1. Introduction

Animal gliders move horizontally through the air by exchanging potential energy for kinetic energy and by producing and controlling aerodynamic forces [1, 2]. To meet ecologically relevant goals, including predator escape, moving to new foraging locations, and finding mates, and has been suggested as an evolutionary pathway to powered flight. Historically, gliding has been conceptualized using the idealized conditions of equilibrium, in which the net aerodynamic force on the glider balances its weight. While this assumption is appealing for its simplicity, recent studies of glide trajectories have shown that equilibrium gliding is not the norm for most species. Furthermore, equilibrium theory neglects the aerodynamic differences between species, as well as how a glider can modify its glide path using control. To investigate non-equilibrium glide behavior, we developed a reduced-order model of gliding that accounts for self-similarity in the equations of motion, such that the lift and drag characteristics alone determine the glide trajectory. From analysis of velocity polar diagrams of horizontal and vertical velocity from several gliding species, we find that pitch angle, the angle between the horizontal and chord line, is a control parameter that can be exploited to modulate glide angle and glide speed. Varying pitch results in changing locations of equilibrium glide configurations in the velocity polar diagram that govern passive glide dynamics. Such analyses provide a new mechanism of interspecies comparison and tools to understand experimentally-measured kinematics data and theory. In addition, this analysis suggests that the lift and drag characteristics of aerial and aquatic autonomous gliders can be engineered to passively alter glide trajectories with minimal control effort.
predictions of performance. For example, heavier individuals with higher wing loading should glide faster than lighter individuals, but both should have the same equilibrium glide angle [3]. Equilibrium theory also predicts that glide range and energy conversion efficiency will be maximized when the lift-to-drag ratio is maximized [4]. These predictions should be valid for any glider, even though species vary greatly in their size, morphology, and diversity of aerodynamic structures. Examples of this diversity include the dorsoventrally flattened body of gliding snakes [5–9], the inter-limb patagial membrane of gliding mammals [10, 11], the rib-wings of gliding lizards [12, 13], the webbed feet of gliding frogs [14], and body/limbs in wingless hexapods [15, 16] and arachnids [17].

However, there is limited evidence of equilibrium gliding in experimental studies. In one study, 52% of *Draco* glides did not reach equilibrium [13]. In experiments with the flying snake *Chrysopelea paradisi*, only one of 14 glide trials originating from a height of 9.6 m appeared to reach equilibrium [18], and no equilibrium glides were found in eight glide trials beginning from a height of 15 m [5]. Two studies of gliders recorded in the wild found similar results. Body-mounted accelerometers attached to gliding colugos generally indicated greater vertical forces than required for equilibrium [11], and no equilibrium glides were found in long horizontal distance (18 m) glides of northern flying squirrels, *Glaucomys sabrinus*. Simulated glides of *G. sabrinus* required time-varying force coefficients to reproduce the observed trajectories in this species [10]. These studies show that non-equilibrium gliding is dominant in real trajectories.

Observations of non-equilibrium gliding are not unexpected given the coupled effects of animal behavior and aerodynamic force production on glide trajectories. All gliders must accelerate to sufficient velocities to produce appreciable aerodynamic forces, so there is always some non-equilibrium portion at the start of any glide. Similarly, slowing the glide before landing and controlling contact with the substrate requires aerodynamic and postural changes [19]. An animal can also modify force production by changing the wing itself, by varying the camber or aspect ratio with relative limb position [20, 21]. Furthermore, gliders can maneuver volitionally, or make small adjustments to the trajectory to achieve a goal such as landing on a targeted tree [22].

The other source of complexity that can affect glide dynamics is the local airflow interaction with the body. During the ballistic and shallowing phases of gliding that precede equilibrium, the relative air velocity changes continuously in magnitude and in direction. Lift and drag forces scale as the velocity squared, and their lines-of-action depend on the instantaneous flow direction. Additionally, lift and drag coefficients depend strongly on the animal’s angle of attack, which changes passively as the glide angle changes, and actively if the animal changes its pitch angle using control. Understanding this coupling of animal behavior and force production requires not only kinematics and force coefficient data, but also modeling to unify experimental observations with physical theory.

