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INTERMITTENT GLIDING FLIGHT IN THE PIPISTRELLE BAT (*PIPISTRELLUS PIPISTRELLUS*) (CHIROPTERA: VESPERTILIONIDAE)

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Summary

The pipistrelle bat *Pipistrellus pipistrellus* intersperses wingbeats in flapping flights with brief (0.1–0.3 s) glides. This *undulating* intermittent flight mode probably saves energy in flight. In large flight cages, captive pipistrelles glided for approximately 13.4 % of flight time, but glides were steep, and the bat accelerated during the glides. The bats sometimes glided during turns. During the glides the bat may have been unable to emit echolocation pulses and, if so, this would explain occasional wide interpulse intervals in wild pipistrelles. The steepness of the glides may be a means of improving undulating flight performance, and may also be unavoidable owing to the very small size and relatively small wings of pipistrelles.

Introduction

Intermittent flight, in which bouts of flapping are interspersed with resting phases, is common in birds, but has not been studied in bats. Compared to continuous flapping it can reduce energy consumption, and can improve an animal's flexibility in speed and in control of its flight path (Rayner, 1985). Two intermittent flight modes have been recognized in birds: 'bounding' flight, in which the wings are folded against the body during the rest phase, and 'undulating' flight, in which the wings are held outstretched and the animal glides. Bats have never been reported to use bounding flight, probably for reasons associated with wing and flight muscle anatomy (Rayner, 1985), but there are occasional anecdotal observations of intermittent gliding or undulating in a number of species of megabats and microbats. All forms of gliding are rare in bats, and hitherto gliding has been studied only in the relatively large megabat *Rousettus aegyptiacus*, flying in a wind tunnel (Pennycuik, 1971, 1973). Gliding can sometimes be observed in larger megabats in the wild, especially when the animals are active during the day and soar on thermal updraughts (J. M. V. Rayner, unpublished observations). Gliding is also used by certain microbats, which is surprising in view of their small

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size: on watching some species in the wild it is apparent that flapping is occasionally interrupted by short glides. This behaviour is often noted in the pipistrelle *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae; Schreber, 1774), the smallest British bat (mass about 5 g); it is occasionally seen in most other British microbats. In this paper we describe intermittent flight in pipistrelles, and consider the functional significance of this behaviour.

Materials and methods

Two male pipistrelles (masses 4.7 and 4.8 g) were allowed to fly freely in large flight cages (5 m×3 m×2 m and 10 m×3 m×4 m), and their flight behaviour was recorded by using a Kodak Ektapro 2000 high-speed video recorder at 250 frames s⁻¹. The camera was stationary, with its optical axis perpendicular to the long axis of the cage at the approximate level of the bats' flight paths.

Wingbeat frequencies and glide durations were measured on a UMATICS slow-motion video analyser with a time resolution of 0.5 ms. Sequences of flapping and of glides in which the bat flew on a path approximately perpendicular to the optical axis of the camera were digitized with a FOR.A VPA 1000 video position analyser, and wingbeat kinematics were subsequently analysed on IBM-compatible personal microcomputers [see Rayner and Aldridge (1985) for details of the analytical techniques employed]. Linear scale was determined from the mean digitized nose–tail distance of the bat. Some bias would be introduced if the flight path was not straight and/or perpendicular to the camera: this may not have been discernible on the video screen owing to the relatively low resolution of the system. We estimate that position, speed and acceleration may be underestimated by at most 5%.

Glides were defined as phases during which the wings were held still relative to the body for a period longer than one wingbeat, in a configuration where appreciable aerodynamic force would have been produced. Detailed kinematic analysis was carried out on some flights in the smaller cage; some results from flights in the larger cage are presented for comparison.

