

# News & views

## Biomechanics

# How wingless salamanders fly

David Lentink

From frogs remaining airborne using their webbed feet to lizards and snakes gliding by expanding their ribcages, biologists might have thought they had seen every unusual aerial strategy – but now they report flying salamanders.

One way to investigate the evolution of flight-associated behaviours is to monitor an animal's response to weightlessness generated by the parabolic-flight method used for astronaut training. Parabolic-flight data<sup>1</sup> indicate that some reptiles and amphibians floating in microgravity adopt skydiving postures, which is unexpected because most of these animals do not have body shapes adapted for aerial behaviour. Many of the animals display aerial righting behaviour (positioning themselves so that their feet can absorb the impact on contact with the ground) and most – including one salamander species – don't vomit, which suggests that they don't develop motion sickness. Such characteristics undoubtedly help tree-dwelling salamanders such as the wandering salamander (*Aneides vagrans*) to move around in the canopy of old-growth redwood trees<sup>2</sup>.

This salamander species can readily jump from branches. From the observation<sup>3</sup> that it adopts a parachuting posture when jumping from a modest height of 75 millimetres, the idea that wandering salamanders might have flying skills was born.

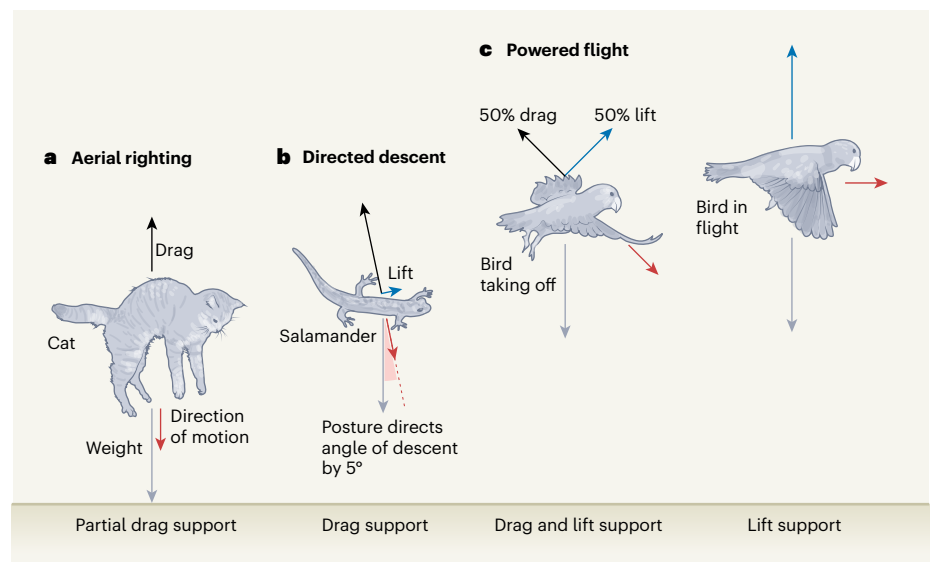
To find out whether this was the case, Brown *et al.*<sup>4</sup>, writing in *Current Biology*, released five of these salamanders in a vertical wind tunnel. The authors report that not only do the animals break their fall by parachuting in a jet of 36 kilometres per hour, but they also actively steer with their limbs and tail to make controlled banked turns and fly forwards at 2.5 kilometres per hour. The discovery that even wingless tree-dwelling salamanders fly in a controlled manner to survive a fall, albeit at steep descent angles that deviate only around 5° from falling straight down (Fig. 1), increases our understanding of how animal flight might have evolved in trees.

The origin of animal flight has long been

debated. Charles Darwin was asked<sup>5</sup>, “what use is half a wing?” Although the debate is continuing<sup>6</sup>, the directed aerial descent of wingless salamanders confirms the idea that life in the trees can spur flight<sup>7,8</sup>. Animals foraging there must watch every step to stay aloft. The need to survive if an animal fails to keep its footing and falls has driven the independent evolution of

effective aerial behaviours in a colourful assembly of tree-dwelling animals – including ants, spiders, salamanders, frogs, lizards, snakes, squirrels, lemurs and marsupials – despite these animals not having wings or having only makeshift ones<sup>6</sup>.

