Mechanisms for mid-air reorientation using tail rotation in gliding geckos

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Abstract
Arboreal animals face numerous challenges when negotiating complex three dimensional terrain. Directed aerial descent or gliding flight allows for rapid traversal of arboreal environments, but presents control challenges. Some animals, such as birds or gliding squirrels, have specialized structures to modulate aerodynamic forces while airborne. However, many arboreal animals do not possess these specializations but still control posture and orientation in mid-air. One of the largest inertial segments in lizards is their tail. Inertial reorientation can be used to attain postures appropriate for controlled aerial descent. Here we discuss the role of tail inertia in a range of mid-air reorientation behaviors using experimental data from geckos in combination with mathematical and robotic models. Geckos can self-right in mid-air by tail rotation alone. Equilibrium glide behavior of geckos in a vertical wind tunnel show that they can steer towards a visual stimulus by using rapid, circular tail rotations to control pitch and yaw. Multiple coordinated tail responses appear to be required for the most effective terminal velocity gliding. A mathematical model allows us to explore the relationship between morphology and the capacity for inertial reorientation by conducting sensitivity analyses, and testing control approaches. Robotic models further define the

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limits of performance and generate new control hypotheses. Such comparative analysis allows predictions about the diversity of performance across lizard morphologies, relative limb proportions, and provides insights into the evolution of aerial behaviors.

1 Introduction

Figure 1: Wind tunnel gliding experiments with *H. platyurus*. A) Sketch of the experimental set up (not to scale), showing layout of key components. B) Composite image of a gecko pitching its tail in flight, with tracked locations indicated. C) Tracked body and tail angles during tail motion in pitch, showing body motion following tail motion. D) Tail motion against body motion in yaw, collecting 7 tracked tail swings, and showing correlation between tail and body motion. E) Example tail yaw swing, showing start and end point, with tracked locations indicated.

Locomotor performance can influence success in nearly all facets of an organism’s life, including avoiding predation, and searching for food or suitable mates.
Arboreal habitats present numerous challenges to locomotor performance due to unsure footing on steep or narrow and often discontinuous substrates. These challenges are made all the more daunting considering animals are often moving on these substrates tens of meters above the ground below. Any mechanism that can provide an additional point of contact with the substrate or to maintain balance in case of the slip of a foot, could prevent a fall or if a fall does occur, the ability to control body posture to land safely can be the difference between life and death. Many organisms use their tails to accomplish these tasks by either increasing contact with the substrate, or by using inertial or aerodynamic forces to aid in postural control.

Numerous primates [3, 4, 5] and other mammals [6] use tails to provide an additional point of contact while reaching [6], climbing or moving on narrow substrates [7, 8, 9], or crossing gaps between branches [10]. Some reptiles including snakes [11] and chameleons [12] also grip with their tails during gap-crossing. Many other animals including birds [13, 14, 15] and mammals [16] use their tail as a prop while climbing steep substrates. The most extreme example of this behavior is the dynamic ‘kickstand’ response elicited by slipping in climbing geckos [17] in which the tail is pressed against the substrate in response to loss of contact between the foot and surface to arrest pitch-back and avoid falling from the vertical surface being climbed.

In addition to these mechanisms to increase contact with the substrate, tails and other appendages can be used to reorient the body using inertia while moving across a surface or while airborne. Cursorial mammals, such as cheetahs [18], and lizards [19, 20] use their tails to change body orientation while running over variable terrain. Tails are also used to change body orientation in mid-air by leaping [21, 22] or saltatory [23] animals. The risks of falling have shaped behavior in a wide variety of arboreal taxa resulting in reorientation after becoming airborne to minimize the risk of injury or control the flight path [24]. Gliding behaviors appear to evolve at the same time as the development of rainforests [25], and the subject of the paper (Hemidactylus platyurus) is known to exhibit ‘parachuting’ locomotion. Despite not possessing the more developed aerodynamic adaptations of other gecko species [26] H. platyurus still exhibits a dorsoventrally flattened body and tail. Aerial-righting behaviors have been described in a wide range of taxa from insects [27, 28, 29, 30] to lizards [31] to cats [32, 33] and often use tail inertia to aid in reorientation while falling.

