs by elongation of the fourth finger to support a skin membrane; in birds by fusing and shortening distal elements and attaching complex feathers; in bats by extreme elongation of digits II–V to support a muscular membrane (Chin & Lentink 2016; Chin et al 2017; Anderson & Ruxton 2020).

Despite these structural differences, the wings of insects, birds and bats converge functionally as lifting surfaces that generate aerodynamic forces through similar kinematic patterns. Comparative aerodynamics has identified a shared reliance on a leading-edge vortex (LEV) that remains attached over much of the wing stroke, delaying stall and augmenting lift in insects, bats and birds alike (Chin & Lentink 2016). Other unsteady mechanisms - rotational circulation, clap-and-fling, wing - wake interactions - are well established in insects and are increasingly recognized or suspected in vertebrates (Chin & Lentink 2016; Hao et al 2025). Dimensionless numbers such as Reynolds number, Rossby number and advance ratio organize these disparate systems into a single framework, showing that all flapping wings operate within a constrained region of parameter space where unsteady aerodynamics and vortex control dominate (Chin & Lentink 2016).

Within this shared design space, miniaturization and gigantism impose repeated morphological solutions. Very small insects shift from fully membranous to bristled wings, reflecting a transition from inertia-dominated to viscosity-influenced aerodynamics, yet still maintain airfoil-like function (Białkowski et al 2025). At larger scales, Mesozoic palaeontinid “giant cicadas” evolved wing planforms that increased speed and maneuverability in response to predation by early birds, an example of convergent optimization of wing loading and aspect ratio under aerial arms-race dynamics parallel to those seen later in birds and bats (Xu et al 2024; Ou et al 2025).

Muscles, **metabolism and power**: **convergent physiological demands**. Powered flight imposes stringent demands on muscle contractility and energetic efficiency. Insects and vertebrates independently evolved specialized striated flight muscles with high mitochondrial densities, modified myofilament proteins and tuned calcium handling that support repetitive, high-frequency contractions (Gau et al 2023; Treidel et al 2024; Hao et al 2025). Insects exhibit two principal muscle actuation modes: synchronous muscles that contract once per neural impulse and asynchronous muscles that are stretch-activated, allowing wingbeat frequencies beyond neural firing limits. Recent phylogenetic and biomechanical work shows that asynchronous actuation likely evolved once and was repeatedly lost, and that synchronous and asynchronous modes represent two regimes of a single dynamical system; small changes in mechanical and physiological parameters can flip the mode, providing a flexible route for evolutionary transitions in flight muscle performance (Gau et al 2023).

In vertebrates, birds and bats convergently evolved powerful pectoral and supracoracoid muscles with highly oxidative fibers. Comparative analyses suggest that while the basic sarcomeric machinery is conserved, bird and bat flight muscles differ in metabolic rates and energetic efficiencies, probably reflecting different evolutionary histories and constraints on oxygen delivery and heat dissipation (Cao & Jin 2020). Across flying vertebrates, wing muscles experience stabilizing selection on combinations of wing loading and muscle mass: in bats, macroevolutionary reconstructions reveal an ancestral morphotype with low wing loading and moderate aspect ratio that persisted for tens of millions of years, with later divergences into high-speed or maneuverable forms linked to ecological shifts such as open-air hawking and foraging strategy changes (Amador et al 2019). Hummingbirds recapitulate this pattern at a smaller scale: basal lineages with weaker wing muscles and convex tails use more linear flight, whereas derived lineages with stronger wing musculature evolve forked or reduced tails and highly maneuverable, bee-like hovering, paralleling the early-constrained-then-radiating trajectory inferred for avian flight more broadly (Bleiweiss 2009).

Developmental and genomic innovations underlying aerial lifestyles. The repeated origin of flight required developmental reorganization and genomic innovation. In insects, genomic and transcriptomic analyses of basal winged groups like mayflies show expansions of odorant-binding proteins and visual opsins associated with transitions from aquatic to aerial life, as well as a conserved set of wing-associated genes expressed in both gills and wings, supporting a shared developmental program for respiratory and flight structures (Almudi et al 2020). The reinterpretation of insect wing origins as gradual elaboration of ancestral body-wall and leg components exemplifies how complex novelties such as wings can arise by differential modification and fusion of pre-existing parts, rather than de novo invention (Moczek 2025).