Experimental observations are compared with theoretical predictions of glide performance made by applying the model of Tucker (1987) with dimensions of a typical pipistrelle (mass 0.0052 kg, wingspan 0.218 m, wing area 0.0063 m²; Norberg and Rayner, 1987). Tucker's model in the form we used here assumes wing profile drag to vary with Reynolds number (i.e. with size and speed) and with lift coefficient, and is based on measurements of aerodynamic performance for bird wings. There are no comparable data for the wings of small bats which might make these predictions more reliable. If profile drag coefficient is assumed to be constant (0.02; see Rayner, 1986) there are only minor changes in the predictions. Statistics are given as mean±standard deviation throughout.

Results

During the normal wingbeat cycle at a flight speed of 2.8 m s⁻¹, movement of the

body of the bat (as indicated by movement of the nose) was approximately steady, and the wingtip described a near-sinusoidal path (Fig. 1). Velocity (Fig. 1C) and acceleration (Fig. 1D) of the wingtip showed similar sinusoidal variations which, as expected, were out of phase with position (Fig. 1A, B) by approximately one-quarter and half a cycle, respectively. There was slight vertical movement of the body (indicated in Fig. 1 by the position of the nose) and, as predicted, peak vertical body accelerations were concentrated in the downstroke, coinciding with the period of maximum lift (Rayner, 1986). Some movement of the nose was probably associated with pitch changes of the whole body. Horizontal acceleration appeared to be positive during the downstroke, but negative during the upstroke, suggesting that at this flight speed all thrust is generated during the downstroke, in agreement with observations of Aldridge (1987*b*) on a range of small microbats. However, this conclusion cannot be certain owing to the following: relatively low resolution of the video image; the poor accuracy of acceleration determined from digitized high-speed film or video (Rayner and Aldridge, 1985; Harper and Blake, 1989); and the possibility that pitching movements of the whole body may obscure gross accelerations.

The bats flew continuously in the small cage, usually turning in flight (flapping or gliding) at either end of the cage, and gliding in the middle. Of the 53 flights analysed in the small cage, 19 contained glides, usually one per flight, with a total of 24 glides recorded from 53 passes totalling 22.7 s of recording time. When flapping, average duration for one wingbeat was 88.10 ± 14.50 ms ($N=82$), giving an average wingbeat frequency of 11.35 Hz. Mean glide duration was 126.31 ± 42.43 ms ($N=16$), corresponding to an average of 1.43 wingbeats. Total time spent gliding during the 22.7 s of tape analysed was calculated as 3.03 s, or 13.36 % of total flight time.

In the larger cage, a different bat flew with a mean wingbeat period of 89.14 ± 9.44 ms ($N=14$), giving an average wingbeat frequency of 11.22 Hz (no different from the bat in the smaller cage). This bat spent 13.43 % of time gliding, a result remarkably similar to that for the other bat in the smaller flight cage.

Six glides in the smaller flight cage out of a total of 53 were examined closely. In these glides the wingbeat cycle was halted halfway through the downstroke, following which the wings were held outstretched through the glide with a slight positive dihedral angle (estimated from lateral view as $15\text{--}20^\circ$). At the onset of a typical glide the bat performed a normal upstroke, then began the downstroke, halting, and holding, the wings just above the horizontal (Fig. 2). During this part-downstroke, lift generation was apparently less than during a normal flapping downstroke, since vertical acceleration of the body was relatively small, albeit positive (Fig. 2D). Velocity and acceleration traces revealed a rapid cessation of motion followed by the assumption of a steady gliding position (zero vertical acceleration) for the remainder of the trace. Flapping flight later resumed with the bat raising the wings from the mid-position, performing in effect the second half of an upstroke. This pattern of transitions was the same in all straight glides.