Theoretical models have been used to study the effects of force coefficients, wing loading, and initial conditions on glider performance and stability. Models from the late 1800’s were developed to understand bird flight [23, 24], but more recent modeling work can be categorized as either particle models or rigid-body models. Particle models consider the glider as a point mass moving in the vertical plane under the influence of lift, drag, and gravity [4, 5, 10, 25]. These models decouple the instantaneous lift and drag coefficients from the glide dynamics, by assuming that the coefficients are either constants or arbitrary functions of time, but not functions of angle of attack. A dominant feature revealed from particle models is damped oscillations in velocity, acceleration, and glide angle time series before the glider reaches equilibrium [4, 5, 24, 25]. Rigid-body models couple both the translational and rotational pitch dynamics of the glider. Jafari *et al* [26] developed two tandem-wing rigid-body models to investigate the passive stability characteristics of flying snakes [26], finding that stable glides are possible, but depend on the initial conditions of pitch and pitch rate. Certain combinations of initial conditions lead to equilibrium glides, whereas other combinations lead to falling with a negligible horizontal velocity.

Here, we used theoretical modeling and a new analysis of the velocity polar diagram (*sensu* Tucker [27]) of horizontal versus vertical velocity to develop a non-equilibrium theoretical framework to understand the mechanics of gliding. This work was specifically motivated by the question, what is the effect of angle-of-attack-dependent lift and drag coefficients on a glider’s trajectory dynamics? We developed a rigid-body model using a new rescaling to isolate the effects of the lift and drag coefficients. This rescaling enabled us to test the effect of lift and drag coefficients using simulated glides, with angle-of-attack-dependent force coefficients taken from previous studies. In particular, we used force coefficients from studies of flying squirrels [10, 20], flying snakes [8], sugar gliders [28], flying fish [29], chukar partridge [30] and dragonflies [31]. This broad sampling of animals helps to elucidate commonalities of non-equilibrium gliding, demonstrating the utility of this non-equilibrium framework across phylogenetically diverse species. As future kinematics studies reveal more detailed glide information, this framework can be used to answer questions about how gliders control the trajectory by varying body posture.

2. Methods

We formulate the equations of motion for a glider translating in the vertical x-z plane (figure 1(e)) under the influence of lift, drag, and gravity. We analyze the glider as a rigid body in which angle of attack changes with glide angle and a specified body pitch angle.
we do not write an equation of motion for the rotational dynamics, but instead use the pitch angle to elicit different system responses. To encapsulate a glider’s motion in an intuitive and informative manner, we use the velocity polar diagram (figure 1(g)) instead of time series of position, velocity, acceleration, and glide angle (figures 1(a)–(d)). The velocity, acceleration, and glide angle information is embedded in the diagram, and equilibrium gliding can be clearly identified as points where the acceleration vector goes to zero and to which velocity trajectories are attracted to or repelled from.

2.1. Rigid-body model equations of motion

Using the free-body diagram in figure 1(f) for a glider of mass \( m \) in an inertial reference frame defined by \( x \) and \( z \), we write the equations of motion in the horizontal and vertical directions as

\[
\begin{align*}
\dot{v}_x &= F_l \sin \gamma - F_D \cos \gamma \\
\dot{v}_z &= F_l \cos \gamma + F_D \sin \gamma - mg,
\end{align*}
\]

(2.1)

where the overdot signifies the time derivative, \( F_l \) and \( F_D \) are the lift and drag forces, \( v_x \) and \( v_z \) are the velocities in the horizontal and vertical directions, and \( a_x = \dot{v}_x \) and \( a_z = \dot{v}_z \) are the accelerations in the horizontal and vertical directions. The instantaneous glide angle, \( \gamma = -\frac{1}{\tan^{-1} v_x/v_z} \), is defined as positive for a clockwise rotation from the horizontal axis (i.e. the glide angle will be positive when the animal glides downward). By definition, the drag force acts counter to the local direction of forward travel along the glide trajectory, lift force acts normal to it, and both are written as

\[
\begin{align*}
F_l &= \frac{\rho v^2 S C_l(\alpha)}{2}, \\
F_D &= \frac{\rho v^2 S C_D(\alpha)},
\end{align*}
\]

(2.2)

where \( \rho \) is air density, \( v = \sqrt{v_x^2 + v_z^2} \) is airspeed, \( S \) is projected surface area of the glider, \( \alpha = \gamma + \theta \) is angle of attack, and \( \theta \) is pitch angle, which specifies the angle between the mean chord line and the horizontal axis (positive counter-clockwise from the horizontal).
Pitch angle is a free parameter in the model, whereas glide angle is not.

