BODY ACCELERATIONS DURING THE WINGBEAT IN SIX BAT SPECIES: THE FUNCTION OF THE UPSTROKE IN THRUST GENERATION

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SUMMARY

The kinematics and aerodynamics of *Rhinolophus ferrumequinum*, *R. hipposideros*, *Myotis nattereri*, *M. mystacinus*, *Plecotus auritus* and *Eptesicus serotinus* in horizontal flight at various flight speeds are described. Three kinematic patterns can be recognized. At low speeds *M. nattereri*, *M. mystacinus* and *P. auritus* use a 'tip-reversal' upstroke in which thrust is generated during the backward 'flick' of the chiropatagium. *R. hipposideros* also uses this kinematic pattern, but does not appear to generate thrust during the upstroke. Both *R. ferrumequinum* flying at $3 \cdot 12 \, \mathrm{m \, s^{-1}}$ and *E. serotinus* flying at $3 \cdot 44 \, \mathrm{m \, s^{-1}}$ accelerate during the 'vertical' upstroke (in which the wings move perpendicularly to the flight path), indicating that their wings are active. When flying at $4 \cdot 16 \, \mathrm{m \, s^{-1}}$, *E. serotinus* also uses a 'vertical' upstroke, but in this case it decelerates, which suggests that thrust is not being generated. At minimum power speed ($4 \cdot 8 \, \mathrm{m \, s^{-1}}$), *R. ferrumequinum* uses a 'reduced-span' upstroke, thrust is not generated during the upstroke and the animal decelerates.

INTRODUCTION

Flying animals flap their wings in order to generate thrust while maintaining weight support, and by altering the configuration of the wings during the upstroke they ensure net positive thrust. As the flight speed of the greater horseshoe bat, *Rhinolophus ferrumequinum*, increases, there is a gradual change in the way in which it moves its wings during the upstroke (Aldridge, 1986). At low speeds it uses a tip-reversal upstroke, in which the chiropatagium is accelerated backwards and upwards (Fig. 1A). This upstroke has also been described in the pigeon, *Columba livia* (Brown, 1948), and in a number of bat species (Eisentraut, 1936; Norberg, 1976; Altenbach, 1979; Aldridge, 1986). Several authors have suggested that the backward and upward flick of the wing at the end of the upstroke generates thrust, but Rayner (1987) thinks this unlikely since large transverse vortices are likely to be developed

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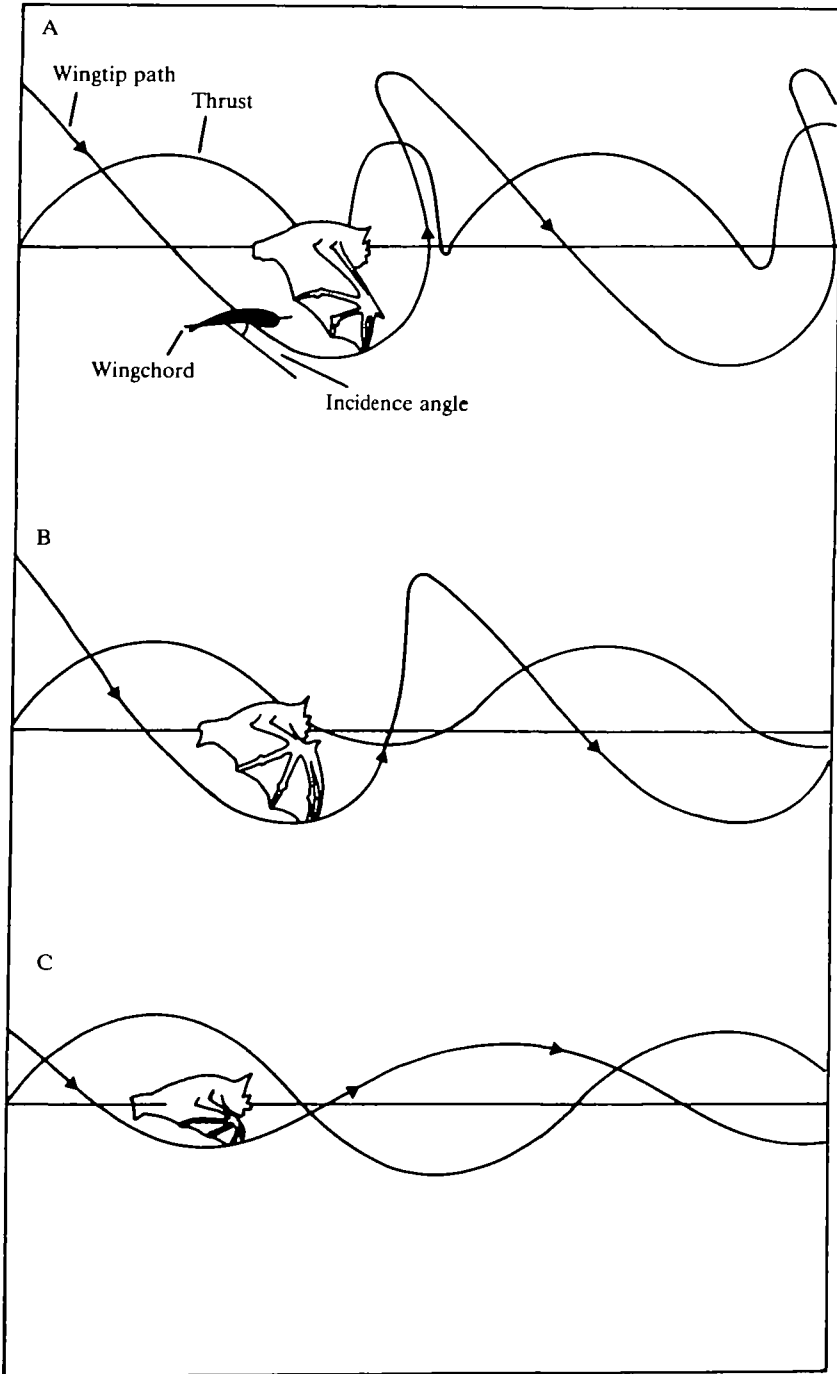
Fig. 1. Flight kinematics and thrust generation in flapping flight. (A) Slow flight kinematics; the tip-reversal upstroke, thrust is generated in both the down- and upstrokes. (B) The vertical upstroke. Thrust is only generated during the downstroke. (C) The reduced-span upstroke. Thrust is generated during the downstroke, negative thrust during the upstroke.

and induced drag increased. The hypothesis that the wings are unloaded during the upstroke in the slow forward flight of birds and bats is supported by the results of Kokshaysky (1979), Spedding, Rayner & Pennycuick (1984), Rayner, Jones & Thomas (1986) and Spedding (1986). The wake in these animals takes the form of small-cored vortex rings shed at the end of the downstroke. It is, however, possible that even if small air movements were generated during the upstroke these might be obscured by the larger air movements generated during the downstroke (Rayner *et al.* 1986).

At $3\cdot12\,\mathrm{m\,s}^{-1}$, *R. ferrumequinum* moves its wings vertically (perpendicular to the flight path) during the upstroke, the so-called vertical upstroke (Aldridge, 1986; Fig. 1B). Incidence angles tend to be low, suggesting that no lift is being generated (Aldridge, 1986). At minimum power speed (V_{mp}), *R. ferrumequinum*, uses a reduced-span upstroke, which has been shown to generate weight support and negative thrust (Spedding, 1987; Rayner *et al.* 1986). The bat ensures net positive thrust by reducing its effective wing span during the upstroke, thereby reducing the magnitude of upstroke lift (Rayner, 1986; Aldridge, 1986).