The glide analysed in Fig. 2 was not steady, and although the bat was flying at

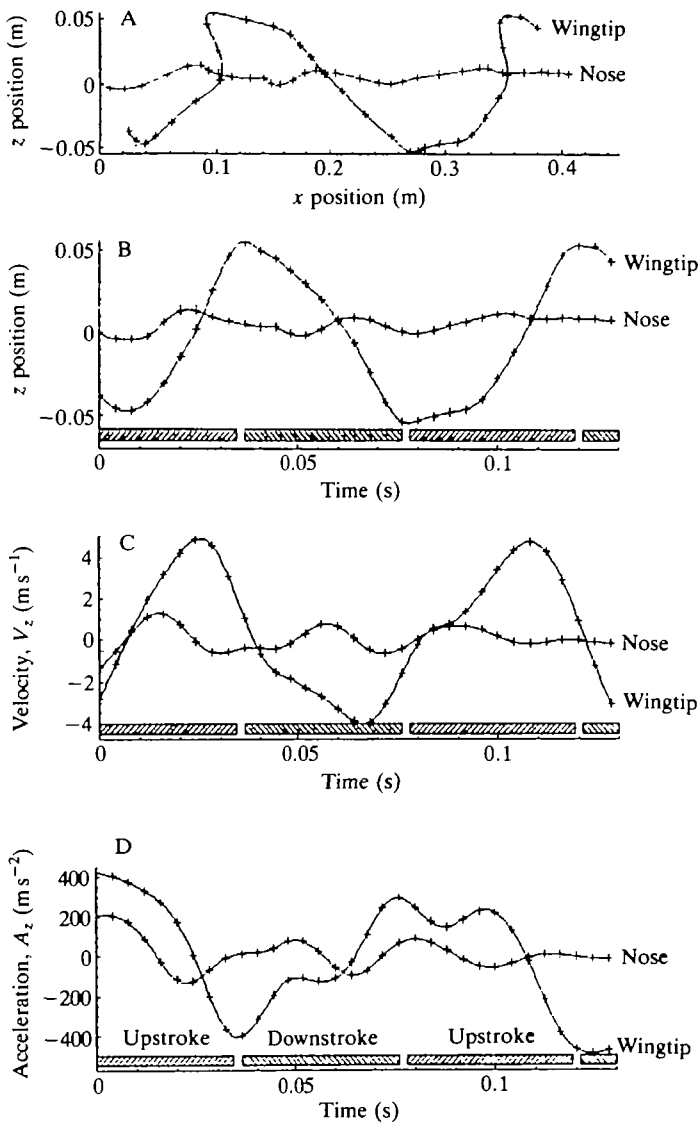


Fig. 1. Wingbeat kinematics of a normal wingbeat of the pipistrelle bat in flapping flight at 2.84 ms^{-1} , showing movements of the nose and proximal (right) wingtip. (A) Lateral view as digitized, showing horizontal and vertical position; (B) vertical position against time, (C) vertical velocity (V_z ; ms^{-1}); and (D) vertical acceleration (A_z ; ms^{-2}). Up- and downstrokes are defined for the purpose of this paper by the sign of the vertical velocity V_z . The body (as indicated by movement of the nose) rises slightly during the downstroke, although some of this movement may reflect pitching of the entire body. The 'pause' in vertical velocity V_z at time 0.085–0.095 s represents the phase at the beginning of the upstroke when the wing is being flexed forwards and supinated prior to accelerating upwards. The increase in A_z of the nose at this point is more likely to represent a pitch-up movement than a vertical acceleration, since it is accompanied by negative A_x . Shaded bars parallel to the time axis indicate the phases of the wingbeat.

close to the optimum (i.e. minimum sink) glide speed, its glide angle of 13.9° was considerably higher than expected from theory. The minimum sink glide speed is calculated as 4.0 m s^{-1} (model of Tucker, 1987); with a vertical sink speed of -0.365 m s^{-1} this corresponds to a glide angle of 5.2° . During the glide, body

