2013-01-9003
Published 12/20/2013

doi:10.4271/2013-01-9003
saeaero.saejournals.org

Detailed Analysis of Variables Affecting Wing Kinematics of Bat Flight

Gaurav Bindal and Sparsh Sharma
Vellore Institute of Technology

Frank Janser and Eugen Neu
Fachhochschule Aachen

ABSTRACT

Body motions of flying animals can be very complex, especially when the body parts are greatly flexible and they interact with the surrounding fluid. The wing kinematics of an animal flight is governed by a large number of variables and thus the measurement of complete flapping flight is not so simple, making it very complex to understand the contribution of each parameter to the performance and hence, to decide the important parameters for constructing the kinematic model of a bat is nearly impossible. In this paper, the influence of each parameter is uncovered and the variables that a specified reconstruction of bat flight should include in order to maximally reconstruct actual dimensional complexity, have been presented in detail. The effects of the different kinematic parameters on the lift coefficient are being resulted. The computation analysis of the lift coefficient for different camber thicknesses and various wing areas is done by unsteady thin airfoil theory and vortex lattice method, respectively.

CITATION: Bindal, G., Sharma, S., Janser, F., and Neu, E., "Detailed Analysis of Variables Affecting Wing Kinematics of Bat Flight," *SAE Int. J. Aerosp.* 6(2):2013, doi:10.4271/2013-01-9003.

INTRODUCTION

Since the dawn of the era, humans have always been fascinated and inspired by the movement of animals through the air. The animal flight has not only aroused passion but also served the most utilitarian function of inspiring design innovations. Nonetheless, the early attempts to develop a flapping wing MAV were bound to fail due to insufficient knowledge of the flapping motion and lack of tools required for the analyses and design of the unsteady flight, and consequently, research concerning flapping flight has been overshadowed by the study of fixed and rotary wing aircrafts for almost 100 years [1]. Interests in bio-inspired flight and rigorous desire to develop highly efficient and maneuverable flapping wing MAVs have resurfaced among the biologists and engineers in the last two decades. The greatly improved capabilities of modern equipments to image animal motion and visualize complex fluid flows have brought the attention back to animal flight research.

Although the tools for the analysis and design of vehicles optimized for steady flight are well developed, the mechanics of highly unsteady flight remains uncertain due to the gap present in our understanding of the basic mechanics of the highly unsteady, three-dimensional and complex character of animal flight. This is an issue of growing interest, driven by the desire to build vehicles that can perform extremely unsteady aerodynamic maneuvers.

Flapping flight is the single most evolutionarily successful mode of animal locomotion: there are today over 1200 species of bats, more than 10 000 living species of flying birds, and somewhere between millions and tens of millions of species of flying insects [2]. Birds, insects and bats apply a variety of flapping patterns in hovering and forward flight to generate lift and thrust but among these, bats are proven to be the most superior and efficient flyers due to their highly articulated motion. Birds and insects can fold and rotate their wings but more than two dozen independently controlled joints overlaid in the flexible wing membrane [2, 3, 4] and highly deformable bones [5,6] enable the bat to fly at either positive or negative angle of attack, dynamically change wing camber and create complex 3D wing topology to achieve extraordinary flight performance. The difference in the wing kinematics of the bats with respect to birds and insects is irrespective of the flight speed and other flight conditions.

Bat wing kinematics is a very complex phenomenon (especially at slow flight speeds) with the wing changing its shape continuously as it flaps [7]. It cannot be simply viewed as a flapping plate, or even as a flapping plate with one or two simple hinges [1]. Many of the joints of the handwing are extended during the downstroke until the lower reversal point, where they begin to flex, and the wingtip moves closer to the body in horizontal direction. At the same time, early in the upstroke, the wingtip moves simultaneously upwards and outwards and the wing adapts an extended posture at the end of the upstroke. Moreover, the motion of the wingtip is not primarily vertical with respect to either gravity or the animal's body, and a strong wing tip vortex is shed from the wing tip during the downstroke and either from the wing tip or a more proximal joint during the upstroke. The wings sweep forward during downstroke, increasing the relative forward velocity, and sweep backward during upstroke alongwith decreasing the angle of attack. Moreover, adding to the complexity of the bat flight, the flight speed and elevation are not constant, but oscillate in synchrony with both the horizontal and vertical movements of the wing.

A bat's wing motion is not governed by one or two variables; instead the wing kinematics is a function of numerous variables, having a significant role in the wing kinematics. The kinematic measurements of such complex motions are very difficult due to the large number of variables involved and thus the contribution of each parameter to performance is not clearly apparent. In this study, the influence of all variables on wing kinematics has been uncovered in detail and priority variables (having the most significant influence on performance) are decided to be focused on for developing a kinematic model of the bat.