Possible independent measures of upstroke function are the accelerations and decelerations of the bat during the wingbeat. The lift generated by a wing is dependent upon the speed at which it moves through the air; therefore, when the wing decelerates at the end of the downstroke, the magnitude of lift (and therefore thrust) will fall and the bat will decelerate. Each wingbeat should, therefore, be characterized by accelerations and decelerations following the accelerations and decelerations of the wings. If the wings are unloaded during the upstroke then this deceleration should continue until the beginning of the downstroke. Alternatively, if the upstroke generates thrust the upstroke deceleration should either be absent or be replaced by an acceleration. I predict therefore that during the tip-reversal upstroke, the bats will accelerate or maintain a constant speed, while during the vertical and reduced-span upstrokes they will decelerate. This deceleration should be higher during the reduced-span upstroke due to the generation of negative thrust. The presence of accelerations and/or decelerations during the upstroke does not, however, unequivocally indicate that thrust is or is not being generated, because the effects of wing inertia and gravity may also be important.

The instantaneous horizontal acceleration experienced by the body of a flying bat during a wingbeat is the product of its mass and the instantaneous resultant force acting on it. This force has three components: inertial, gravitational (important if the bat is climbing or descending) and aerodynamic. The movement of the wings during the wingbeat will result in an inertial force acting on the centre of mass of the body, which in turn should result in small changes in the horizontal acceleration of the body, the magnitude of which will depend upon the relative masses of the wings and the body and the acceleration of the wings' centres of mass. At all speeds the wings are moved backwards and upwards for some period during the upstroke and, as a result, the body should experience a force (proportional to the combined masses of the two wings and their backward and upward accelerations) directed forwards and

downwards. This effect is likely to be most noticeable at low speeds when strokeplane angles tend to be small. If this horizontal force is large, then the accelerations of the body caused by it should be detectable.

The aim of this study was to measure the changes in body speed during the wingbeat for bats using all three of the kinematic patterns described above (Fig. 1) and, after accounting for the accelerations due to wing inertia and gravity, to test the hypotheses that (1) the tip-reversal upstroke generates thrust, (2) the vertical upstroke is inactive and (3) the reduced-span upstroke is active, generating weight support and negative thrust.

MATERIALS AND METHODS

Husbandry

Six microchiropteran bat species were used in this study, *Rhinolophus ferrumequinum* (Schreber), *R. hipposideros* (Bechstein), *Plecotus auritus* (L.), *Myotis mystacinus* (Kuhl), *M. nattereri* (Kuhl) and *Eptesicus serotinus* Schreber (Table 1). The bats were housed in plywood boxes similar in design to those described by Racey (1976) and Aldridge (1986). Food consisted primarily of the larvae of *Tenebrio molitor* (plus a vitamin supplement). Water was available *ad libitum* in Petri dishes placed in the boxes. The bats were fed by hand every day during their training sessions, during which they were allowed to fly unimpeded about the experiment room for up to 4 h. The basic training schedule has already been described for *R. ferrumequinum* (Aldridge, 1986), and the same methods were used for the other species.

Photography

The bats were photographed as they flew through a flight tunnel, illuminated by a stroboscope (Rayner & Aldridge, 1985; Aldridge, 1986). Two stroboscope flashing

Table 1. *Morphological parameters for* Plecotus auritus, Eptesicus serotinus, Myotis nattereri, M. mystacinus, Rhinolophus ferrumequinum *and* R. hipposideros

Species	m (kg)	b (m)	S (m²)	Q_s (N m⁻²)	R
Rhinolophus ferrumequinum	0·0215	0·36	0·0223	9·45	5·8
R. hipposideros	0·0065	0·24	0·0094	6·78	5·9
Plecotus auritus	0·0095	0·26	0·0128	7·28	5·1
Myotis mystacinus	0·0059	0·23	0·0080	7·23	6·6
M. nattereri	0·0095	0·27	0·0130	7·16	5·6
Eptesicus serotinus	0·0260	0·38	0·0190	13·42	7·6

m, body mass; b, wing span; S, wing area; Q_s, wing loading; R, aspect ratio.

frequencies were used; 100 Hz and 200 Hz. For each flight, two photographs were obtained showing dorsal and lateral views of the bat as it flew through the cage. Only those photographs in which the upstroke occurred at the middle of the recorded time sequence were used for further analysis.

Analysis

The method of analysis has been described in detail elsewhere (Rayner & Aldridge, 1985; Aldridge, 1986), suffice it to say that from these photographs the positions of the bat and various parts of it (e.g. wrist and wingtip) were calculated in three dimensions at regular time intervals. These data were then used to calculate the velocities and accelerations of the body (defined by a point midway between the humeral joints horizontally and in the middle of the thorax vertically), the wrist, the wingtip and the tips of the second, fourth and fifth digits. From these data, I estimated the angles made by wingchords with the horizontal (a wingchord is defined as a straight line drawn between the leading and trailing edges of an aerofoil). The angle of incidence of a wingchord is defined as the angle between the wingchord and the resultant airflow (Fig. 1). I calculated angles of incidence by determining the local velocity vectors of the two ends of the wingchord and finding the angle between the chord and the resultant of a line parallel to these velocities and induced velocity. Induced velocity was estimated using Pennycuick's (1975) equation.

Accuracy and errors

Rayner & Aldridge (1985) have discussed in detail the sources and magnitudes of the errors in the technique. With a camera tilt angle of $5°$, they found that the maximum error due to the resection technique alone was approximately 1%. The overall error of the system, including digitizing inaccuracies and errors in test cube construction, was approximately 2%. For this study I digitized one pair of photographs five times and found that the maximum variation in coordinate estimation was approximately 4%. These errors are random, being due primarily to operator error, and can therefore be accounted for by using the smoothing technique of Lanczos (1957) (Rayner & Aldridge, 1985). The calculation of velocities and accelerations from this corrected position series was done using the method of Lanczos (1957) (Rayner & Aldridge, 1985), and it is possible that small irregularities in position estimation will be amplified and make the velocity and acceleration traces meaningless. In Fig. 2, I have plotted the changes in the acceleration of the body for *R. ferrumequinum* over 0·025 s calculated from five data sets obtained by five digitizing events. It is clear from this figure that, although the numerical values of the accelerations vary, the positions of the maxima and minima remain the same, and it is these positions that are important in this study. I think, therefore, that although quantitatively the technique may not be very accurate the results are good enough for the aims of this study.
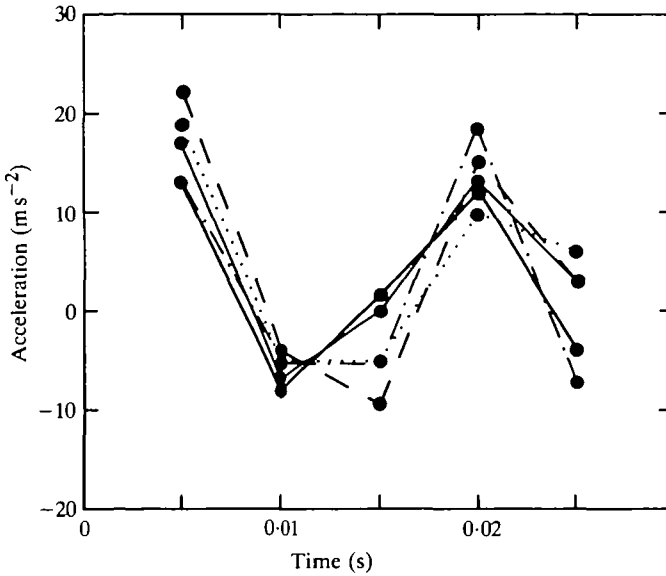
Fig. 2. Change in the acceleration of the centre of mass of *Rhinolophus ferrumequinum* over a 0·025 s time interval calculated from five separate estimates of the animal's position.