The first step in the evolution of aerial recovery from falling was probably gaining the ability to right the body in mid-air. This maximizes the projected area (the area perpendicular to the airflow) to generate aerodynamic drag (a force acting in the opposite direction to that of motion) to oppose gravity, breaking the animal's fall and allowing it to position its legs optimally to absorb the impact with the ground. Cats twisting their bodies and geckos swinging their tails to reorient in mid-air are examples of this phenomenon<sup>9</sup>. Wingless salamanders show how the next addition to the flight toolkit might have been the ability to change body posture with respect to the incoming airflow in a controlled fashion, as a way of directing aerial descent. Now that this rudimentary form of flight has been discovered in salamanders, a capacity that has also been observed in tree-dwelling ants<sup>7</sup> and spiders<sup>10</sup>,



**Figure 1 | The role of drag in the evolution of flight.** Animals use a range of aerial strategies to harness aerodynamic forces for weight support. **a**, A cat falling from a moderate height can right itself in the air to land on its feet. In this situation, in which the cat does not reach its maximum (terminal) velocity, the force providing partial weight support is mainly drag, which acts in the opposite direction to the (directly downwards) direction of motion. **b**, Brown *et al.*<sup>4</sup> analysed wandering salamanders (*Aneides vagrans*) falling in a vertical wind tunnel. As well as being able to right themselves, these creatures adopted a parachuting posture that generated drag and lift (a force acting perpendicular to the direction of motion), and enabled the animals to control their descent and land at an angle of about 5° away from the location expected from a directly downwards descent. **c**, Drag also provides weight support in winged flight. As a Pacific parrotlet (*Forpus coelestis*) takes off, lift and drag contribute equally to weight support, because drag counterbalances the downward wing stroke<sup>14</sup>. Once a bird or other winged creature has taken off by beating its wings, lift, rather than drag, is the dominant weight-supporting mechanism. Arrow size indicates the relative contributions of drag and lift to weight support.

wings seem surprisingly irrelevant for understanding the origin of flight across different types of body plan.

But how is ‘wingless flight’ not simply a contradiction in terms? Our common understanding of flight hinges on the aerodynamic theory developed for aircraft, which assumes that wings generate the aerodynamic lift (a force acting perpendicular to the direction of motion) needed to support weight, which is necessary for aircraft flight<sup>6,11</sup>. This obviously cannot explain wingless flight.

Instead, the answer can be found by considering the aerodynamics of oddly shaped bodies. A century’s worth of measurements of aircraft and rocket fuselages, as well as sky-diver models, in wind tunnels has shown that such odd shapes generate both a rise in drag and appreciable lift when held at extremely high angles (called high incidence) that are almost 90° away from the direction of airflow<sup>12</sup>. Furthermore, similar to the effect felt when sticking your hand out of the window of a moving car, flattened, disk-like surfaces such as hands (or feet) effectively generate drag in the direction of airflow and lift perpendicular to it when held at high incidence<sup>11,12</sup>.

Brown and colleagues report that the wandering salamander makes exquisite use of this phenomenon by adjusting the angle of incidence of its trunk, tail, legs and feet with respect to the incoming airflow. The appreciable lift provided pulls the salamander forwards along the horizontal direction, which enables

it to perform a directed aerial descent. This modulation of body posture gives the animal control over the lift-to-drag ratio, which generates a descent at an angle of 5–6° away from falling straight down. By modulating the net aerodynamic force with respect to its centre of gravity, the salamander steers left and right. Whereas lift is indispensable for directing flight, it is clear that salamanders rely predominantly on high drag to slow their descent. Given this expected role of drag, it seems counter-intuitive to consider the possibility that drag could also enable take-off.

Yet, two decades ago, an aerodynamic simulation of an insect wing flapping down under a steep angle demonstrated that drag can, in principle, be pointed upwards to counteract gravity<sup>13</sup>. Although the lift-based flight paradigm<sup>6,11,12</sup> made this idea seem quirky at the time, direct lift and drag measurements during foraging of Pacific parrotlets (*Forpus coelestis*) confirmed this phenomenon *in vivo*<sup>14</sup>. These birds are generalists, rather than specialists, in terms of their body shape and flight style, suggesting that their aerial behaviour is characteristic of that of many other bird species. On take-off, parrotlets flap their wings downwards to orient drag upwards so that it supports half of their body weight, after which they switch to harnessing lift as expected<sup>14</sup>. Taken together, these results reveal how drag is useful for supporting the body weight of modern flying animals ranging from ‘entry-level’ wingless salamanders to fully fledged birds. This new

appreciation of the full spectrum of wingless to winged body plans that can all aerodynamically support body weight continuously boosts our understanding of the evolution of flight.

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