The flight of bats, much like that of birds has often been modeled to first approximation as quasi-steady, with wings treated as rigid plates [8, 9, 10]. The assumption of steady flight was largely necessitated by the lack of analytical and experimental tools to analyze the complex flows, but this situation has changed considerably in the past few years. Recently, numerous experiments on bats have been done by many scientists and engineers to study the importance of various parameters of the bat wing kinematics. In 2006, Tian [2] experimented and analyzed the bat flight kinematics and observed that bats possess unique flight characteristics at relatively low flight speeds, including a flexion of the wing during upstroke. Riskin [7], in 2008, used proper orthogonal decomposition method (POD) for assigning importance to kinematic variables, using dimensional complexity metric, concluding that it does not change with flight speeds. While in 2010, Riskin [11], Hubel [12] and Leigh [13] performed different studies on bats to analyze the variation in their wing posture and kinematics on account of varying body mass, flight speed and power output required, respectively. Leigh [13] found out that variation of kinematics alone can increase sufficient aerodynamic power to accommodate even a 21% increase in body weight. In 2012, Riskin [14] analyzed kinematics of the folding and unfolding of the bat wing during upstroke motion for inertial cost of flight, while Rhea [15] studied the three-dimensional wingbeat kinematics of a bat to determine how factors affecting the lift production vary across flight speed and within wingbeat.

This paper explains the influence and importance of different variables on the wing shape and kinematics of a bat flight. The focus has been given on parameters which are critically important for the construction of the kinematic model of bat flight in order to maximally reconstruct actual dimensional complexity.

EFFECT OF PARAMETERS ON WING KINEMATICS

Bat wings have a high potential to adjust wing morphology according to the aerodynamic demands due to their highly flexible wings with flexible wing bones and a compliant wing membrane, enabling them to carefully control their wing shape and motion. The morphology and kinematics of a bat wing determines the resulting aerodynamic lift through the regulation of the flight speed, wing area and lift coefficient. Thrust and weight support of the bat is generated by the aerodynamic lift (L) of the wing, which is determined by the density of the medium (ρ), the speed of the wing relative to the air (U_{eff}), the wing area (S) and the lift coefficient (C_l) given by equation (1) [16]:

$$L = \frac{1}{2}\rho S U_{eff}^2 C_l \quad (1)$$

Each of these factors, except density, is controlled by different parameters of the wing morphology and kinematics. The speed of the wing is determined by the combination of flight speed and flapping speed, with the latter being determined by the amplitude and frequency of the wing beat. Wing area can be controlled by retracting or extending the wing. Finally, the lift coefficient depends on the shape of the wing profile (e.g. camber and thickness) and the angle of attack, the angle between the chord line and the direction of the airflow.

To have a more clear understanding of the correlation between the wing kinematics and aerodynamic variables, a detailed explanation has been presented for the effect of these variables on the wing morphology and the performance of the bat.

Wing Speed

Due to the strong dependency of generated aerodynamic lift on speed of the wing, bats are expected to alter their kinematics and wing morphology across flight speeds to generate sufficient weight support and thrust.

The stroke plane angle (β), increases from less than 30° at low to about 75° at high flight speed [15], indicating a change from a horizontal to a more vertical stroke plane (as depicted in fig.1) while the downstroke ratio and span ratio, both increases when going from low to medium flight speed and then decreases slightly when flight speed is increased further,

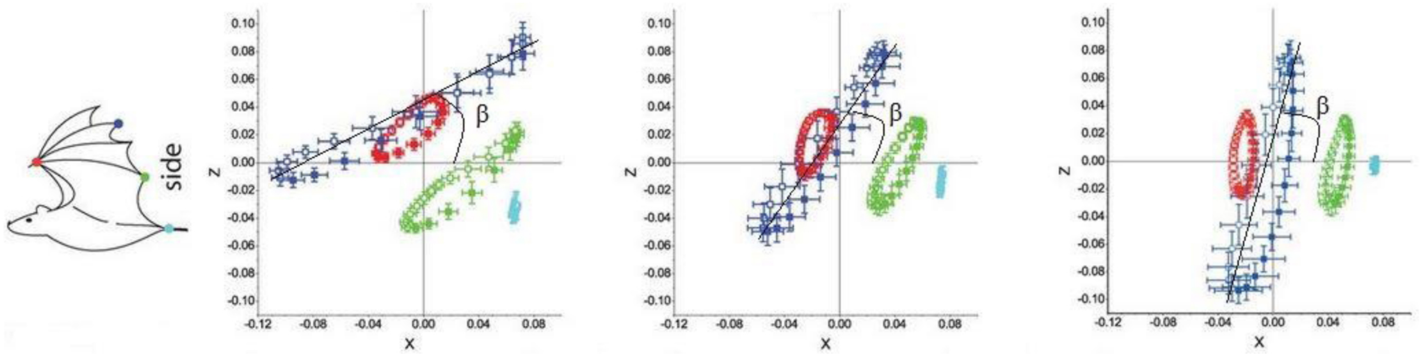


Fig.1. The trace of the wrist (red), the wingtip (blue), the tip of the 5th finger (green) and the foot (sky blue) for one wing beat with the shoulder as the origin for three different speeds (0 m/s, 3 m/s, 7 m/s respectively). Filled symbols represent the downstroke, open symbols the upstroke. The variation of stroke plane angle is clearly visible varying from around 30° at low speeds to 75° at the high speeds. All distances are shown in meter [15].

while the body angle is relatively constant throughout the stroke across speeds, with higher body angle at low speeds.