Accelerations due to inertial and gravitational forces

The angular velocity of a wing during a wingbeat is,

$$d\phi/dt, \tag{1}$$

where ϕ is the positional angle (Fig. 3). The wing's angular acceleration is, therefore,

$$d^2\phi/dt^2. \tag{2}$$

The acceleration of the wing's centre of mass is, therefore,

$$a_w = r(d^2\phi/dt^2), \tag{3}$$

where r is the distance of the centre of mass from the humeral joint. I assumed that r was 1/6 wing length. The total force acting at the centre of mass is,

$$F_w = m_w a_w, \tag{4}$$

where m_w is the mass of the wing. I did not measure the masses of the wings of the bats in this study, but measurements of individuals of six other microchiropteran species (*Myotis lucifugus*, *Eptesicus fuscus*, *Antrozous pallidus*, *Megaderma lyra* and *Macrotus californicus*) showed that there was a significant positive correlation ($r = 0·96$, $P < 0·01$) between total wing area and wing mass,

$$m_w = 0·761 S^{2·12}, \tag{5}$$

where S is wing area, and I used this to estimate wing mass. The horizontal component of F_w is,

$$F_{wh} = F_w \cos\gamma, \tag{6}$$

where γ is strokeplane angle. Therefore the total horizontal force experienced by the bat due to the acceleration of the wings is,

$$F_{bh} = 2(F_w \cos\gamma). \tag{7}$$

The horizontal acceleration experienced by the bat is therefore,

$$a_{bh} = 2(F_w \cos\gamma)/m_b, \tag{8}$$

where m_b is the bat's total body mass.

If the animal is climbing or descending, gravity will have a horizontal component defined by:

$$g_h = g\cos(90 + \alpha), \tag{9}$$

where α is the angle between the horizontal and the animal's flight path, and g is the acceleration due to gravity.

Some of the flights of *R. ferrumequinum* which I used in a previous paper (Aldridge, 1986) were used again in this study. The slow horizontal flight of *P. auritus* was described in detail by Norberg (1976), while the flights of *E. serotinus*, *R. hipposideros*, *M. mystacinus* and *M. nattereri* are described here for the first time.
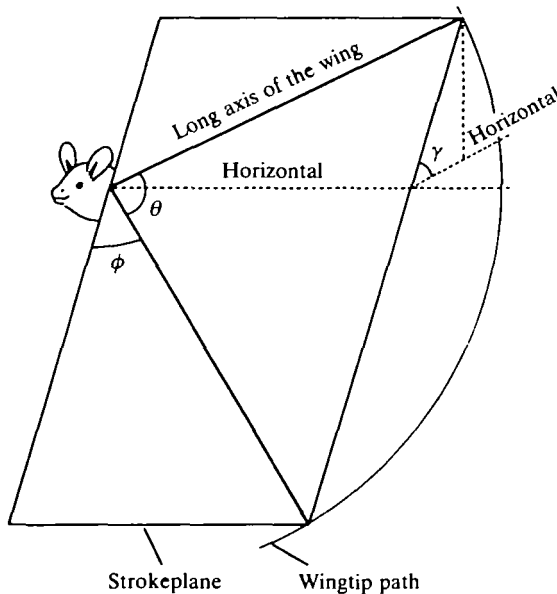

Fig. 3. Diagram showing various terms used in the text (after Norberg, 1976). γ is the strokeplane angle, ϕ is the positional angle and θ is amplitude.

RESULTS

The tip-reversal upstroke: the slow forward flight of P. auritus, M. nattereri,
M. mystacinus *and* R. hipposideros

I examined four flights for *P. auritus*, two flights each for *M. mystacinus* and *R. hipposideros* and one flight for *M. nattereri* (Table 2). Kinematically these flights were similar (Table 2; Figs 4, 5, 6), but two patterns of body acceleration were recorded. The first pattern was recorded in two of the four flights of *P. auritus* and the flights of *R. hipposideros*. The bats decelerate during the upstroke and accelerate during the downstroke, suggesting that thrust is being generated during the downstroke, but not during the upstroke. In both bats, incidence angles during the upstroke are positive and therefore if lift is being generated it will be directed backwards and upwards. In both cases, the wings decelerate during the upstroke, suggesting that they are unloaded. The absence of upstroke thrust in *R. hipposideros* may be the explanation for the bats' overall deceleration and loss of height (Fig. 5).

The remaining flights of *P. auritus* and the flights of *M. mystacinus* and *M. nattereri* were characterized either by an increase in the acceleration of the body during the upstroke, or by the maintenance of the acceleration observed during the downstroke (Figs 4, 6). In *P. auritus*, the body's acceleration is associated with an acceleration of the wing backwards and upwards during the upstroke, at the end of which the wingchords are perpendicular to the flight path. Two upstrokes are illustrated in Fig. 4. In the first of these, the backward flick of the wing results in incidence angles approaching 90°: the bat is generating propulsion by means of a forward-directed drag force. In the second upstroke smaller negative incidence angles are produced, and thrust is probably generated as a consequence of the generation of a negative upstroke circulation.

The vertical upstroke: the flight of R. ferrumequinum *and* E. serotinus

I examined seven flights of *R. ferrumequinum* and three of *E. serotinus*, in which the vertical upstroke was used (Table 2; Figs 7, 8, 9). The wingbeat kinematics of these bats is similar to those already described, except that there is a decrease in the backward movement of the wing during the upstroke and an increase in strokeplane angles. In both species and all flights, the downstroke is initiated by an acceleration of the wing, an increase in incidence angles and a deceleration of the body. Assuming that the wing is acting in a quasi-steady fashion, weight support and thrust are generated during the downstroke, and as the wings' speed increases there is an increase in thrust production and the bats accelerate (Figs 7, 8, 9). This acceleration reaches a maximum at the middle of the downstroke as the wing reaches maximum velocity and thrust reaches a maximum. As the wing decelerates towards the end of