During glides, tails have also been implicated in the volitional maneuvers of many taxa, both living (e.g. [34, 35, 36]) and extinct (e.g. [37, 38]). These mechanisms could rely on appendage inertia [17] or aerodynamic forces acting on an outstretched appendage (e.g. [39, 30]). In reptiles, numerous anecdotal descriptions have been made of tail use in maneuvering flight (e.g. [40, 26]), but little quantitative data exists on the mechanics of tail use during maneuvers in gliders, especially the independent contributions of inertia and aerodynamic forces. Quantitative studies of tail rotational inertia in geckos have shown that tail inertia can be used to change pitch and yaw during gliding [17] using similar movements as during aerial righting [17, 31, 27]. By comparing lizard species with different tail proportions it was shown that longer tail lengths can reduce
the tail motion required to elicit maneuvers of similar magnitude [31, 27].

In cases where animal performance data is limited, it is possible to use robotic modeling to inform the mechanical basis of locomotor behavior [41]. Wind tunnel testing of models is widely used to inform aerodynamics [39], and recently the development of precise miniaturized mechatronic components have allowed testing of active robotic models in free flight conditions, allowing access to a wider envelope of motion, that includes free rotation relative to the free stream (as opposed to the prescribed body orientations used in a statically mounted wind tunnel test), incorporating dynamic as well as static effects.

Many robotic models testing the uses of tails in locomotion have been presented recently. Inertial tails have been used for robot steering on the ground [42, 43, 44], and in aerial righting. Tail inertia has also been used to control roll orientation during free-fall [31] and pitch orientation during jumping [19, 45, 46], and to passively absorb perturbations in terrestrial locomotion[47]. The combination of aerodynamic and inertial control has also been employed to yaw a robot [48].

To understand the role of tail mechanics in pitch and yaw control and the independent effects of both rotational inertia and aerodynamic forces on reorientation during gliding in lizards, a combination of animal data and mathematical and robotics models were used. Kinematic data from the Asian Flat-Tailed Gecko (Hemidactylus platyurus) was examined to determine what tail movements result in reorientation of the body in pitch and yaw. Based on these data, a mathematical model was developed to describe the effect of tail movements on turning performance. Finally, a robotic model was used to determine the independent effects of tail inertia and aerodynamic forces on body reorientation in pitch during gliding.

2 Materials and Methods

2.1 Animal Experiments in a Wind Tunnel

In this paper, we expand upon an experimental set up previously described in [17, 31], presenting tracked kinematics of separate data sets acquired through high speed videography and testing the cross-correlation of tail and body motion. The gliding behaviors of geckos were investigated with an open circuit vertical wind tunnel, with a working section flow speed of 2 - 8 m/s. The animals were placed in the transparent tunnel working section, above the contraction and fan, with Plexiglas and mesh screens use to prevent animals from leaving the tunnel or entering the contraction. A tree stimulus was placed within sight of the working section, as a target for the animals, and cameras (AOS X-pri) were placed outside the tunnel to record motion (Fig. 1A). Anemometers (VelociCalc; TSI, Inc.) were used to measure airspeed, and geckos were found to glide at speeds between 4 and 7 ms$^{-1}$, depending on the mass and surface area of the individual.

We analyzed four gecko ‘flights’ across the vertical wind tunnel cross section
Figure 2: Examples of Relative tail size variation across several lizards species. Body length was measured snout to vent, tail length was measured from vent to tail tip. Geckos (H. platyurus) have relatively short tails compared to body length. Dimensions taken from preserved specimens in the Harvard Museum of Comparative Zoology.