The lift and drag coefficients, \( C_L(\alpha) \) and \( C_D(\alpha) \), are functions of angle of attack in this model, as determined from lift and drag curves specific to each glider. In general, these curves depend on airfoil shape and Reynolds number [32], and must be determined experimentally. For this analysis, we chose characteristic lift and drag curves for a particular Reynolds number and wing shape, using angle of attack as the only free parameter that determines the instantaneous lift and drag coefficients. Although the lift and drag coefficients are velocity-independent, the lift and drag forces are not. Combining equations (2.1) and (2.2), we arrive at the following expression for the glider’s accelerations,

\[
\ddot{x} = \frac{\rho v^2}{2m} [C_L(\alpha) \sin \gamma - C_D(\alpha) \cos \gamma] \tag{2.3}
\]

\[
\dot{\gamma} = \frac{\rho v}{m} [C_L(\alpha) \cos \gamma + C_D(\alpha) \sin \gamma] - g \tag{2.4}
\]

2.2. Dimensional analysis

We non-dimensionalize the equations of motion using the chord length \( c \) as the characteristic length scale. For a flying snake, the chord length is nominally the flattened aerial width of the animal [5, 8], and for a gliding mammal, it is the distance between the wrist and the ankle along the stretched patagium [21, 33].

The non-dimensional time scale, \( T = \sqrt{c/g} \), is found by normalizing by the gravitational acceleration \( g \); it follows that the characteristic velocity scale is \( c/T = \sqrt{c g} \). We define the non-dimensional time, velocity, and positions as

\[
\hat{t} = \frac{t}{\sqrt{c g}}, \quad \hat{v} = \frac{v}{\sqrt{c g}}, \quad \hat{p} = \frac{p}{c}.
\]

where \( v \) is either \( v_1 \) or \( v_2 \) and \( p \) is either \( x \) or \( z \). After substituting the non-dimensional groups into the equations of motion (2.3) and (2.4), we find

\[
\frac{d\hat{v}_1}{dt} = \rho \hat{v}^2 [C_L(\alpha) \sin \gamma - C_D(\alpha) \cos \gamma] \tag{2.5}
\]

\[
\frac{d\hat{v}_2}{dt} = \rho \hat{v}^2 [C_L(\alpha) \cos \gamma + C_D(\alpha) \sin \gamma] - 1 \tag{2.6}
\]

where prime notation is used as a shorthand for rescaled time derivatives \( \frac{d}{d\hat{t}} \). These equations are integrated to construct the velocity polar diagram trajectories. The polar form of the equations, written in terms of the airspeed \( \hat{v} = \sqrt{\hat{v}_1^2 + \hat{v}_2^2} \) and glide angle \( \gamma = -\tan^{-1} \hat{v}_2/\hat{v}_1 \), is

\[
\gamma' = -\hat{v} C_L(\alpha) + \frac{\cos \gamma}{\hat{v}} \tag{2.7}
\]

\[
\hat{v}' = -\hat{v}^2 C_D(\alpha) + \sin \gamma \tag{2.8}
\]

Note that the rescaled equations do not depend on body size or wing loading, but only on the lift and drag coefficients. Therefore, any differences in glide performance must result from differences in the lift and drag curves.

2.4. Equilibrium gliding

Equilibrium gliding occurs when the resultant aerodynamic force balances the gravitational force on the glider, producing a constant glide angle and speed. This condition requires that the left-hand sides of expressions (2.5) to (2.8) are zero, resulting in the equilibrium states \( (\hat{v}_1^*, \hat{v}_2^*) \) and \( (\gamma^*, \hat{v}^*) \). Once the equilibrium glide angle \( \gamma^* \) is known, the equilibrium airspeed \( \hat{v}^* \) is determined from equations (2.7) or (2.8), and the equilibrium horizontal and vertical velocities are found using \( \hat{v}_1^* = \hat{v}^* \cos \gamma^* \) and \( \hat{v}_2^* = -\hat{v}^* \sin \gamma^* \). Simple algebraic manipulation of the equilibrium equations of motion results in the well-known expression for the equilibrium glide angle

\[
\frac{F_L}{F_D^*} = \frac{C_L(\alpha^*)}{C_D(\alpha^*)} = \frac{C_L(\gamma^* + \theta)}{C_D(\gamma^* + \theta)} = \cot \gamma^*, \tag{2.9}
\]