The wing area varies sinusoidally over the wing beat cycle with the largest area found at the time of mid-downstroke while the lowest is present in the middle of the upstroke. On increasing the flight speed both the minimum and maximum areas tend to decrease slightly and increase on decreasing the flight speed. The innermost part of the wing is aerodynamically relatively inactive at the lowest flight speed range due to the low speed of the flow across the wing, but potentially more important at intermediate flight speeds when the upstroke is more or less inactive [17].

A higher angle of attack produces higher lift, but also higher drag, and therefore the bats are expected to reduce the angle of attack with increasing flight speed when the demand of a high lift coefficient is reduced (as shown in fig.2).

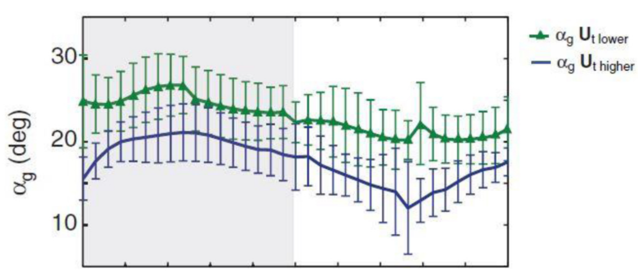


Fig.2. Geometric angle of attack, vertical wrist and wingtip excursion at lower and higher wind speeds averaged over four bats. Grey shading indicates downstroke [12].

The leading edge flap angle has a very large variation with the flight speed, varying from around 5° at high speeds to around 25° at low speeds, with an increase in the lift force during the downstroke, and a decrease during the upstroke. At high speeds, the entire upstroke shows negative values.

The mean angular velocity directly affects the performance of the flyer. It shows a minimum at the speed of maximum lift to drag ratio, suggesting a simple way to determine the optimal speed from kinematics alone.

The wing velocity (*V*) is a function of forward velocity (U_∞) and flapping velocity (V_f) as given by equation (2) [18] :

$$V = \sqrt{U_\infty^2 + V_f^2} \tag{2}$$

Forward velocity

Several changes in the kinematics of bats are being observed with changes in the flight velocity. The horizontal velocities of bats are much greater than vertical velocities, so flight paths are more close to horizontal [2]. When flight speed is reduced, sustaining weight support becomes more demanding and bats need to compensate for the lower velocity over the wings by increasing the wing area, flapping speed or lift coefficient. This is particularly important during hovering and slow flight.

Flapping velocity

The flapping velocity of the wing is determined by the stroke amplitude (ϕ_0) and the flapping frequency of the wing beat (*f*) given by the equation (3) [18]:

$$V_f = 4 f \emptyset_0 R \tag{3}$$

where *R* is the half of the total wingspan of the wing.

Amplitude

The vertical amplitude of the wing beat increases with increasing the speed while the horizontal amplitude decreases (as shown in fig.3). The angular amplitude in the stroke plane follows a U-shaped pattern with high values at low flight speed, with decreasing and then increasing values with increasing speed. It is highest at low speeds at around 90°, drops to 65° at 3 m/s and rises back to about 80° at high speeds [15]. Stroke plane and wing stroke amplitude at the

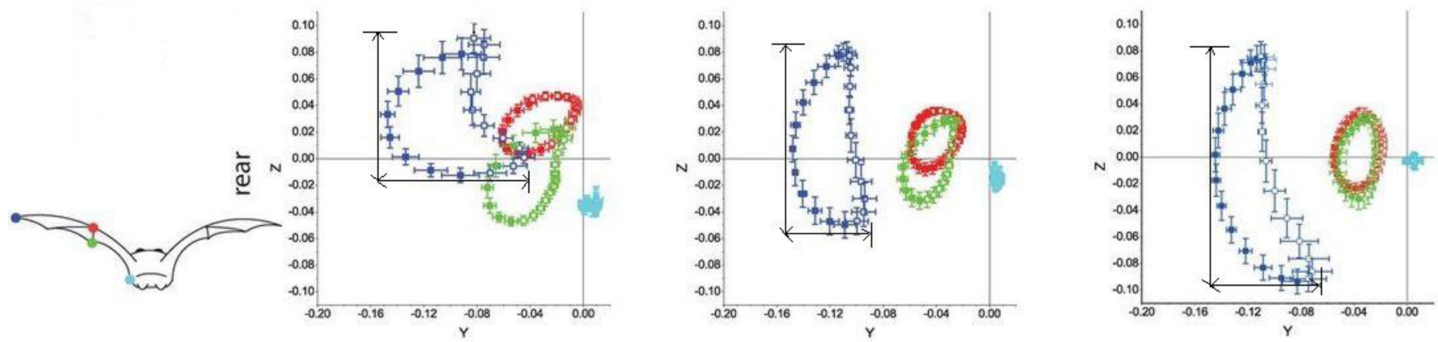


Fig. 3. The trace of the wrist (red), the wingtip (blue), the tip of the 5th finger(green) and the foot(sky blue) for one wing beat with the shoulder as the origin for three different speeds (0 m/s, 3 m/s, 7 m/s respectively). Filled symbols represent the downstroke, open symbols the upstroke. The variation in the stroke amplitude is clearly visible with the vertical amplitude increasing and the horizontal amplitude decreasing on increasing flight speed. All distances are shown in meter [15].