While H. platyurus tails are typically around the same length as their body, many other lizard families exhibit much larger tail lengths (Fig. 2). To gain more insight into the mechanics of inertial reorientation with tails, a simulation was developed in Matlab/Simulink, using the Simscape Multibody package. The simulation models the animal’s tail and body as two rigid bodies, connected by
Figure 3: Simulating a planar yaw over a range of tail lengths. A) Graphical output from the simulations, showing a tail motion sequence, and the final position after a tail swing for four different tail lengths. B) Illustrative plot of how actuation changes as tail length is increased - accelerating and decelerating torque is kept constant, but actuation time changes. C) Body angle change after 180° tail swing. D) Maneuver speed shows diminishing returns, as the actuation time increases more rapidly than total body movement.

Two pin joints in the roll and yaw axes. The body and tail are all modelled as rigid bodies of uniform density, with the torso represented as a rectangular prism, the legs as cylinders and the tail as a cone. Dimensions and masses for *H. platyurus* are taken from [31].

Initially, we modelled a simple planar 180° swing of the tail in yaw, in a motion similar to the maneuvers observed in the wind tunnel testing (Fig. 1E), and used the model to test the effect of tail length (Fig. 3A). To produce the swing in the simplest possible manner, we applied a constant torque to the tail for 90° of swing, followed by an equal decelerating torque for the next 90°, such that the tail came to rest at 180° (Fig. 3B). The tail was then scaled up, while keeping tail base diameter and material density constant. The resulting body motion was analyzed in terms of both the angle moved (Fig. 3C) and the time taken for the swing (Fig. 3D). As tail length was scaled up, we held actuator torque constant, reasoning that the available muscular torque to accelerate the tail would scale with tail thickness rather than length.
2.3 Tail Motion in Multiple Degrees of Freedom

Previous work on lizard tails has focused on tail motion with a single degree of freedom [31]. However, a planar yaw or pitch swing eventually requires some return movement in the opposite direction, in order for the tail to be used repeatedly [50]. And because inertial forces are conservative, this will produce the opposite body motion to the initial movement. In practice, tail motion for inertial reorientation needs to be cyclic, with the tail returning to its neutral position (Fig. 4A). However, even a two degree of freedom tail with limited motion ranges presents an impractically large range of possible tail trajectories that produce useful body motion. The multibody gecko model provides an opportunity to apply trajectory optimization techniques to the tail, and attempt to ‘reverse engineer’ the motions observed in nature [51].

As our animal experiments indicated both an inertial and an aerodynamic role for the tail, we also used the model to investigate the effect of external forces on inertial reorientation. While an accurate aerodynamic model of the gecko would require significant computational complexity, beyond the scope of this paper, we represented aerodynamic forces in simplified form, as a pair of linear torsion springs acting on the roll and pitch axes of the body, such that the body is at equilibrium with a pitch and roll angle of zero, while the yaw axis of the body is unconstrained. This was felt to be a reasonable abstraction of small perturbation around an equilibrium gliding posture at terminal velocity, in which only pitch and roll rotations produce movement into the airflow direction. The springs added to each axis represent a simplified version of the aerodynamic restoring torques that keep a stably gliding object at an equilibrium orientation. Our approximation ignores any effect from tail position on the aerodynamic torque, and is only dependent on body motion. Including these simple external forces was enough to modify the tail trajectory found by a trajectory search (Fig. 4B) in a way which made the simulated motion better reflect the motion observed in gliding geckos (Fig. 4C).

In this paper we have set up an optimization of the tail trajectory using a genetic algorithm to search the space of possible trajectories. To bound the dimensionality of the problem, we have parameterized the trajectory with 6 collocation points (three in pitch and three in roll, Fig. 4D), equally spaced in time, and defined the trajectory of the tail as a cubic spline through the points [52]. These six points are used as input to the search algorithm, with each point constrained to be between -180° and +180°. The tail is constrained to start and finish at the same position, parallel to the body. This ensures that the resulting motion is cyclic, and can be repeated. The collocation points were spread over a 0.5 second timespan, to reflect the movement speed of the tail motions observed in the wind tunnel (Fig. 1C).