where \( \alpha^* = \gamma^* + \theta \). This transcendental equation for the equilibrium glide angle \( \gamma^* \) can have multiple solutions, which depend on the number of times the lift-to-drag ratio curve \( \frac{C_L}{C_D} \) intersects the \( \gamma^* \) curve. Furthermore, the location and number of equilibria depend on the pitch angle \( \theta \). Because lift and drag are not analytical expressions of angle of attack, the equilibrium glide angle is found numerically. From equation (2.9), changing the pitch angle shifts the equilibrium glide angle, and to find these values, we consecutively shifted the lift-to-drag ratio curve over a range of specified pitch angles and used the Newton–Raphson root-finding method to locate the intersections. This technique is shown in figure 2, where two equilibrium glide states exist for a pitch of \( 10^\circ \) and only one equilibrium for a pitch of \(-10^\circ \).
2.5. Equilibria type and stability analysis

To determine the stability type and location of equilibrium points in the velocity polar diagram, we use linear stability analysis [34] by classifying the eigenvalues of the Jacobian matrix of partial derivatives for the polar coordinate equations (2.7) and (2.8) evaluated at equilibrium. For this system of two equations, the eigenvalues \( \lambda_{1,2} \) are

\[
\lambda_{1,2} = \frac{C_D}{2(C_L)^2 + C_D^{MU4}} \left(-\tau \pm \sqrt{\tau^2 - 8\Delta}\right),
\]

\[
\tau = \left(\frac{C_L}{C_D}\right) + 3
\]

\[
\Delta = \left(\frac{C_L}{C_D}\right)^\gamma + \left(\frac{C_L}{C_D}\right)^2 + 1
\]

where \( \left(\frac{C_L}{C_D}\right)^\gamma \) denotes the slope of the lift-to-drag ratio curve. The stability type depends on both the magnitude and slope of the lift and drag curves at equilibrium. This system permits five common types of equilibrium points, based on the signs and magnitudes of \( \tau \) and \( \Delta \): stable and unstable foci, stable and unstable nodes, and saddle points. A summary of these equilibrium types is shown in figure 3.

If lift and drag coefficients are independent of angle of attack, then the primed terms in equations (2.11) and (2.12) are zero, and only stable equilibria are possible. That is, the simulated glider will never have a horizontal velocity of zero and will always reach an equilibrium with some horizontal velocity. Additionally, that equilibrium will be a stable focus if lift-to-drag ratio exceeds the low value of \( \gamma^\ast \approx 0.354 \) \( (\gamma^\ast > 70.53^\circ) \), and otherwise will be a stable node. If lift and drag coefficients are dependent on angle of attack, more dynamical behavior is possible.

2.6. Model input from experimentally measured lift and drag curves

To test the effect of angle-of-attack-dependent force coefficients and the applicability of the non-equilibrium gliding framework, we use aerodynamic coefficient curves (figure 4) from a range of animal gliders, including flying squirrel [20], flying snake [8],

---

Figure 2. Pitch as a bifurcation parameter. Increasing the body pitch angle \( \theta \) shifts the lift-to-drag ratio curves horizontally to the left, which changes the number of intersections with \( \cot \gamma \). Each intersection is an equilibrium point, which are indicated by round markers at the intersection points for varying pitch angles. Force coefficient data are for a flying snake cross-sectional shape [8] at \( Re = 11,000 \).

Figure 3. Summary of equilibrium type as a function of lift and drag curves. The equilibrium type is uniquely determined by the lift and drag curves and their slopes evaluated at the equilibrium angle of attack. Previous models of animal gliding, which assumed constant lift and drag coefficients, only observed stable node and stable focus type equilibrium points, as indicated by the horizontal gray line.
sugar glider [28], and flying fish [29], as well as two active flyers, juvenile chukar partridge at 20 days post hatch (d.p.h.) [30], and dragonfly [31]. These species vary in size, Reynolds number, and aerodynamic force-producing structure. The chukar at 20 d.p.h can sustain level flight, but lacks the locomotor capacity of adults, as the wing is still developing and produces only small amounts of lift. Dragonflies use brief periods of gliding, lasting up to 0.5 s and covering 1 m. However, gliding is often interrupted by wingbeats, so glide durations are short (less than 0.2 s, mean of 0.13 s [31]). Coefficient curves are classified in three ways, based on data from previous studies (table 1). The ‘airfoil’ curves are from wind tunnel experiments of a representative airfoil model. The ‘whole animal’ curves are from wind tunnel measurements of a deceased and taxidermically-prepared animal. The ‘kinematics’ curves are reconstructed from recorded glide trials of flying squirrels, and are further discussed below. The coefficient values were smoothed with third-order B-splines to provide a continuous representation for simulations and stability calculations.