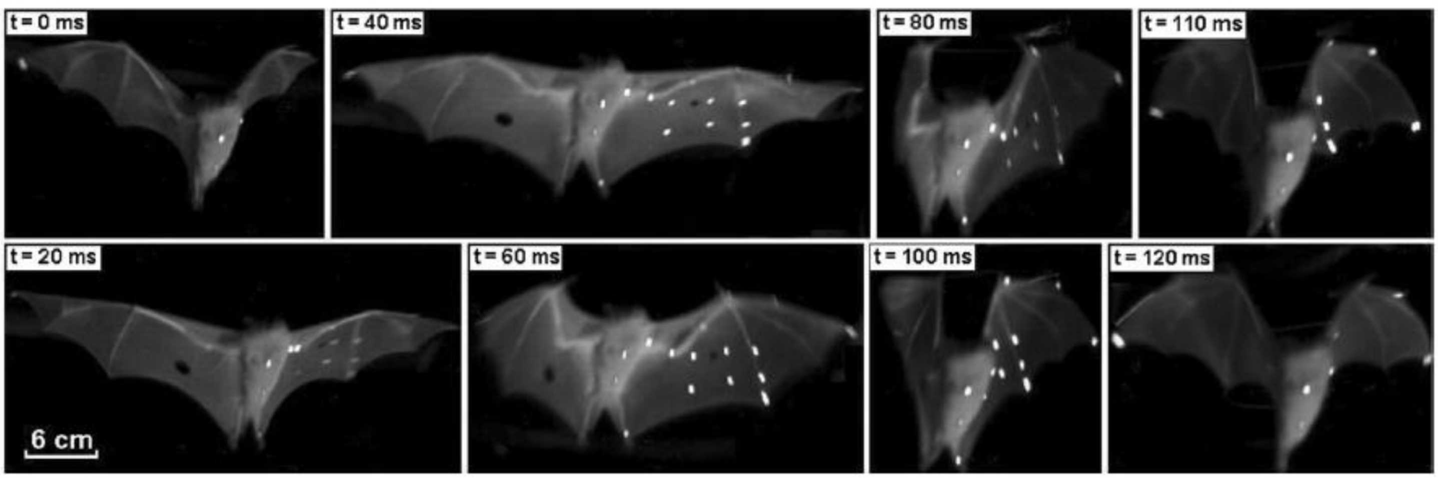


Fig.4. Sequences of images from one high-speed video camera. During the downstroke, the wing is largely extended, although the joints do not reach full extension. During the upstroke, the substantial flexion of elbow, wrist and finger joints is evident [2].

wrist does not change significantly with body mass or wing size.

Flapping frequency

Flapping increases the flight speed of a bat by increasing its Reynolds number as seen from the wings. The wingbeat frequency of bat is about 13.8 Hz during hovering flight and decreases to 10.5 Hz for intermediate and high speeds. It is controlled by the muscular contraction frequency and is expected to decrease with increasing body size [19-20]. The flapping frequency decreases with increasing the flight speed [21, 22, 23]. Small variations in the flapping frequency of consecutive wing beat cycles led to a variable number of computed values of the velocity field and circulation during each cycle [1].

Wing Area

A bat's wing comprises of highly compliant skin membranes that interconnect a jointed skeleton capable of many degrees of freedom. By its very morphological structure, the area of a bat wing is highly variable throughout every wingbeat cycle. As a result, measurements of the wing area for bats can vary substantially when compared with those of the insects or birds, depending especially on the degree to which the membrane is stretched before measurement.

The area of the wing is largely controlled by the angle between the hand wing and the arm bones. The area of a bat's wing varies sinusoidally throughout the wingbeat cycle and depends greatly on the positions of the carpus and elbow, and the degree of extension and abduction of the digits. The large bats extend the wing more fully on the downstroke, but not on the upstroke, with the largest area found at the time of mid-downstroke while the lowest is present in the middle of the upstroke (see fig. 4). This makes sense, since the majority of lift production occurs on the downstroke. On increasing the flight speed both the minimum and maximum areas tend to decrease slightly, and increase on decreasing the flight speed.

Lift Coefficient

The most general mechanism for increasing the lift coefficient is to increase the angle of attack (AoA). In addition, potential high-lift features, such as high camber of the wing [24-25] and the use of the leading edge vortices, being generated by leading edge flaps, are well known mechanisms to increase the lift coefficient. It improves the gust alleviation and dynamic stall of the wing by increasing the stall angle of attack, which is very important in case of hovering. The variation in camber and AoA is possible due to flexible bones and dozens of joints present in the membrane of the bat wing. Studies suggest that flexible airfoils have greater thrust/input power ratio than rigid airfoils. A thinner airfoil (generally t/c < 0.06) with sharp leading edge shows much better results.