The genetic algorithm (adapted from [53]) conducts a stochastic search of the space of possible trajectories according to the value of an objective function (see appendix 1 for details, including a link to a code repository). This objective function was calculated using the body pose at the end of the simulation (at 1 second simulation time). The trajectory optimization is run with a population
Figure 4: Tail motion in multiple degrees of freedom, produced via trajectory optimisation in a simulated tail. A) Graphical simulation output, showing axis definitions. B) Without external forces, trajectory optimisation produces ‘figure eight’ motion, that does not resemble nature, but with external forces, tail motion resembles gecko observations. C) The cyclic tail swings which produce a yawing of the body in the gliding gecko. Lines show the position of the tail base (blue ‘+’) and the tail tip (red ‘o’). D) without restoring forces, the tail must repeatedly change directions on the way to a 30° yaw. E) with restoring forces on the pitch and roll axes, a simple tail swing is enough to produce a 30° yaw, and tail motion resembles nature.
size of 20 for 20 generations, requiring 400 simulations of the model, each with a different set of collocation points. An extended description of the model and parameter list can be found in appendix 1.

We ran the optimization routine twice, once with no external forces on the pitch and roll axes (Fig. 3B), and once with external forces active (representing tail motion with and without aerodynamic reaction forces, Fig. 4D). The external forces act only on the body roll and pitch axes, such that an external torque acts on the body:

\[ T_\alpha = C_1 \alpha + C_2 \dot{\alpha} \]

\[ T_\beta = C_1 \beta + C_2 \dot{\beta} \]

where \( T_\alpha \) and \( T_\beta \) are the torques acting on the pitch and roll axis respectively, and \( C_1 \) and \( C_2 \) are constants. No other external forces act on the body. While a coarse representation, the inclusion of external torques can approximate oscillations about an aerodynamic equilibrium point. Many natural modes of flying systems are well approximated by damped harmonic oscillation [39] (the short-period pitch oscillation, for example), and the representation is enough to illustrate the effect that aerodynamic torques could potentially have on the motion of a gliding animal with an inertial tail.

2.4 Biorobotic Gliding Experiments

Based on the importance of aerodynamics indicated by the modelling and analysis, we sought to quantify the aerodynamic effect of the tail by conducting a gliding test of a simple biorobotic model with an active tail. We built a small robot modelled on the posture of \( H. \ platyurus \) during gliding (Fig. 5A-C). We tested pitch motion of the tail, rather than yaw, as this kept the robot tail motion in the same plane as the glide motion.

Our robot has a body length of 80 mm, and a mass of 12 g. The body of the robot is made from 0.25 mm thick carbon fiber sheet, with a small nylon hinge to create a tail joint. The carbon fiber is hand cut with scissors and a dremel multitool. The arms and legs of the gecko were laser cut from 1 mm polypropylene sheet, and bent upwards with a heat gun to mimic the gecko’s ‘skydive’ posture, which is presumed to have a relevant positive influence on roll stability via the dihedral effect. The tail was actuated using a small linear servo (Spektrum SPMH2040L), chosen because the leadscrew mechanism would not backdrive, unlike more common spur gear servos. Spring steel wire and kevlar twine are used to connect the servo output to the tail. The robot uses a SAMD21 microcontroller from TinyCircuits (ASM2021-R) powered by a LiPo battery, (150mAh, TY502020). The robot also includes an SD card reader (ASD2201-R) which is not used in this paper, but contributes to the robot’s weight (Fig. 5B).

For the glide tests, the robot was dropped and allowed to descend freely from a height of 3m. An 0.5m aluminum channel was used as a launch rail,
Figure 5: Biorobotic active tail experiments. A) Image of *H. platyurus*’ gliding posture, Copyright (2008) National Academy of Sciences [17]. B) Close up view of the robot, showing the tail servo. C) Image sequence from two glides with tail raised and lowered. D) Descent velocity across runs. No statistically significant changes in velocity resulted from changes in tail position. E) Angle of attack with different tail positions - a raised tail produces a positive pitch up, while a flat tail tends to follow the robot’s direction of travel. F-G) Example runs with an active tail motion mid flight. In both cases, the initial upward swing of the tail produces a simultaneous pitch of the body. Once the tail is raised, the body continues to pitch upward slowly from the aerodynamic torque.
to ensure consistent orientation at the start of the glide. Tail movement mid glide was done open loop, occurring at a fixed time after release. The lower section of the robot glide was filmed with a high speed camera (AOS S-motion) at 500 Hz (Fig. 5C), and videos were tracked using DeepLabCut [54], with pixel calibration based on the length of the robot body, such that the length of a pixel was set by averaging the length of the body in pixels over each run to give a calibration length.