In birds, comparative genomics of paleognaths has revealed that repeated losses of flight in ratites are associated less with convergent amino-acid changes in structural proteins and more with convergent acceleration and modification of regulatory elements controlling limb development (Sackton et al 2019). These results imply that acquiring and losing flight in vertebrates frequently involves tweaking gene regulatory networks governing limb growth, muscle patterning and feather development, rather than wholesale innovation of new structural proteins. Together with developmental insights into interdigital webbing in ancestral bats, these findings highlight a common evolutionary tactic: incremental repurposing and redeployment of ancestral developmental modules to construct aerodynamic forelimbs suited for flapping or gliding (Almudi et al 2020; Anderson & Ruxton 2020).

Ecological and macroevolutionary consequences: **dispersion**, **migration and loss of flight**. Once established, flight transforms lineage trajectories in parallel ways across insects, reptiles, birds and mammals. Flying taxa often display exceptional dispersal ability, broad geographic ranges and elevated diversification rates. Long-range seasonal migration in insects, enabled by efficient flight and atmospheric exploitation, has profound ecological and epidemiological consequences, paralleling the global migratory networks of birds and bats (Chapman et al 2015). In groups such as beaded lacewings, long-term biogeographic analyses reveal that improvements in flight efficiency are tightly coupled to niche shifts and range expansions over more than 100 million years, illustrating how aerial adaptability facilitates dynamic responses to climatic and tectonic change (Ou et al 2025).

At the same time, flight is also repeatedly lost when its benefits no longer outweigh its substantial developmental and metabolic costs. Flightlessness has evolved convergently in multiple bird lineages, particularly in island ratites and rails, via shared regulatory changes affecting forelimb growth and pectoral musculature (Sackton et al 2019). Among insects, many lineages have independently reduced wings or abandoned flight under conditions where dispersal is risky or energetically wasteful, such as in stable, resource-rich or wind-exposed habitats (Chapman et al 2015; Treidel et al 2024). These parallel gains and losses underscore that the conquest of the air is not an irreversible apex but a contingent strategy whose maintenance depends on ecological context.

A unified pattern of aerial evolution. Despite anatomical, developmental and phylogenetic diversity, a broadly similar pattern underlies the conquest of the air across insects, reptiles, birds and mammals. First, pre-existing behaviors of falling, righting and gliding provide immediate fitness advantages and select for improved aerial control (Dudley & Yanoviak 2011). Second, anterior appendages are progressively transformed into wings that function as airfoils, exploiting convergent unsteady aerodynamic mechanisms such as leading-edge vortices within a shared physical parameter space (Chin & Lentink 2016). Third, musculoskeletal and metabolic systems are remodeled to support high power output and endurance, with convergent evolution of specialized striated flight muscles and fine-tuned actuation modes (Amador et al 2019; Cao & Jin 2020; Gau et al 2023; Treidel et al 2024). Fourth, developmental and genomic changes repurpose ancestral modules - gills, limbs, feathers, interdigital webbing - into aerodynamic surfaces, often through modifications of gene regulation rather than novel structural proteins (Sackton et al 2019; Almudi et al 2020; Anderson & Ruxton 2020; Moczek 2025). Finally, the acquisition of flight feeds back on macroevolutionary dynamics, enabling exceptional dispersal and diversification, but also repeated secondary losses of flight under altered ecological regimes (Bleiweiss 2009; Chapman et al 2015; Sackton et al 2019; Xu et al 2024; Ou et al 2025).

Seen in this light, the independent aerial radiations of insects, flying reptiles, birds and mammals reflect not isolated evolutionary accidents but recurrent solutions to a common set of biomechanical and ecological challenges posed by life in a gravitational field with a fluid atmosphere.

Conclusions. Flight evolution proceeds along a predictable behavioral continuum, from controlled descent and gliding to flapping flight, providing immediate survival and dispersal benefits. Morphological convergence transforms anterior appendages into wings capable of generating lift via shared aerodynamic mechanisms, despite distinct structural solutions. Musculoskeletal and metabolic systems are repeatedly remodeled to meet the high power demands of flight, with convergent adaptations in muscle structure, actuation modes, and energetic efficiency. Developmental and genomic innovations often involve repurposing pre-existing modules and modifying regulatory networks, rather than evolving entirely new proteins. The acquisition of flight enhances ecological versatility, range expansion, and diversification, but flight can also be lost when ecological costs outweigh benefits, reflecting its contingent nature. Overall, the independent emergence of flight across diverse animal lineages reflects recurring evolutionary solutions to common biomechanical and ecological challenges, rather than isolated evolutionary events.

Conflict of interest. The authors declare that there is no conflict of interest.

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