The leading edge flap increases both the effective angle of attack and camber of the wing, thus contributing towards increasing the lift force of the wing. The leading edge flap angle varies during the entire wing beat at all speeds, with the flapping pattern being consistent. The angle is mostly positive during the downstroke with more constant values than the upstroke, during which the angle is mostly negative. An increasing deflection of the leading edge with decreasing speed suggests a higher lift coefficient at lower flight speeds. The deflection of the leading edge flap also increases the curvature of the front part of the wing, which would promote the separation of the flow, similar to what has been suggested as the function of the alula in landing steppe eagles [26], and facilitates the generation of the leading edge vortices at low speeds. Moreover, the leading edge vortices [27], produced by flap motion, stay attached to the wing during the downstroke and contribute up to 40% of the total lift at mid-downstroke at low flight speeds.

Angle of attack

When it comes to controlling the lift coefficient of the wing, the angle of attack (α) and camber are considered to be among the most important factors [16]. The angle of attack of the outer wing stays nearly constant during the downstroke, with higher values for lower speeds and decreases during the upstroke until mid-upstroke, with minimal values for low speeds. For all speeds, the angle of attack is positive during the downstroke and negative during the upstroke. The highest values of the angle of attack are reached for hovering flight (80° to −60°). Although steady aircraft airfoils show stall and loss of lift already above an angle of attack of about 15° at these Reynolds numbers [25], the bats operate at mean downstroke angles of attack up to 50° [11,15, 28, 29, 30] without apparent lift loss [30]. This suggests that bats must have some mechanisms to maintain lift throughout the downstroke at these high angles of attack. AoA increases significantly with body mass and the overall change occurs as a result of changes in α_1 but not α_2 (shown in fig. 5) [11].

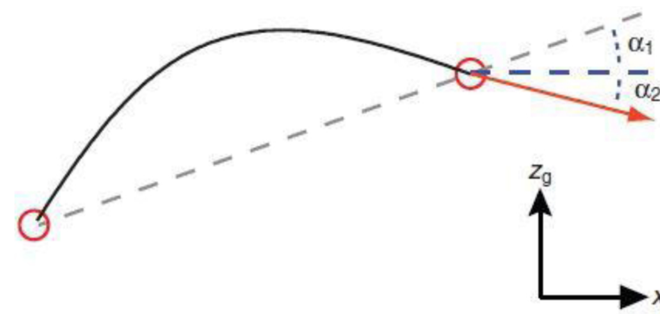


Fig.5. Angle of attack (α) is calculated as $\alpha_1 + \alpha_2$, where α_1 is the angle of the wing chord line above horizontal (blue dashed line), and α_2 is the angle between horizontal and the velocity vector of the wrist (red arrow) in the x_g -z_g plane [11].

Camber

Wing camber is a dynamically changing variable. It is controlled by multiple mechanisms along the span, including the deflection of the leg relative to the body, the bending of the 5th digit, the deflection of the leading edge flap and the upward bending of the wingtip. All of these measures vary throughout the wingbeat suggesting active or aeroelastic control. The camber of the outer wing is mainly controlled by the leading edge flap, the flexion of the phalanges of the 5th digit and the bending of the 5th digit. Since the wing camber is being controlled by a number of mechanisms and parameters, thus it seems to have a large impact on the performance of a bat flight.

The camber has a very large variation during downstroke and upstroke at low flight speeds while it remains constant over time at higher speeds. The slaking of the wing membrane results in a more favorable camber of the outer wing during the supinated upstroke. A passive mechanism for camber control at the outermost part of the wing may be the bending and sweeping of the wing tip. At the outermost part of the wing the fingers run more closely in the spanwise direction than in the chordwise direction, making camber control by the fingers, similar to the 5th digit, less likely. Due to the flexibility of the finger bones [31,32], both the bend and sweep of the wingtip are affected by the aerodynamic forces on the wing and could passively affect the camber of the outer wing [33], while the camber of the innermost part of the wing is actively controlled by the tail-to-body angle.

Body Mass/ Wing Size

Many aspects of wing kinematics vary with body size, but the way kinematics change with velocity and acceleration is relatively consistent with body sizes. The body mass has a direct relationship with the downstroke, which helps to offset the consequences of higher wing loading that accompany increased body size. Larger bats open their wings more completely than smaller bats do in flight [11] and have higher lift coefficient to compensate for the increase in the body mass. This highlights the importance of wing posture as a confounding variable for hypothesis about ecological function based solely on two-dimensional shape of an outstretched wing. Thus aspect ratio of bats is generally quite low as a large component of lift is generated by tip vortices at low AR. Wing loading as well as the speed at which bat flies increases with the size of the bat, but in the mass range of 0.020 to 0.1 grams, it makes negligible difference.