Fig. 4. Kinematics and aerodynamics of *Plecotus auritus* in slow flight at 1.87 m s^{-1} and 2.15 m s^{-1}. (A) The acceleration and velocity of the body centre of mass. (B) Changes during the wingbeat in the positions of the wrist and wingtip chords and their incidence angles. The arrows indicate the direction of lift but not its magnitude. (C) Wingtip and wrist speed changes during a wingbeat. The dotted lines in C indicate the changes in the wings' velocity parallel to the flight path.
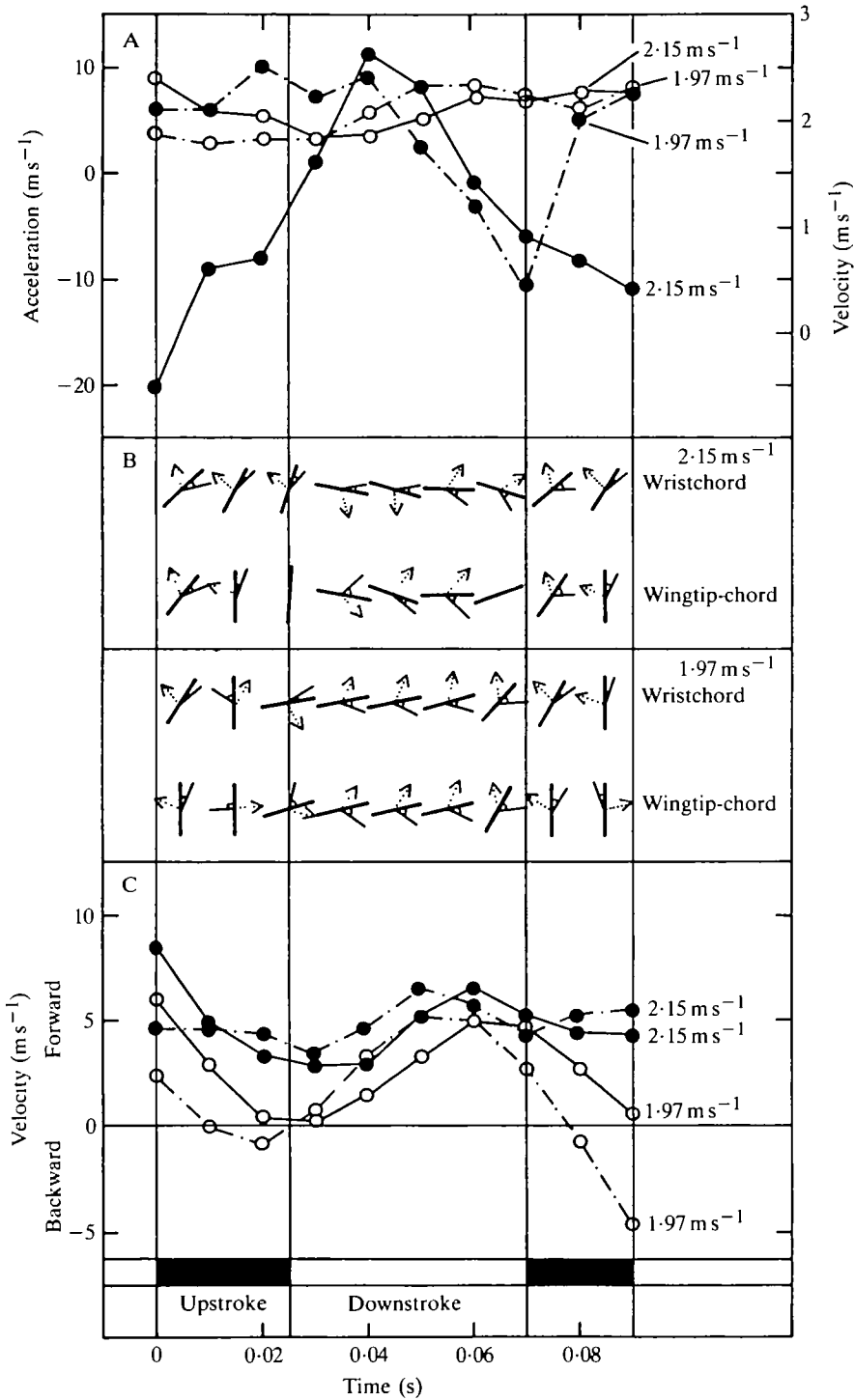
Fig. 4

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Table 2. *Kinematic parameters for representative flights of* Rhinolophus ferrumequinum, Plecotus auritus, Myotis nattereri, M. mystacinus *and* Eptesicus serotinus *and the nature of the change in body horizontal velocity for each flight*

Upstroke type	Speed $(m s^{-1})$	Frequency (Hz)	Amplitude (degrees)	Strokeplane angle Wrist (degrees)	Strokeplane angle Wingtip (degrees)
Tip-reversal					
P. auritus					
Deceleration (Fig. 4)	2·15	14·28	50·0	78·0	70·0
Deceleration (Fig. 4)	2·03	14·28	50·3	73·0	69·0
Acceleration (Fig. 4)	1·97	14·28	57·0	81·0	61·0
Acceleration (Fig. 4)	2·11	14·28	62·1	73·7	65·0
R. hipposideros					
Deceleration (Fig. 5)	2·65	16·67	59·5	74·0	61·0
Deceleration (Fig. 5)	2·58	16·67	51·9	79·0	70·0
M. nattereri					
Acceleration (Fig. 6)	1·81	11·81	42·7	63·0	49·0
M. mystacinus					
Acceleration (Fig. 6)	1·57	14·28	40·1	77·0	72·0
Acceleration (Fig. 6)	1·83	14·29	74·8	89·0	79·0
Vertical					
R. ferrumequinum					
Acceleration (Fig. 7) (from Aldridge, 1986)	3·12	11·11	65·8	89·0	65·0
Acceleration	3·12	11·11	50·1	81·0	66·0
Acceleration	3·85	12·50	98·0	89·0	83·0
Acceleration	3·52	11·11	59·0	70·0	66·5
Acceleration	4·00	11·11	71·6	90·0	80·0
Acceleration	3·55	12·50	58·0	86·0	82·0
Acceleration	3·48	12·50	76·0	83·0	78·0
E. serotinus					
Deceleration (Fig. 8)	4·16	8·33	51·0	90·0	76·0
Acceleration (Fig. 9)	3·44	12·50	41·2	90·0	81·6
Acceleration (Fig. 9)	3·90	9·10	86·3	88·0	77·0
Reduced-span					
R. ferrumequinum					
Deceleration (Fig. 10) (from Aldridge, 1986)	4·84	9·09	64·0	90·0	85·0