Because the aerodynamic coefficients for the entire animal will be different from those of the airfoil alone [35],

Figure 4. Lift, drag, and lift-to-drag ratio coefficient curves used in this study. Airfoil-based curves for (a) flying squirrels [20], (b) flying snakes [8], and (c) chukar partridge [30], and whole-animal curves for (d) sugar gliders [28], (e) dragonflies [31], and (f) flying fish [29]. Measured values are indicated with markers, and spline-fit values are indicated with solid lines.
we also analyzed force coefficient curves (figure 7(a)) derived from kinematic measurements of flying squirrels gliding to a tree located 18 m from the launch platform [10]. These ‘kinematics’ coefficient curves were back-calculated from individual glides, as well as from an ensemble of all glides (see supplemental information). To reconstruct the angle-of-attack-dependent coefficients, first the force coefficients were calculated by rearranging equation (2.2). Second, the time-varying angle of attack was approximated as the sum of the calculated glide angle and an assumed pitch angle of zero degrees. We had to approximate the pitch angle because it was not available from the kinematics data. In general, the force coefficient curves measured from wind tunnel tests are of higher quality because (1) the velocities and angles of attack are precisely known, (2) they cover a wider angle of attack range, and (3) noise-magnifying numerical derivatives [36] are not present. Nonetheless, these coefficient curves were included to help synthesize theoretical predictions with observed glides.

2.7. Model assumptions

The complete non-equilibrium glide framework consists of the equations of motion, equations (2.5)–(2.8), and lift and drag coefficients determined from experiments. The model assumes angle-of-attack dependent, but velocity independent, quasi-steady lift and drag coefficients that are representative of the animal mid-glide. Although lift and drag coefficients are velocity independent, the lift and drag forces depend on the instantaneous velocity. Additionally, we do not explicitly model the rotational motion of the glider, but instead treat only one rotational direction, pitch, as a parameter that is systematically varied to elicit different glide performance. Finally, we treat motion in the vertical x–z plane only, ignoring side forces and full three-dimensional glide trajectories resulting from yaw and roll rotations. The above assumptions provide the simplest model to explore the effect of angle-of-attack dependent lift and drag coefficients on a glider’s trajectory dynamics.

3. Results

3.1. Structure of the velocity polar diagrams

Velocity polar diagrams for the airfoil and whole-animal-based lift and drag curves are shown in figure 5 for two different pitch angles. In these plots, initial conditions from the animal gliders originate near the origin of the diagrams, with a near-zero vertical velocity and low horizontal velocity. These plots show that only certain equilibrium glides can be reached for the initial conditions typically observed in real glides. The velocity polar diagrams generally have multiple equilibria including stable nodes and saddle points. The stable and unstable manifolds of the saddle point delineate the basins of stability of stable glides. The upper stable branch of the saddle point, which runs vertically through the diagrams, acts as a separatix (sensu Strogatz [34]) and can block accessibility to low glide angle equilibrium points. Additionally, saddles show that there are stable and unstable directions in the velocity polar diagram; these directions determine the glider’s trend toward equilibrium.