Angle of attack increases significantly with the increment in body size. The influence of body size on locomotion is no less striking, and biomechanical investigations have revealed that just as body shape changes with size, so do locomotor's kinematics [34, 35, 36].

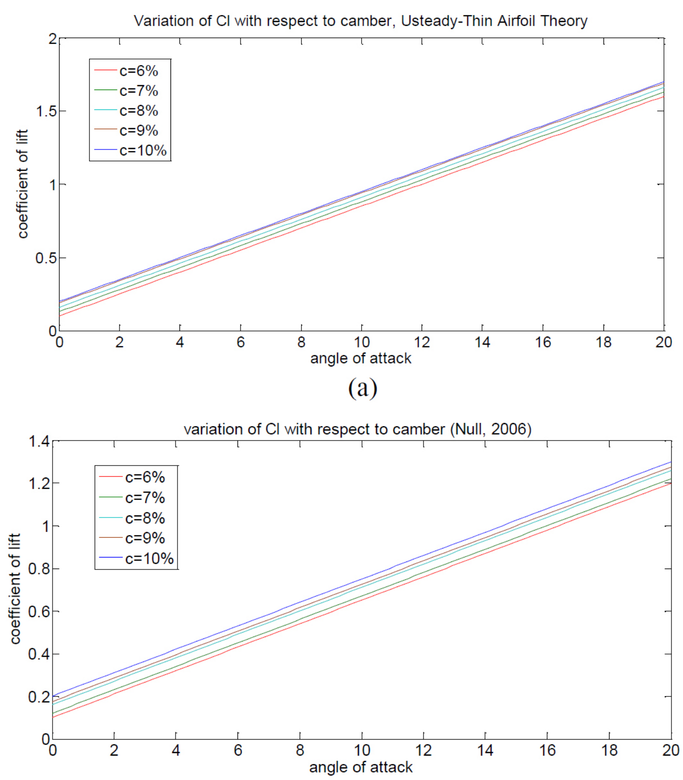
Concluding Remarks

The aerodynamic lift generated by a wing is proportional to the square of the local speed of the wing, i.e. the vector sum of the forward flight speed and the flapping speed of the wing. Altering flight speed changes the forward velocity component over the wing, and bats alter the kinematics to sustain weight support and to generate sufficient thrust. The unique flexibility and controllability of bat wings suggest a multitude of mechanisms to control the lift generated by the wing. Using this study, it is concluded that all parameters that adjust lift, namely flight speed, wing area and the lift coefficient, are adjusted on account of changing each other. The flapping speed of the wing, which has the largest impact on lift production, shows a U-shaped pattern across flight speed. Wing area is highest during the downstroke and also increases with decreasing flight speed. The lift coefficient is determined by the camber and angle of attack of the wing, which both increase with decreasing flight speed. The angle of attack is highest during the downstroke, hovering and at low flight speeds, increasing the probability of unsteady mechanisms being used to further increase the lift [27]. The studies show an increasing camber with decreasing speed for all positions along the span, until the transition speed when the wing is flipped upside down with a more complex change of camber at lower speeds. The studies also suggest that the bats adjust kinematics to control the flow over the wings and to reduce the drag generated. The bats alter their stroke plane angle, in order to maintain favourable flow characteristics across flight speeds [30].

RESULTS

Maintaining weight support and generating thrust to overcome drag are the main challenges in level flapping flight. After having a detailed study of the effects of every flapping parameter variation, it is concluded that bats vary their wing camber and angle of attack during the entire wingbeat cycle to enhance their performance, which makes their flight most complex. Variation in any one of them results in changing the overall coefficient of lift. This unique flexibility and controllability of their wings allow bats to alter the flight speed and wing area during flight.

The change of lift coefficient with angle of attack for different wing cambers is being analyzed using unsteady thin airfoil theory, which is an inviscid theory ignoring thickness and applies the linearized boundary condition on a mean surface. Results of the variation of the lift coefficient with angle of attack for 6, 7, 8, 9, and 10% cambers at Re 1×105 are being plotted in fig. 6 and compared with the results obtained by Null [37]. It is clearly evident from the results that the lift coefficient C_l, is highest for 10% camber airfoil at this Reynold's number, and the slope of the lift curve increases with the wing camber. Computational results show some discrepancies when compared with the experimental data, because of the limitations of the unsteady thin airfoil theory and computational errors. For all cambers, there is negligible difference in $C_{l_{min}}$ values of computational and wind tunnel data but a quite significant difference of 0.4 occurs in the $C_{l_{max}}$ values. Due to the fact that this is an inviscid theory and doesn't predict the flow separation and stall phenomenon, it results in computing larger values of lift coefficient than the experimental results for high angle of attack, still the theory can be unquestionably used for low values of angle of attack.



(a)

(b)

Fig.6. Variation of lift coefficient with 6,7,8,9 and 10% camber thickness by (a) unsteady thin airfoil theory, (b) wind tunnel data, Null [37].