the downstroke, the animals' accelerations fall and they attain their maximum speeds. In both species the upstroke is initiated by a deceleration of the body. In *E. serotinus* flying at $4·16 m s^{-1}$, this deceleration continues throughout the upstroke and occurs simultaneously with a decrease in wing speed (Fig. 9). The rate of change of this deceleration does, however, decrease towards the end of the upstroke, and the wingtip chord incidence angles suggest that some thrust may be generated at this time. As the upstroke proceeds, *R. ferrumequinum* accelerates, reaching maximum upstroke velocity just prior to the start of the downstroke (Fig. 7). Calculated incidence angles suggest that during the last half of the upstroke some positive thrust is produced by both wingchords. When flying at $3·44 m s^{-1}$, *E. serotinus* shows two patterns of acceleration (Fig. 8). During the first upstroke, the bat decelerates and this deceleration appears to be associated with a relatively low wing speed. During
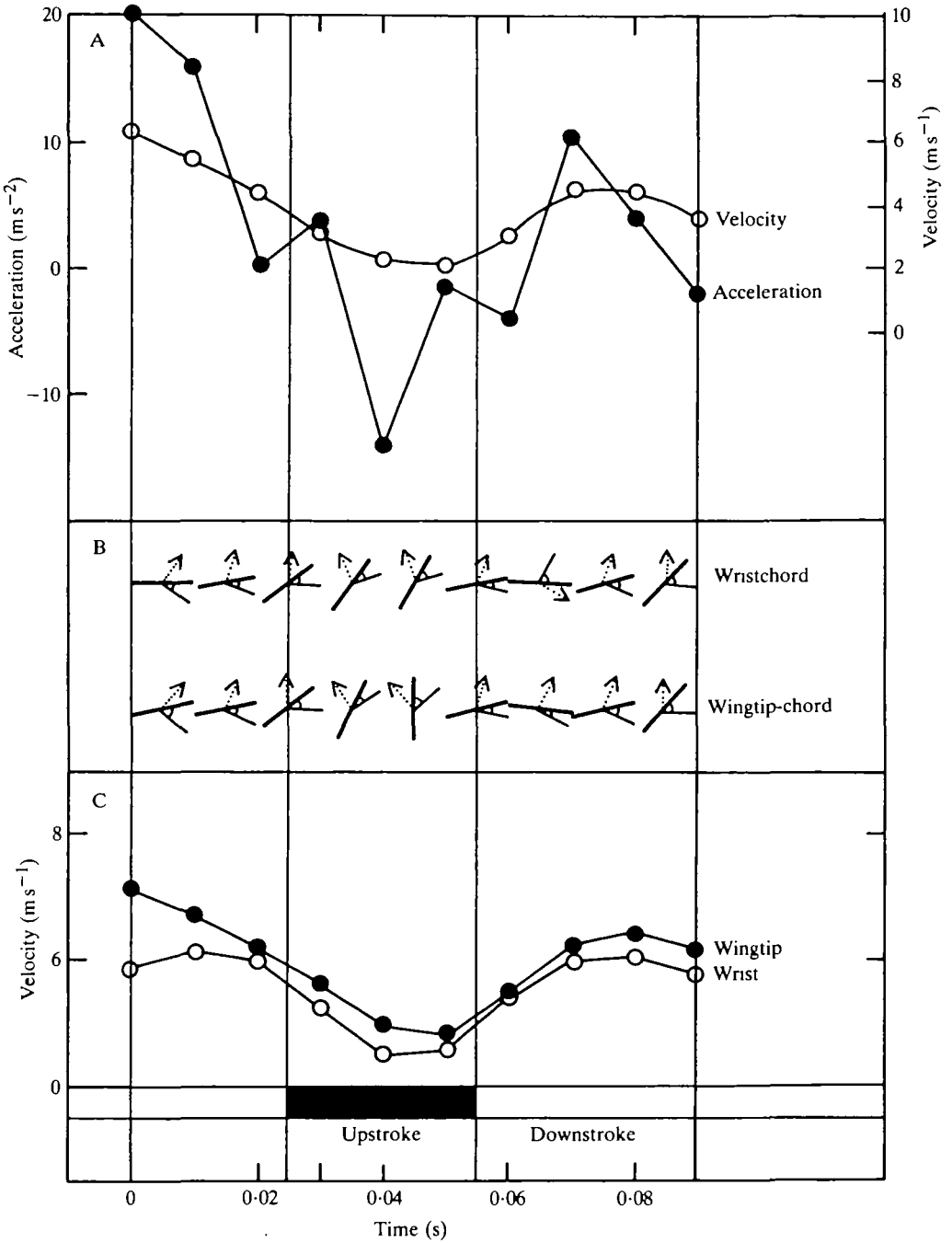
Fig. 5. Kinematics and aerodynamics of *Rhinolophus hipposideros* in slow flight at 2·65 m s⁻¹. Other conventions as in Fig. 4.
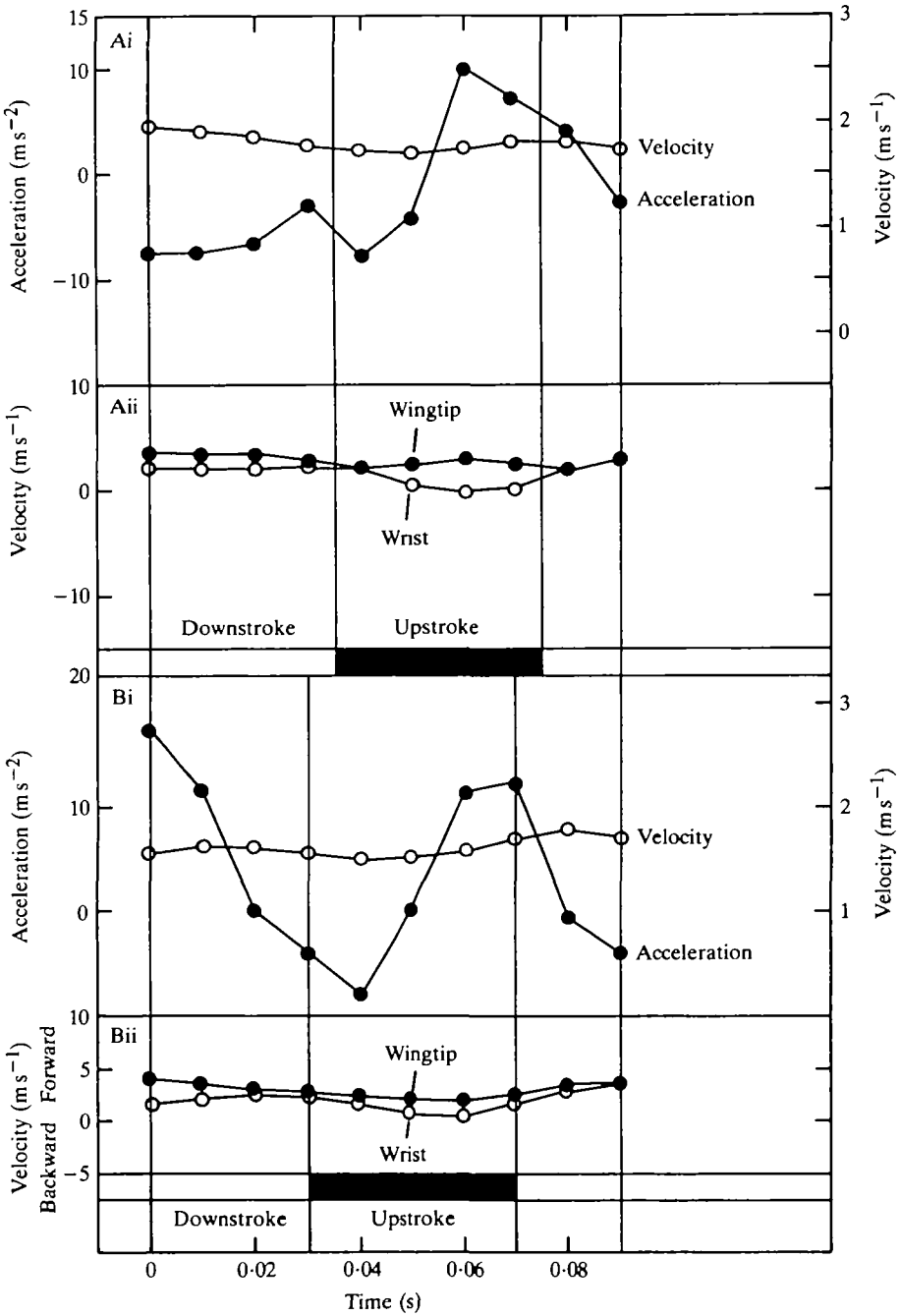
Fig. 6. Kinematics and aerodynamics of (A) *Myotis nattereri* and (B) *Myotis mystacinus* flying at 1.81 m s^{-1}. (i) The acceleration and velocity of the body centre of mass and (ii) wingtip and wrist speed changes during a wingbeat.
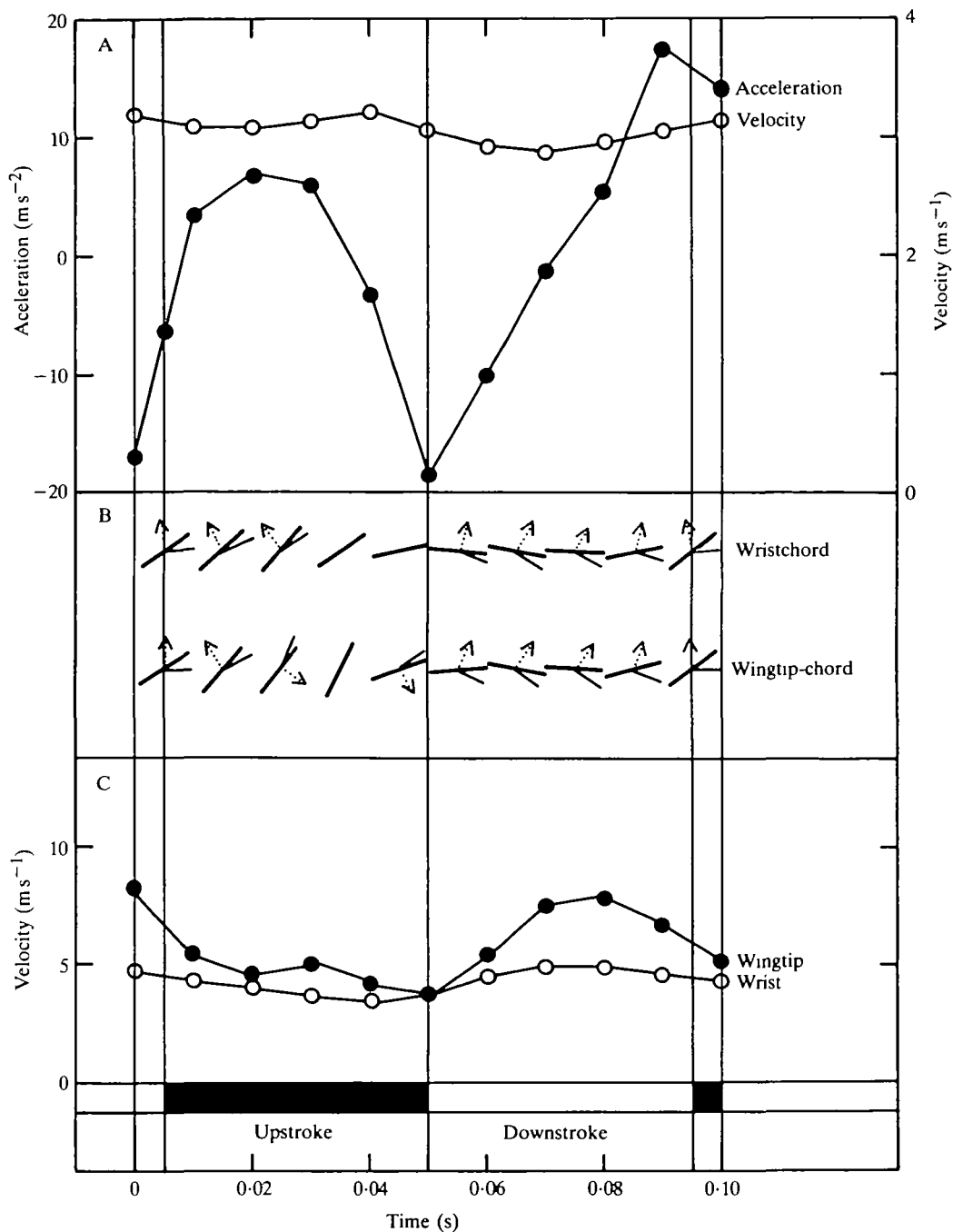
Fig. 7. Kinematics and aerodynamics of *Rhinolophus ferrumequinum* in slow flight at
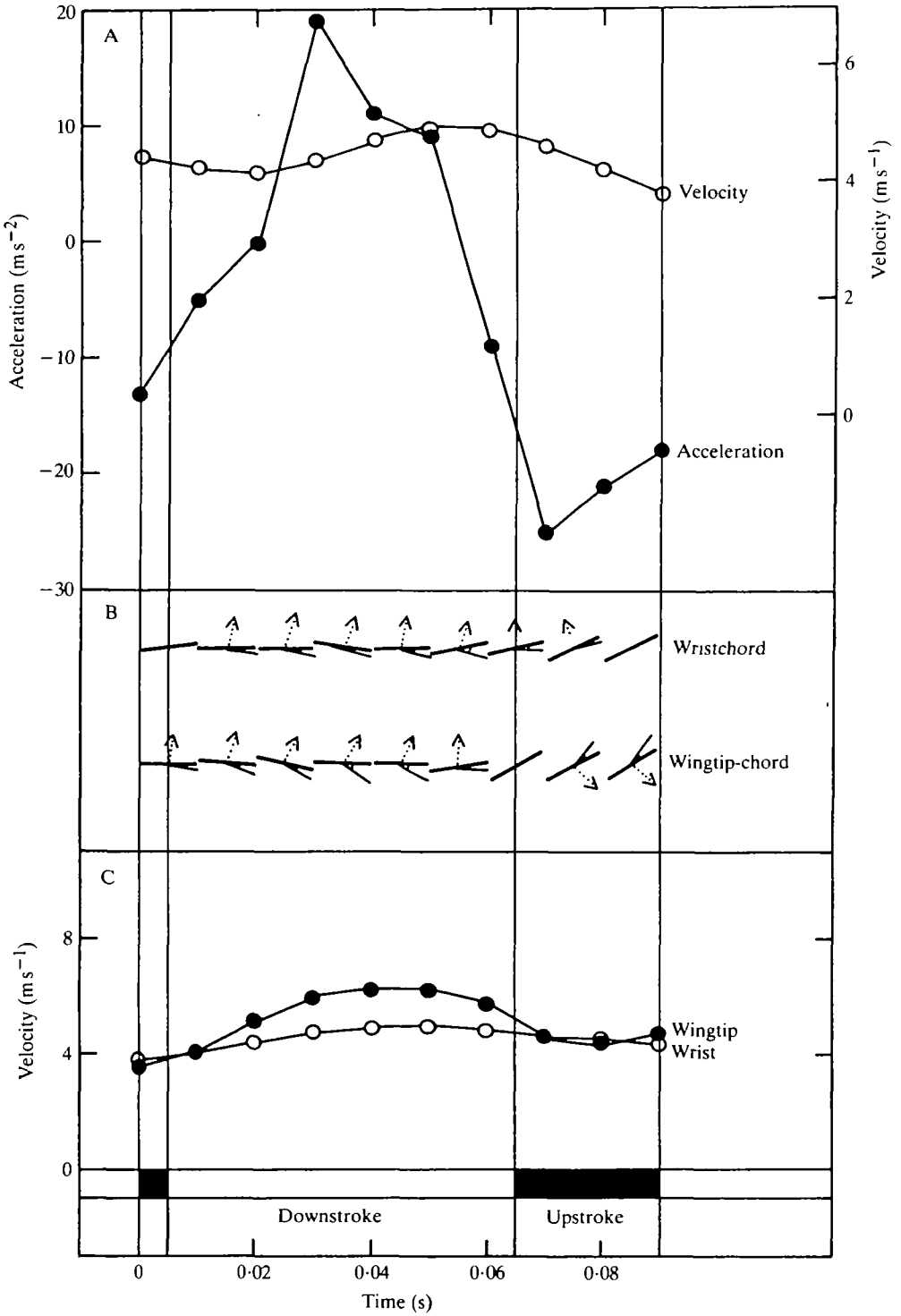3·12 m s⁻¹. Conventions as in Fig. 4.