3.1.1. Structure of the terminal velocity manifold

Nearly all velocity trajectories in figure 5 (except for figure 5(dii)) fall quickly onto a one-dimensional manifold. If the trajectory originates in the basin of stability of the equilibrium point, the trajectory moves along the manifold and stable gliding is achieved. Otherwise, the trajectory is pushed to a steep glide where the horizontal velocity is low and the animal is in effect falling. The initial quick descent of the glider to the manifold corresponds to the ballistic phase of gliding (figures 1(d) and (g)), and movement along the manifold corresponds to the shallowing phase of gliding. We designate this one-dimensional manifold as the ‘terminal velocity manifold’ as it is a higher-dimensional analog of the terminal velocity, and dynamics along it are a relatively slow evolution toward stable equilibrium. The terminal velocity manifold is approximated by the curve of zero vertical acceleration, the v_z nullcline, along which equation (2.6) is zero. A trajectory in the vicinity of the nullcline would be in a near-vertical force balance, with the vertical component of the total aerodynamic force balancing the weight of the gliders. Nullclines are shown on the flying snake and chukar velocity polar diagrams (figures 5(bii), (cii), and (fii)). These curves pass through any equilibrium points present in the velocity polar diagram, and best approximate the terminal velocity manifold locally around the stable node. If a saddle point exists (e.g. figures 5(aii), (bi), (bii), (cii), and (fi)), then the terminal velocity manifold is also approximated by the unstable branch of a saddle point and the less-stable manifold of a stable node. Furthermore, we can
Figure 5. Velocity polar diagrams. Two different pitch values, indicated by (i) and (ii), are shown for (a) flying squirrels, (b) flying snakes, (c) chukar partridge, (d) sugar gliders, (e) dragonflies, and (f) flying fish. Pitch values are specified by vertical lines in figure 6. Gray lines are simulated glide trajectories, and arrows indicate motion along the trajectory through time. Equilibrium gliding is indicated by circle markers, and the glide angle is read as the angle subtended from the horizontal axis as before to the equilibrium point(s). Saddle points and their stable and unstable branches are indicated in red, with separatrices running vertically to the saddle points. The inset in (bii) shows 2nd and 3rd-order accurate analytical approximations of the terminal velocity manifold in the vicinity of the saddle point equilibrium. Vertical velocity nullclines, where the vertical acceleration is zero, are shown in (bi), (ci), and (cii), as the solid purple line passing though the equilibrium points and near the terminal velocity manifold. (ai) Flying squirrel, $\theta = 0$. (aii) Flying squirrel, $\theta = 2$. (bi) Flying snake, $\theta = 0$. (bii) Flying snake, $\theta = 5$. (ci) Chukar 20 d.p.h., $\theta = 0$. (cii) Chukar 20 d.p.h., $\theta = 13$. (di) Sugar glider, $\theta = 0$. (dii) Sugar glider, $\theta = 10$. (ei) Dragonfly, $\theta = -10$. (eii) Dragonfly, $\theta = -25$. (fi) Flying fish, $\theta = -10$. (fii) Flying fish, $\theta = -25$. 

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approximate the terminal velocity manifold analyti-
cally (see Supplemental Information), as shown in the
inset of figure 5(bii).

Low-acceleration regions \((a \leq 0.1 \text{ g where } a = \sqrt{a_1^2 + a_2^2})\) are identified by shading in all velocity polar diagrams in figure 5. These regions are located around the equilibrium points and along terminal velocity manifolds, which indicates that the glider will exhibit little change in velocity while far from equilib-
rium, with glide dynamics dictated by the direction of
the manifold. Trajectories can also leave the low-acce-
leration region (figures 5(bi) and (biii)) while moving along the terminal velocity manifold towards

The flying snake bifurcation diagram in figure 6(b)) is
similar to the flying squirrel bifurcation diagram,
except that more than four equilibria are possible at

The equilibrium points and corresponding equilibrium

3.2. Pitch bifurcation diagrams
The equilibrium points and corresponding equilibrium

The bifurcation diagrams show multiple co-existing
equilibrium points at high and low angles of attack,
which persist over a range of pitch angles. The flying

The flying squirrel bifurcation diagram (figure 6(a)) shows that

To demonstrate how these analytical methods can
be applied to experimental data, we used mean force
coefficients from a flying squirrel glide experiment

4. Discussion
We have developed a dynamical systems framework to
understand non-equilibrium animal gliding based only
on the lift and drag coefficients. In this conceptualiza-
tion of gliding, equilibrium is represented as a point in the
velocity polar diagram where the accelerations are zero; trajectories will progress towards or away from
equilibrium depending on the initial conditions and
the equilibrium type. Analysis of the velocity polar
diagram indicates that pitch angle has a large effect
on the glide trajectory and that animal gliding has more complicated dynamics than previously realized.
However, these dynamics can be systematically explored
using the velocity polar diagram and by incorporating
the lift and drag coefficient curves into the equation of
motion.