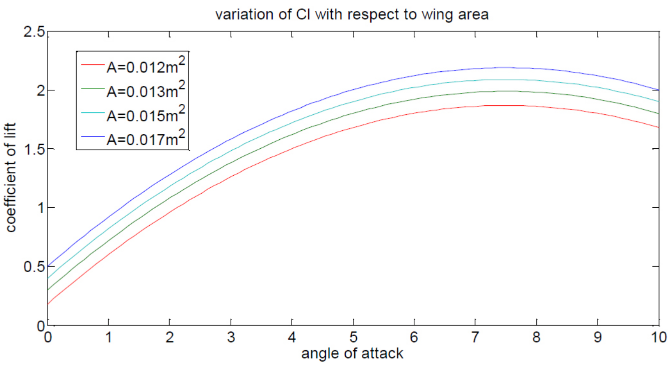


Fig.7. Variation of lift coefficient with different wing areas

In bats, mass is directly proportional to the wing size. Although the wing area increases on account of increasing the wing mass, increasing the lift force, but the increment is not sufficient to compensate for the increased weight, and hence bats increase their lift coefficient by increasing their wing camber and angle of attack. The effect on lift coefficient is being analyzed for different wing areas by using the vortex lattice method [38], and the results are plotted in fig. 7. It is clearly evident from the figure that the lift coefficient increases with the wing area to support the added weight. The results are also in conjugation with the biological data of the species: *Plecotus auritus, Leptonycteris yerbabuenae* and *Cynopterus brachyotis*, where wing span increases with the body mass [2, 15, 39, 40, 41].

CONCLUSION

In this study, it is concluded that the bats' flight is the function of various kinematic variables. All parameters that adjust lift, namely flight speed, wing area and the lift coefficient are adjusted on account of changing each other. The lift coefficient mainly depends on the angle of attack and wing camber, which is largely controlled by active deformations in the highly flexible wing membrane. The lift coefficient increases on increasing the wing camber, the effective angle of attack and the wing area.

ACKNOWLEDGEMENTS

The authors would like to acknowledge and thank Prof. Frank Janser (FH Aachen UAS, Germany) for his valuable suggestions and guidance, Eugen Neu (Ph.D. scholar, FH Aachen UAS, Germany), for his assistance and support in computational analysis of the results, Vishnu Ganesh for his significant help in reviewing the paper and finally our wonderful parents.