Fig. 8. Kinematics and aerodynamics of *Eptesicus serotinus* in slow flight at $3·44 \, m \, s^{-1}$. Conventions as in Fig. 4.
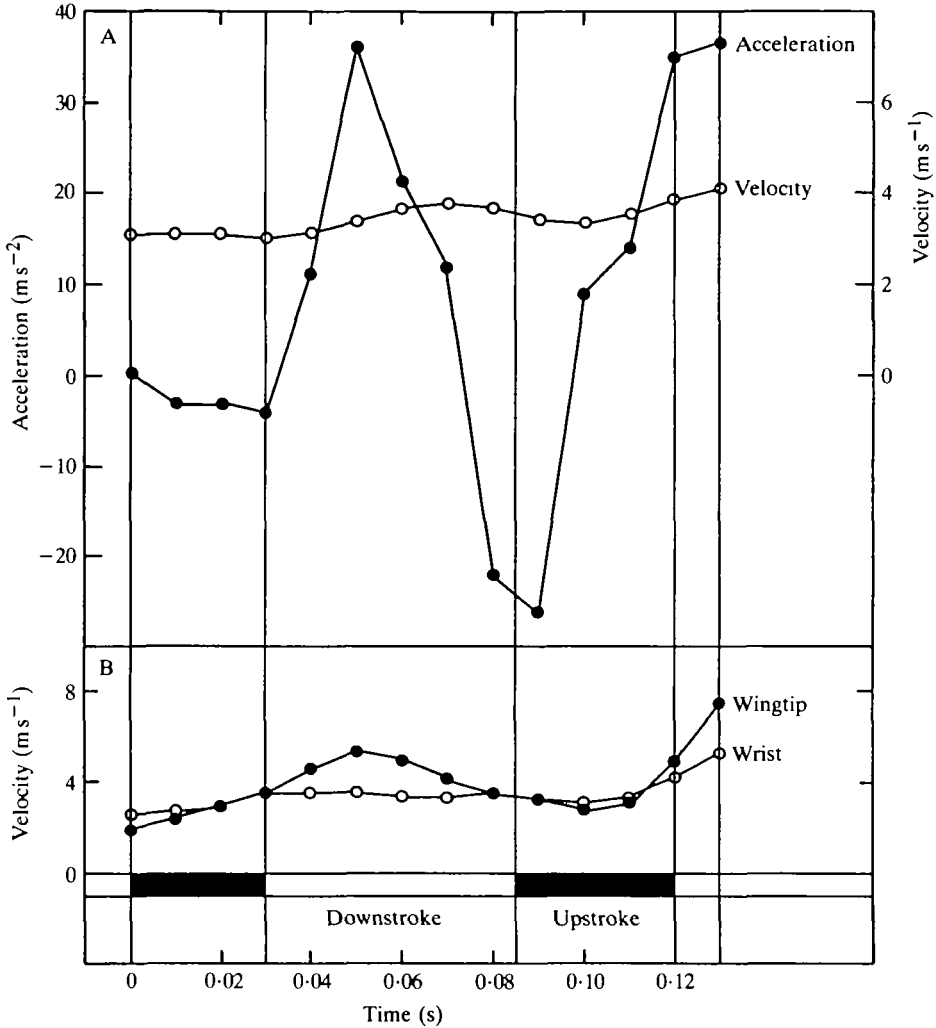
Fig. 9. Kinematics and aerodynamics of *Eptesicus serotinus* in flight at $4.16 \, \text{m s}^{-1}$. (A) The velocity and acceleration of the body centre of mass and (B) wingtip and wrist speed changes during a wingbeat.