4.1. Effect of lift and drag coefficients
Because lift and drag coefficients are the only model
inputs, the analysis presented here can be viewed as
a parametric study of representative lift and drag
curves and how the structure of these curves affects
non-equilibrium gliding. The analytically derived
expressions for equilibrium type (figure 3) and the
general topology of the velocity polar diagrams (figure 5)
indicate commonalities in how glide trajectories
proceed based solely on the lift and drag curves. First,
multiple equilibria are possible, and these generally
occur for slightly negative to positive pitch values.
Second, unstable equilibria are possible, particularly
saddle points which appear along a terminal velocity
manifold. Third, spiraling motion in the velocity polar

3.3. Velocity polar diagrams from kinematics data

The chukar, sugar glider, and dragonfly bifurcation
diagrams (figures 6(c)–(e)) show a flat equilibrium
glide angle region over a large range of pitch angles.
Due to the low lift-to-drag ratio of the dragonfly, equi-
librium glides are steep, being nominally 70° in glide
angle. The flying fish and dragonfly bifurcation dia-
grams show that only negative pitch angles allow stable
equilibria; in this condition, a flying fish or dragonfly
would be nose-down at equilibrium.
The difference in velocity polar diagram structure when there is a terminal manifold or when there is a focus-type equilibrium suggests future extensions of this work to investigate if gliders switch between different glide motifs. The motion around a focus-type equilibrium in the kinematics-based flying squirrel velocity polar diagrams (figures 7(c)–(e)), with a decrease in vertical velocity throughout the trajectory, is not seen in the airfoil-based velocity polar diagrams (figure 5). These different gliding motifs could provide complementary means to modify the glide path, but
how the animal switches between them is unknown. For example, the focus-based motif should lessen landing forces, because the vertical velocity is near zero or merely slightly positive at the end of the glide. However, the animal would have higher accelerations throughout the glide, which in theory would require more control.
authority to maintain stability. In the terminal velocity manifold motif, accelerations are lower for the majority of the glide, but a large pitch-up maneuver would be required for landing to lower the airspeed. How the animal switches between these motifs with changes to lift and drag coefficients, or with unsteady aerodynamic and/or fluid-structure interaction effects [37–39], are important considerations for future work.

Calculating the kinematics-based lift and drag coefficient curves was done as a way to compare measured animal trajectories to model predictions. The velocity polar diagrams derived from wind tunnel measurements (figures 5(ai), (a(ii), (d(i), and (d(ii)) are substantially different from the kinematics-based ones (figures 7(c)–(e)). There are several possible reasons for this. One possibility is that the kinematic data are insufficient (due to undersampling, noise, or experimental error) to derive force coefficient curves. The kinematics data lack the ballistic phase of the glide, and the assumption of zero pitch angle used to derive the kinematics-based curves is likely to be invalid over part of the glide. Another possibility is that wind tunnel coefficient curves do not accurately represent the whole-animal aerodynamics in flight. This is most likely true for the artificial membrane curves, in which a thin latex sheet represents the patagial membrane, but does not include the limbs and tail of the flying squirrel. The sugar glider coefficient curves provide an intermediary to understand whole-animal lift and drag characteristics, as it is of a taxidermically prepared mammal in a likely flight configuration. In fact, these curves show spiraling in the velocity polar diagram (figure 5(d(ii)) for certain positive pitch angles, which is a likely flight posture used by flying squirrels [19]. Spiraling is also seen in the kinematics-based velocity polar diagrams in figures 7(c)–(e).

4.2. Comparison to other modeling studies of gliding

In the model presented here, the magnitude and orientation of the aerodynamic force vectors are modulated by pitch angle. Previous particle models were not directional, with the aerodynamic force vectors being modulated by pitch angle in the pitch bifurcation diagram (see figure 5(b), where moving from negative to slightly positive pitch leads to a saddle-node bifurcation). The newly presented non-dimensionalization and rescaling of the equations of motion is a significant difference from previous studies. This rescaling reduces the difference between species to their lift and drag coefficient curves only. The universal glide scaling parameter ($\epsilon \propto \sqrt{A}$) not only facilitates modeling and normalization of experimental trajectories, but provides a metric to compare gliders based on their chord length and wing loading. Under geometric scaling of isometry, and assuming $L \propto m^{1/3}$, one would expect chord length to scale as $\epsilon \propto m^{-1/3}$. Experimental data suggest that wing loading scales isometrically, $W_s \propto m^{1/3}$ [1], so one would therefore expect $\epsilon = \text{constant}$ for a given species. The universal glide scaling parameter is shown in figure 8 for a variety of animal gliders across several orders of magnitude of mass. The scaling of $\epsilon$ with mass is not as evident as with wing loading [1], but there appear to be three distinct groupings. The first grouping has an $\epsilon$ value of 0.1 and includes dragonflies only. The next grouping has an $\epsilon$ of 0.04 and includes Draco, squid, and mammals. The third grouping, with an $\epsilon$ of 0.003, includes flying snakes and flying fish. For flying snakes, $\epsilon$ is nearly constant over two orders of magnitude in mass, and for Draco, $\epsilon$ is nearly constant over one order of magnitude in mass. These different scaling groups suggest that the chord length used to non-dimensionalize the equations of motion has a large effect on $\epsilon$ for different gliding species.