3 Results and Discussion

Using a combination of animal data with mathematical and robotic models, we have shown that lizards can reorient in mid-air using both inertial and aerodynamic forces from their large tails. Tail motions were associated with reorientation of the body in both pitch and yaw. From these data, two major patterns emerged. First, over the range of tails observed in most arboreal lizards, increasing tail length relative to body length increased the rate of body reorientation (Fig. 3). Second, while the lizards use both inertial and aerodynamic forces to reorient, inertial forces result in more rapid reorientation than do aerodynamic forces (Fig. 5).

3.1 Animal Data

In one glide across the wind tunnel, repeated tail motions were observed in pitch (Fig. 1B-C). Cross correlation analysis of body and tail angle showed that tail motion slightly lagged body motion, with a peak cross correlation at 16 ms time lag. The same was observed in another run with three repeated swings of the tail in yaw, with a time lag in this case of 24 ms. The time lag indicates the presence of an aerodynamic effect. If the body motion were due entirely to inertial effects, we would expect peak cross correlation at zero time lag, because the motion derives from conservation of momentum, meaning instantaneous body angular velocity would be correlated with instantaneous tail angular rate. On the other hand, aerodynamic torques and the resulting angular accelerations are principally proportional to tail position (a large tail deflection typically presents a larger area to the oncoming flow, and so produces more aerodynamic force), such that the change in body angular velocity from aerodynamic force generated by the tail will be given by the integral of tail position with respect to time, resulting in a time lag between tail movement and body movement.

However, despite the presence of aerodynamic effects, the dominant effect of the tail appears to be inertial. Collecting tail motions in the yaw plane (seven tail swings across five trials) (Fig. 1D-E), we can show correlation between tail angle change and the body angle change during the same time period as the tail motion ($R^2 = 0.57, n = 7$). However, the correlation is not complete, likely a consequence of aerodynamic rotations from feet and tail motion, superimposed upon the inertial effect. While geckos appeared to steer towards the stimulus at
the wind tunnel wall, they were not always able to successfully reach it. This could be attributed to the fact that the visual environment does not reflect the optical flow that would be experienced during a true arboreal glide, and more ecologically relevant testing would be needed to assess the aerodynamic authority of *H. platyurus*.

### 3.2 Planar Tail Motion Modelling

The consequences of scaling the tail up and down in length for a planar yaw are shown in Fig. 3C-D. We see that the angle moved by the body increases as the tail length increases, as would be expected, but when looking at the maneuver speed, calculated as the total angle moved by the body divided by the time taken, we see diminishing returns with increasing tail length. Since inertial reorientation is used for rapid movements with little available time (e.g. falling), the decreasing maneuverability improvement with increasing length will limit the pressure for longer tails. In fact, a maximum maneuver speed is found with a tail that is five times body length for the model parameters used here. 5:1 is a tail length ratio that can be observed in nature (e.g. *Takydromus*), but at such large tail lengths, the rigid body assumptions of the model are not valid, and here we only consider tail lengths up to 3:1, which is more representative of tail size among arboreal lizards.

### 3.3 Tail Trajectory Search

Without reaction forces, the final output of the tail trajectory search was a ‘figure-eight’ tail motion, with the tail having to trace opposing motions in pitch and roll to ensure only a pure yaw. This involved repeated changes in tail direction that did not resemble any natural motion observed in the gliding geckos (see supplementary movie). When the reaction forces were added, the tail motion was simpler, and the yawing could be produced in a similar fashion to the cyclic yaw motions observed in the wind tunnel (Fig. 4C). While the trajectory search is somewhat prescriptive (for example, the cost function could take many forms), the difference between the simulations illustrates the importance of aerodynamic reactions to the tail maneuvers seen in the gliding gecko; aerodynamic forces simplify the tail trajectory in certain situations, allowing quick inertial movements in one axis, followed by dissipative recovery strokes using aerodynamic reaction forces.