the second upstroke, however, the bat accelerates suggesting thrust generation, possibly associated with the acceleration of the wing (Fig. 8).

The reduced-span upstroke: the flight of R. ferrumequinum *at* $4.8 \, \text{m s}^{-1}$

I analysed one flight of *R. ferrumequinum* flying at V_{mp}, in which the bat uses the reduced-span upstroke already described for this species by Aldridge (1986), and the strokeplane angle is 90° (Fig. 10). At the beginning of the downstroke, the animal decelerates, this deceleration decreasing as the downstroke proceeds. By the end of the downstroke, the bat has an acceleration of $11 \, \text{m s}^{-2}$. The bat continues to accelerate during the upstroke, but as a result of the generation of negative thrust the rate of acceleration falls. By the middle of the upstroke, the bat has a deceleration of

$10 \, \text{m s}^{-2}$, and this continues for 20 ms. Towards the end of the upstroke, the wing accelerates and a small thrust may be produced, and cause a small upstroke acceleration.

DISCUSSION

The results seem to support the three hypotheses I postulated in the Introduction. In some flights in which the tip-reversal upstroke is used, a body acceleration occurs
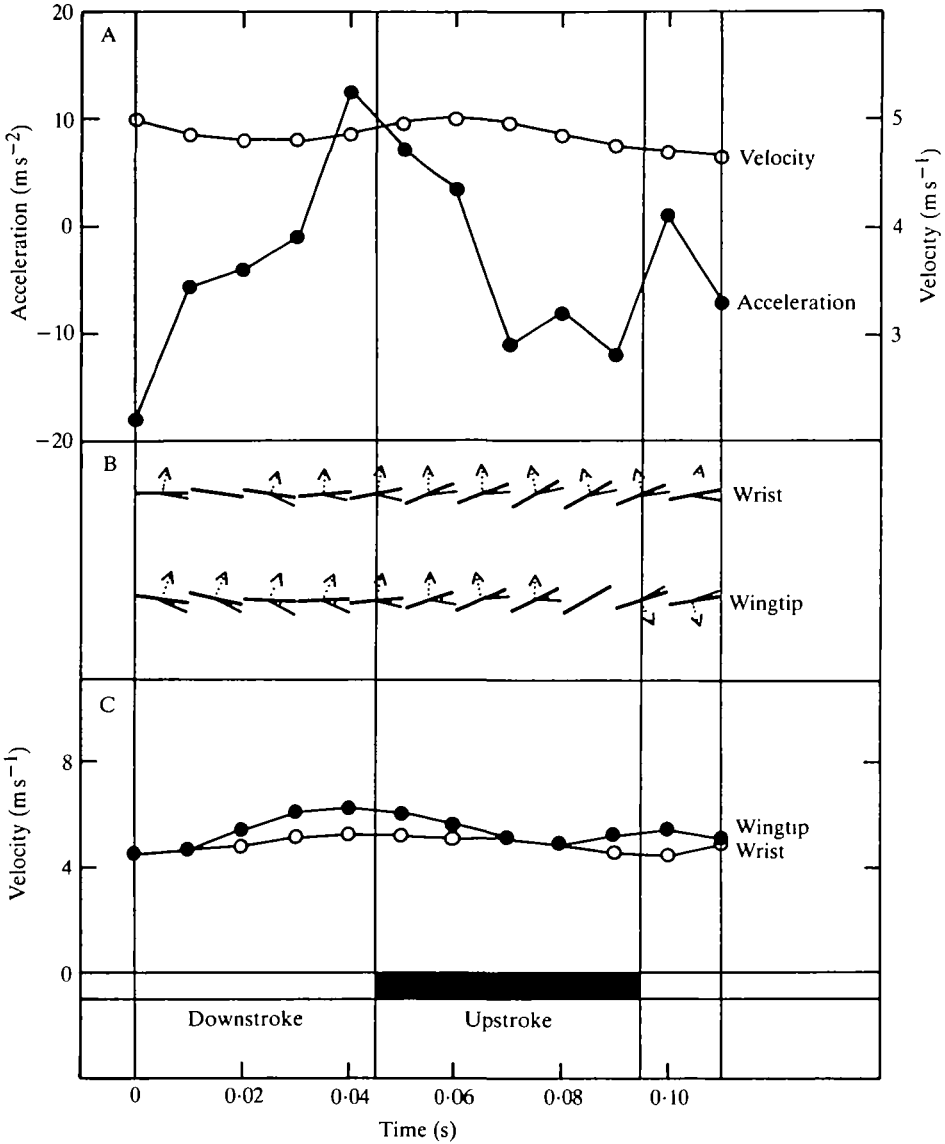