The universal glide scaling parameter also helps to explain why smaller individuals with lower wing loading are generally better gliders, covering more
horizontal distance from a given take-off height. The framework presented here identifies equilibrium points in the velocity polar diagram, but it does not specify the time required to reach equilibrium. By converting both time and velocity back to physical units using $\varepsilon$, we see that both dimensional time and velocity are proportional to the square root of wing loading. Because the time to equilibrium is fixed in (4.1), the glider with lower wing loading will reach equilibrium sooner. If a large and a small individual were to take off from the same physical height and with the same initial conditions in the velocity polar diagram, the smaller individual would traverse more of the velocity space before landing. This would correspond with a higher shallowing rate, lower velocity, and greater horizontal distance traveled.

4.3. Implications for animals that glide

The global view of gliding developed here provides insight into how a glider’s translational motion changes with pitch. The results of this work show that once the glider is at equilibrium, changing pitch angle has only a small effect on glide angle. For example, for the sugar glider (figure 6(d)), the equilibrium glide angles change only $\pm 10^\circ$ over a pitch range of $25^\circ$. A similar trend holds for the other wind-tunnel based bifurcation diagrams, in which the low glide angle equilibrium is relatively insensitive to pitch. The initial launch parameters and the ballistic glide phase are therefore important because they determine how close to the basin of stability the glider is, and if control is needed to select a stable equilibrium. This analysis suggests that animals could select pitch values to avoid unstable features in the velocity polar diagram, with a worst-case scenario resulting in a fall with negligible horizontal velocity. A negative pitch angle shortly after launch and through the ballistic phase will confer greater translational stability, and will also act to direct the lift vector horizontally.

Additionally, hysteresis effects are possible as the pitch angle changes. The equilibrium glide angle can increase rapidly if the pitch angle increases above a critical threshold (figures 6(a) and (b)). To re-establish a low glide angle equilibrium glide, a glider would have to decrease its pitch to a negative value so that only the upper stable branch of equilibria are possible. Therefore, a pitch-up maneuver prior to landing would not only slow the animal, but may remove all equilibria from the velocity polar diagram, so the animal would begin to fall. Only very steep glides are possible for some animals, such as dragonflies (figures 6(e)) and gliding arthropods. Arthropod glide trajectories consist of large glide angles between $70^\circ$–$75^\circ$ and small lift-to-drag ratio of approximately 0.3 [15–17]. Although lift and drag coefficient data are not available, these steep trajectories suggest velocity polar diagram structure similar to figure 5(e), with steep glides to a stable equilibrium.

The framework presented here also helps to address the question of if and when equilibrium is reached in gliding, as it clearly distinguishes true equilibrium where accelerations are zero, from equilibrium-like gliding in the shallowing phase and along the terminal velocity manifold where accelerations are small. Measured fluctuations of the glide path, which indicate non-equilibrium gliding, can occur for several reasons. One possibility is the animal in such a trajectory is using small postural changes to maintain a particular pitch angle or to slightly alter the glide path. Another possibility is that experimental errors, from digitization and numerical derivatives of position data, give the appear-
in the velocity polar diagram. The autonomous glider would then only need small actuations in pitch angle to passively switch to different glide states.

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References

in northern flying squirrels Glaucomys sabrinus J. Exp. Biol. 210 1413–23
[22] Vernes K 2001 Gliding performance of the Northern flying squirrel (Glaucomys sabrinus) in mature mixed forest of Eastern Canada J. Mammal. 82 1026–33
[34] Strogatz S H 2001 Nonlinear Dynamics and Chaos with Applications to Physics, Biology, Chemistry, and Engineering (Boulder, CO: Perseus Books)