### 3.4 Robot Data

To test the aerodynamic impact of tail deflection, drop tests were performed with the tail held static deflected upward to 45 degrees and with the tail held parallel to the body (Fig. 5C, E). These tests showed that upward tail deflection produced a constant pitch up change in angle of attack as the robot descended (202.9 ± 10.9°/s, n = 6, mean ± s.e.) while a flat tail posture produced a pitch down at (51.7 ± 3.4°/s, n = 6, mean ± s.e.). Plotting velocity showed that
the robot was slowly accelerating, with velocity changing by a mean of 1.8m/s over the course of a glide (Fig. 5D). The change in posture did not result in a significant change in mean velocity ($p = 0.38$, paired two-tailed t-test).

We also tested actuating the tail in mid-flight, with a rapid up and down motion of the tail commanded, switching between the two positions tested statically. These trials showed the expected inertial response of the body, with the body pitching up at the same moment the tail was swung (4° and 6° body pitch). The raised tail then produced a slower pitch up (53°/s and 27°/s), generated by the aerodynamic forces observed in the static trials. Taken together, the robots trials demonstrate that while inertial forces are dominant, aerodynamic reactions also exert a strong influence on the path of a gliding gecko.

Pressure acts on maneuver speed in several ecological scenarios including signaling mates or conspecifics (e.g. [55]) for predator evasion [56, 57] or prey capture [58], and traversing complex habitats (e.g. [59]). The large tails of lizards aid in reorientation during locomotion over complex terrain [60] or while airborne [31]. Here we show that longer tails result in more rapid reorientation (Fig. 3). For example, *H. platyurus* has a tail length to body length ratio of 0.93 and *Anolis carolinensis* has twice the relative tail length ratio of 1.80 [31, 27], which results in smaller tail flicks sufficing for reorientation during free fall, and greater effectiveness for turning during gliding. Our modeling results show that this results in a 50% increase in turning rate (60°/s in *H. platyurus* compared to 90°/s in *A. carolinensis*). It should be noted that as tails get even longer, the benefit of a longer tail in reorientation rate diminishes rapidly above a tail length ratio of 2. This relationship between tail length and running rate poses another challenge for animals with autotomized tails (self-amputated/shed, typically for self defense). If much of the tail is lost, geckos lose the ability to successfully complete righting after falls [17]. Further, the ability to reorient the body to control a glide trajectory will also be reduced. For example, if a gecko tail is autotomized to 40% of its original length, the turning rate is halved (Fig. 3).

In squamate locomotion, lateral tail oscillation is a common occurrence in the context of back bending that is used in running, climbing, and swimming [61]. While we do observe similar planar tail oscillations during aerial behavior (Fig. 1) the observed tail kinematics often have more out of plane motion (See supplementary movie) than during lateral undulation in terrestrial locomotion. During aerial motion, if no external force is applied to the system, then there must be conservation of angular momentum. Thus, if the tail moves to the left and the body responds, when the tail is moved back to the center, the body will in turn respond in the opposite direction, resulting in no net reorientation. The observed out of plane motions of the tail, allow the tail to continue rotating in one direction to allow a maneuver to occur over multiple sweeps of the tail.

Our analyses also found a significant but not dominant aerodynamic role for the tail. It is important to note here that our experiments examine the gecko at or near to terminal velocity, whereas previous observations of the air righting reflex in geckos have been made at the onset of a fall, i.e. where velocity is zero. The importance of terminal velocity falling to the animal’s life cycle is difficult to quantify, but we can gain insight into the relevance
of terminal speed by calculating the distance the animal must fall to reach terminal velocity (see appendix 2 for full calculation). Based on the typical glide speed (6 m/s), mass (2.9 grams) and approximate projected area (890 mm$^2$) of *H. platyurus*, we can estimate its drag coefficient as 1.9 (this drag coefficient is significantly higher than a flat plate of equivalent area, reflecting some aerodynamic adaptation). Based on that drag coefficient, the distance a falling gecko must descend vertically to reach 75% of terminal speed can be estimated as 1.6 m. To reach 95% terminal speed, the gecko must descend 4.1 m. These are feasible falling heights for wild geckos, given the height of the canopy they inhabit.