Fig. 10. Kinematics and aerodynamics of *Rhinolophus ferrumequinum* in flight at $4 \cdot 84 \, \text{m s}^{-1}$. Conventions as in Fig. 4.

during the upstroke, suggesting thrust generation. In *P. auritus* I recorded two
upstrokes; during the first of these, thrust is generated as a consequence of a forward-
directed drag force (Altenbach, 1979), while in the second the wings are acting more
conventionally, thrust being generated in a manner similar to that described for this
species by Norberg (1976). In her study, Norberg (1976) showed that most of the
required thrust was generated during the upstroke, while weight support was
produced during the downstroke. The pattern of body accelerations observed in
P. auritus, *M. mystacinus* and *M. nattereri* suggests a similar pattern of lift
generation. The wake in this wing stroke should take the form of a series of linked
vortex rings of opposite circulation in the up- and downstrokes. This kinematic
pattern, or 'gait', is similar to that postulated by Alexander (1986) for hovering
hummingbirds and represents a possible intermediate stage between hovering and
slow forward flight using an unloaded upstroke. This conclusion does not, however,
agree with the findings of Rayner *et al.* (1986), who found that the wake of slow-
flying *P. auritus* (and *N. noctula*) consists of discrete vortex rings similar to those
described in the pigeon, *Columba livia* (Spedding *et al.* 1984), and the jackdaw,
Corvus monedula (Spedding, 1986), which indicates that the upstroke is unloaded.
There are two possible explanations for this discrepancy. First, it is possible that the
flight of *P. auritus* reported by Rayner *et al.* (1986) was similar to the first flight of
P. auritus and the flights of *R. hipposideros*, in which the wings are unloaded during
the upstroke. Alternatively, as pointed out by Rayner *et al.* (1986), the circulation
generated during the upstroke will be relatively weak and might be obscured by the
more dominant vortices produced during the downstroke. It is significant that as
P. auritus increases its flight speed from $1 \cdot 97 \, \text{m s}^{-1}$ to $2 \cdot 15 \, \text{m s}^{-1}$, the upstroke
apparently becomes unloaded. Presumably the wake in this case takes the form of
discrete vortex rings as described by Rayner *et al.* (1986).

The development of a negative circulation is only possible if the wing is accelerated
backwards during the upstroke. Increases in forward velocity make this more
difficult, incidence angles become positive and therefore the upstroke generates
weight support and negative thrust, even though the animal's kinematics remain the
same. Further increases in speed will increase the magnitude of this negative thrust
up to a speed at which it exceeds the thrust generated during the downstroke. By
reducing upstroke wing velocity, eliminating the backward flick and/or reducing
incidence angles, the bat ensures that the wings are unloaded when this speed is
reached.

I postulated in my previous paper on the flight kinematics of *R. ferrumequinum*
(Aldridge, 1986) that the vertical upstroke was functionally equivalent to the
feathered upstroke used by slow-flying birds (Brown, 1948). If this were so, we
might expect the bat to decelerate during the upstroke and accelerate during the
downstroke. This occurs in *E. serotinus* flying at $4 \cdot 16 \, \text{m s}^{-1}$, but not in *R. ferrum-
equinum* flying at $3 \cdot 12 \, \text{m s}^{-1}$ or *E. serotinus* flying at $3 \cdot 44 \, \text{m s}^{-1}$, in which there are
upstroke body accelerations and evidence that negative incidence angles generate
thrust but at the expense of weight support. The flight of *E. serotinus* at $4 \cdot 16 \, \text{m s}^{-1}$
appears to represent that typical of slow-flying animals, and I predict that the wake

would take the form of a series of discrete circular vortices shed at the end of the downstroke. The flight of *R. ferrumequinum* and that of *E. serotinus* at $3.44\,\mathrm{m\,s^{-1}}$ would appear to be intermediate between the tip-reversal upstroke with negative circulation and the vertical upstroke with no circulation. The wake is probably similar to that described above for the active tip-reversal upstroke, except that the air movements generated during the upstroke are much smaller. At this stage it appears that the downward force generated during the upstroke is balanced by weight support generated during the downstroke. It is significant that as the flight speed of *E. serotinus* increases from $3.44\,\mathrm{m\,s^{-1}}$ to $4.16\,\mathrm{m\,s^{-1}}$ the upstroke becomes inactive. As flight speed increases, it is probable that this downward force plus the animal's weight exceed the upward force generated during the downstroke and the upstroke has to become inactive.

At minimum power speed *R. ferrumequinum* uses a reduced-span upstroke similar to that described for birds in cruising flight (Brown, 1952; Scholey, 1983; Spedding, 1987) and bats (Rayner *et al.* 1986; Aldridge, 1986). This wingbeat is characterized by a vertical strokeplane, up- and downstrokes of equal duration, and small changes in incidence. As noted in the kestrel, *Falco tinnunculus* (Spedding, 1987), the large accelerations and decelerations associated with the wingbeat at lower flight speeds are absent and, thus, it is likely that lift is generated throughout the stroke. Because of wing supination during the upstroke, lift is directed backwards and upwards, although my results suggest that the negative thrust generated is relatively small. The bat ensures that net thrust is positive by reducing its effective wingspan and the magnitude of upstroke lift. The advantages of lift generation in the upstroke in this gait are quite clear; by generating weight support throughout the stroke the animal may reduce wing angular velocity and therefore power output. Also, upstroke lift will tend to raise the wing during the upstroke thus further reducing the need for muscular work (Aldridge, 1986). More importantly perhaps, by keeping the sense of the circulation constant the bat eliminates transverse vortices and reduces induced drag (Rayner, 1986).

Rayner (1986) has suggested four distinct gaits for flying animals of which three appear to apply to most birds and bats.

(1) Rigid wing flapping with negative upstroke circulation, generating thrust. This gait has been demonstrated in the bats, *P. auritus* and *R. ferrumequinum* (Norberg, 1976; Aldridge, 1986). The wake of this gait probably takes the form of linked vortices of opposite sense. An extreme form of this gait is thought to be used by hovering animals (Alexander, 1986).

(2) Wing flapping with little or no upstroke circulation. The wake is a series of separate vortex rings shed during the downstroke, and there is no upstroke lift generation (Kokshaysky, 1979; Spedding *et al.* 1984; Rayner *et al.* 1986).

(3) Wing flapping with constant circulation, net positive thrust being ensured by flexed, swept wings or unloaded wingtips. The wake takes the form of a pair of distorted trailing vortices (Rayner *et al.* 1986; Spedding, 1987).

The results presented here seem, in general, to confirm the lifting patterns which are associated with these gaits. However, they also suggest that intermediate

patterns may exist between them, confirming the idea of a gradual change in upstroke function with increasing flight speed (Rayner, 1986; Aldridge, 1986; Scholey, 1983).

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