REFERENCES

1. Hubel Tatjana Y. et al, “Time-resolved wake structure and kinematics of bat flight”, Exp. Fluids, Springer-Verlag 2009
2. Tian Xiaodong et al, “Direct measurements of the kinematics and dynamics of bat flight”, Bioinspiration & Biomimetics, 2006
3. Vaughan T. A., “The skeletal system the biology of bats”, Vol 1, Ed. Wimsatt W. A. (New York: Academic) pp 98-139, 1970
4. Swartz S. M., “Allometric patterning in the limb skeleton of bats: Implications for the mechanics and energetics of powered flight”, J. Morph. 234 277-94, 1997
5. Swartz S. M. et al, “Wing bone stresses in free flying bats and the evolution of skeletal design for flight”, nature 359 726-9, 1992
6. Swartz S. M. et al, “Dynamic complexity of wing form in bats: Implications for flight performance functional and evolutionary ecology of bats”, Ed. Akbar Z., McCracken G. and Kunz T. H. (Oxford: Oxford University Press), 2005
7. Riskin D. K. et al, “Quantifying the complexity of bat wing kinematics”, J. Theor. Biol. 254:604-615, 2008
8. Pennycuick C. J., “Power requirements for horizontal flight in the pigeon: Columba Livia”, J. Exp. Biol. 49:527-555, 1968
9. Rayner J.M.V., “A vortex theory of animal flight, Part 2: the forward flight of birds”, J. Fluid Mech. 91:731-763, 1979
10. Tobalske B.W., Hedrick T. L., Dial K. P., Biewener A. A., “Comparative power curves in bird flight”, Nature 421:363-366, 2003
11. Riskin Daniel K., Iriarte-Díaz José, Middleton Kevin M., Breuer Kenneth S. and Swartz Sharon M., “The effect of body size on the wing movements of pteropodid bats, with insights into thrust and lift production”, The Journal of Experimental Biology 213, 4110-4122, 2010
12. Hubel Tatjana Y., Riskin Daniel K.2, Swartz Sharon M. and Breuer Kenneth S., “Wake structure and wing kinematics: the flight of the lesser dog-faced fruit bat, Cynopterus brachyotis”, The Journal of Experimental Biology 213, 3427-3440, 2010
13. MacAyeall1 Leigh C., Riskin1 Daniel K., Swartz Sharon M. and Breuer Kenneth S., “Climbing flight performance and load carrying in lesser dog-faced fruit bats (Cynopterus brachyotis)”, The Journal of Experimental Biology 214, 786-793, 2011
14. Riskin Daniel K., Bergou Attila, Breuer Kenneth S. and Swartz Sharon M., “Upstroke wing flexion and the inertial cost of bat flight”, Royal society publishing, 2012
15. Rhea et al, “Kinematics and wing shape across flight speed in the bat, Leptonycteris yerbabuenae”, Biology Open 1, 1226-1238, 2012
16. Anderson J. D., “Fundamentals of Aerodynamics”, p.772. New York: McGraw-Hill, 1991
17. Johansson L. C., Wolf M., Von Busse R., Winter Y., Spedding G. R. and Hedenstrom A., “The near and far wake of Pallas' long tongued bat: Glossophaga soricina”, J. Exp. Biol. 211, 2909-2918, 2008
18. Lentink Stefan R. et al, “The scalable design of flapping micro-air vehicles inspired by insect flight”, Flying Insects and Robots, 2009
19. Pennycuick C. J., “Modelling the flying bird”, p. 480. Amsterdam: Academic Press, 2008
20. Bullen R. D. and McKenzie N. L., “Scaling bat wingbeat frequency and amplitude”, J. Exp. Biol. 205, 2615-2626, 2002
21. Schnitzler H. U., “Fledermause im Windkanal”, Z. Vgl. Physiol. 73, 209-221, 1971
22. Lindhe Norberg U. M. and Winter Y., “Wing beat kinematics of a nectar feeding bat, Glossophaga soricina, flying at different flight speeds and strouhal numbers”, J. Exp. Biol. 209, 3887-3897, 2006
23. Hubel T. Y., Hristov N. I., Swartz S. M. and Breuer K. S., “Changes in kinematics and aerodynamics over a range of speeds in Tadarida brasiliensis, the Brazilian free-tailed bat”, J. R. Soc. Interface 9, 1120-1130, 2012
24. Norberg U. M., “Bat wing structures important for aerodynamics and rigidity (Mammalia, chiroptera)”, Zoomorphology 73, 45-61, 1972
25. Laitone E. V., “Wind tunnel tests of wings at reynolds numbers below 70 000”, Exp. Fluids 23, 405-409, 1997
26. Carruthers A. C., Thomas A. L. R. and Taylor G. K. “Automatic aeroelastic devices in the wings of a steppe eagle Aquila nipalensis”, J. Exp. Biol. 210, 4136-4149, 2007
27. Muijres F. T. et al, “Leading-edge vortex improves lift in slow-flying bats”, Science 319, 1250-1253, 2008
28. Norberg U. M., “Aerodynamics, kinematics and energetics of horizontal flapping flight in the long-eared bat Plecotus auritus”, J. Exp. Biol. 65, 179-212, 1976
29. Aldridge H. D. J. N., “Kinematics and aerodynamics of the greater horseshoe bat, Rhinolophus ferrumequinum, in horizontal flight at various flight speeds”, J. Exp. Biol. 126, 479-497, 1986
30. Wolf M., Johansson L. C., Von Busse R., Winter Y. and Hedenstrom A., “Kinematics of flight and the relationship to the vortex wake of a Pallas' long tongued bat (Glossophaga soricina)”, J. Exp. Biol. 213, 2142-2153, 2010
31. Swartz S. M., “Allometric patterning in the limb skeleton of bats: Implications for the mechanics and energetic of powered flight”, J. Morphol. 234, 277-294, 1997
32. Swartz S. M., Bishop K. and Ismael-Aguirre M. F., “Dynamic complexity of wing form in bats: Implications for flight performance”, In Functional and Evolutionary Ecology of Bats, (ed. Akbar Z., McCracken G. F. and Kunz T. H.), 2006

33. Neuweiler G., "The biology of bats", New York: Oxford University Press, 2000

34. Biewener A. A., "Allometry of quadrupedal locomotion: The scaling of duty factor, bone curvature and limb orientation to body size", J. Exp. Biol. 105, 147-171, 1983

35. Biewener A. A., "Biomechanical consequences of scaling", J. Exp. Biol. 208, 1665-1676, 2005

36. Heglund N. C. and Taylor C. R., "Speed, stride frequency and energy cost per stride: How do they change with body size and gait", J. Exp. Biol. 138, 301-318, 1988

37. Null W. and Shkarayev S., "Effects of camber on the aerodynamics of adaptive wing micro air vehicles" 2nd AIAA Flow control conference, Portland, Orgeon, June 28-1, 2004.

38. Hall K. C., Hall S. R., "A rational engineering analysis of the efficiency of flapping flight", In Fixed and Flapping Wing Aerodynamics for Micro Air Vehicle Application, Progress in Astronautics and Aeronautics, Vol. 195, pp. 249-274. New York, NY: Academic Press, 2002

39. Horner M. A., Fleming T. H. and Sahey C. T., "Foraging behaviour and energetics of a nectar-feeding bat, Leptonycteris curasoae (Chiroptera: Phyllostomidae)", J. Zool. 244, 575-586, 1998

40. Iriarte-Díaz J. and Swartz S. M., "Kinematics of slow turn maneuvering in the fruit bat, Cynopterus brachyotis", J. Exp. Biol., 211 3478-89, 2008

41. Iriarte-Díaz J., "Flight performance in bats and its ecomorphological implications", PhD Thesis, Department of Ecology and Evolutionary Biology, Brown University, 2009