Falling at terminal velocity changes the dynamics of reorientation significantly, and as terminal velocity changes with size [62], we can also expect the relative contribution from aerodynamic and inertial effects to change significantly. The available torque that can be applied to the body in an inertial reorientation is simply the torque that can be applied to the inertial appendage, which in this instance would be proportional to the muscle cross section (length$^4$) multiplied by a lever arm length, giving an overall scaling of length$^3$. An aerodynamic torque depends on appendage area, lever arm length and velocity, i.e. length$^3$ multiplied by velocity$^2$. At terminal velocity, velocity$^2$ is proportional to mass divided by area, or proportional to length$^1$ (where mass scaling is isometric). This would mean that the available aerodynamic torque is proportional to length$^4$. The faster scaling up of aerodynamic torque relative to inertial torque as size increases may partially explain why a larger arboreal mammal such as *Sciurus carolinensis* [63] exhibits a smaller relative tail mass (3% body mass, vs 10% in *H. platyurus*), but has adaptations to increase aerodynamic area through fur growth (tail fur produces a significant increase in aerodynamic area [50]).

The effects of inertial forces at low speeds during righting (e.g. [17]), leaping (e.g. [21]), or running [60] are well described. Similarly, the aerodynamic torques used by falling or gliding animals to reorient using an outstretched limb or tail are well established from wind-tunnel studies [39, 37, 29]. By examining descent at higher speeds our data show that both inertial and aerodynamic forces interact to affect reorientation and their relative contributions vary with increasing speed. This interaction between inertial and aerodynamic forces needs to be further explored, particularly in animals that do not appear specialized for gliding. The robot and code presented in this paper both use rigid tails, but advances in soft robotics [47, 64, 65] mean that testing the effect of lifelike, compliant tails in future studies is now possible. Numerous arboreal animals are at risk of falling and once airborne this interaction of forces plays a role in their ability to reorient and land safely.

4 Conclusion

Lizard tails vary widely in form and function, shaped by their role in signaling, camouflage, and locomotion. Tail proportions are often associated with habitat
and those differences can have an influence on the mechanics of locomotion. In arboreal lizards, that risk falls from height, tail proportions affect an animal’s ability to reorient in the air and control trajectory to land safely. For tree-dwelling lizards, relatively longer tails allow for more rapid reorientation and control of body position through use of both inertial and aerodynamic forces. It takes coordinated responses of these forces to successfully control posture in the air. These data only reinforce the versatility of tails and their importance in the evolutionary success of lizards and other tailed animals.

In this paper we have examined the role of tails in gliding locomotion with several new experiments and analyses. The data shows that multiple coordinated responses are necessary to successfully control posture in the air. Future work will combine the trajectory optimization shown here with advanced versions of the presented robot, to test tail use in multiple degrees of freedom across a range of glide conditions.

5 Appendix 1: Trajectory Optimization Detail

The Matlab code for both the multibody simulink model and the optimization procedure is available for download, see the ‘Data Availability’ section. The demanded tail trajectory is input to the simulation as a cubic spline between three collocation points at fixed points in time (Fig. 4D-E). The resultant tail motion in each axis is determined by a PID position controller, where the process variable is the angle of each tail joint and the setpoint is the demanded tail value at a given instant in time. The controller determines the instantaneous torque applied to each tail axis, and the same PID gains are used on both axes. These gains are listed in table 1.

The trajectory optimization is run using the inbuilt genetic algorithm function in Matlab 2020b. We ran the optimization using default settings, with a fixed ‘population’ and number of ‘generations’, in this case 20 and 20 respectively, requiring 400 simulations of the model, with the best value after 20 generations taken as the result (Fig. 6). The objective function is made up of a path length constraint (found by integrating the motion of the tail pitch joint $\theta$ and roll joint, $\psi$), the absolute difference between the final body angle and the demanded body angle change (which in this case was 0° in pitch, $\alpha$, 0° in roll, $\beta$, and 30° in yaw, $\gamma$), and a body velocity penalty such that the cost function, $F_{\text{cost}}$ was

$$F_{\text{cost}} = F_{\text{angle}} + F_{\text{velocity}} + F_{\text{path}}$$

$$F_{\text{angle}} = |\alpha| + |\beta| + ||\gamma| - \pi/6|$$

$$F_{\text{velocity}} = |\dot{\alpha}| + |\dot{\beta}| + |\dot{\gamma}|$$

$$F_{\text{path}} = \int |\theta| + |\psi|dt$$
Figure 6: A) Trajectory optimization progression for the result displayed in Fig. 4D, without restoring forces. B) Trajectory optimization progression for the result displayed in Fig. 4E, with restoring forces. C) Example of trajectory optimization result with no seeding, and no external forces included. The optimization finds a local minimum with no net body motion. To avoid this, 50% initial population seeding was added with a coarse representation of the observed gecko tail motion.

To limit the search space, half of the population of initial guess collocation points (i.e. 10 tail trajectories out of 20 in the population) are prescribed as [90°, 90°, 90°] in tail pitch and [90°, 0°, -90°] in tail roll, with the other 10 guesses generated randomly within the possible tail motion range (±100° in tail pitch and ±370° in tail roll). The ten prescribed guesses represent a coarse representation of the observed gecko tail motion (see supplementary video), to focus the trajectory search. Removing this seeding and beginning the trajectory search with entirely random collocation points resulted in a local minima with a net body yaw motion of 0.5° vs the 5.5° yaw produced by seeding the optimization with approximate animal motion (Fig. 6C). The remaining parameters for the model are tabulated in table 1, including the external torque constants $C_1$ and $C_2$ (equations 1 and 2). Body mass and length parameters are taken from [31].

Table 1: Specifications and variable definitions of the multi body model.

| Parameter                      | Value                        |
|--------------------------------|------------------------------|
| Body mass                      | 2.9 g [31]                   |
| Body length                    | 54.0 mm [31]                 |
| Tail mass                      | 0.29 g [31]                  |
| Tail length                    | 50.0 mm [31]                 |
| External Rate, $C_1$           | $5 \times 10^{-7} Nm/deg$    |
| External Damping, $C_2$        | $0.5 \times 10^{-7} Nm/deg/s$|
| Tail axis gains:               |                              |
| Proportional gain              | 0.1 Nm/rad                   |
| Integral gain                  | 0.05 Nm/rad/s                |
| Derivative gain                | 0.02 Nm.s/rad                |
6 Appendix 2: Terminal Velocity Fall Distance

For an object falling under quadratic drag, terminal velocity will be reached when drag balances body weight, such that

\[ \frac{1}{2} \rho AC_D v_T^2 = mg \]  

(7)

where \( m \) is mass, \( A \) is area, \( C_D \) is drag coefficient, \( g \) is acceleration due to gravity and \( \rho \) is air density. The terminal velocity is then

\[ v_T = \left( \frac{2mg}{\rho AC_D} \right)^{\frac{1}{2}} \]  

(8)

For an object descending vertically in a straight line from rest, the instantaneous velocity, \( v \), at time \( t \) is

\[ v = v_T \tanh \left( \frac{tg}{v_T} \right) \]  

(9)

which can be integrated to give distance, \( x \) as a function of time:

\[ x = \frac{v_T^2}{g} \ln \left( \cosh \left( \frac{tg}{v_T} \right) \right) \]  

(10)

These equations can be used to find the distance traveled before a falling object reaches a significant proportion of its terminal velocity.

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Data Availability

A video file is included with the paper, and the model code can be found here: dx.doi.org/10.17617/3.6k or here: github.com/robjds/Tailobatics. The other data presented in this paper will be made available upon reasonable request.

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