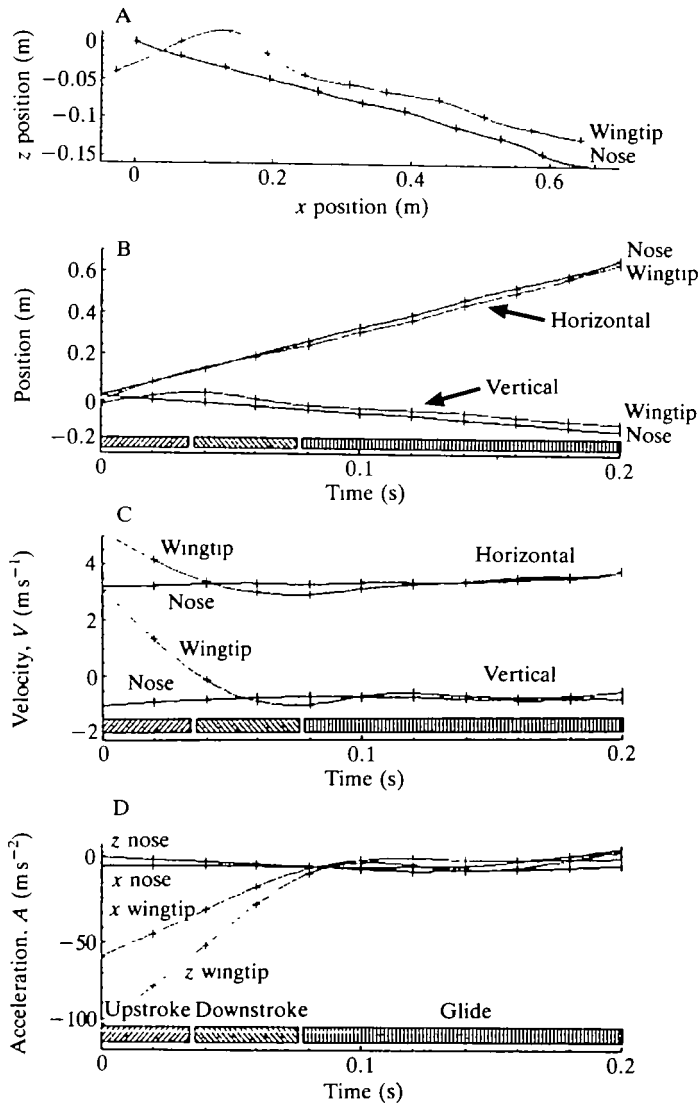


Fig. 2. Kinematics at the onset of a glide, showing movements of the nose and proximal (right) wingtip against time. (A) Lateral view as digitized, showing horizontal (parallel to long axis of flight cage, and approximately parallel to flight path) and vertical position; (B) horizontal and vertical positions; (C) horizontal and vertical velocities (V_x, V_z); and (D) horizontal and vertical accelerations (A_x, A_z). The glide begins at approximately $t=0.09$ s. Shaded bars parallel to the time axis indicate the phases of the wingbeat and of the glide.

accelerations were much smaller than when flapping, but they were not zero, and the nose of the bat accelerated forwards (from 3.3 to 3.7 m s^{-1} from time 0.14 to 0.2 s) and downwards (-0.82 to -0.85 m s^{-1} in the same interval). The total acceleration of the nose was substantial (about 6 m s^{-2}), but only a fraction of this can be explained by the steepness of the glide angle. The bulk of this apparent change of speed was associated with a pitch down movement of the body axis which caused the head to move downwards and forwards. The acceleration of the centre of gravity was much less, but could not be measured owing to the low resolution of the video image.

Because of drag, a gliding bat must either lose speed or lose height. In the glide described here, the bat chose to descend more rapidly than necessary: not only was potential energy expended against drag, but potential energy was also converted to kinetic energy by increasing speed. Height was regained during the subsequent flapping phase so that the bat maintained a constant overall speed and height.

In several cases the bat executed a turn while gliding, and in one such gliding turn the bat initiated the glide halfway through the upstroke.

Discussion

This analysis reports the first experimental observation of gliding flight in a microchiropteran bat. The pipistrelles were gliding for only 13.4% of their time in the flight cages, and the glides were always of brief duration, comparable to between 1 and 2 wingbeats. The bats were flying at between 2.5 and 4 m s^{-1} , which is somewhat slower than the speed used by foraging bats in the wild (4.5 m s^{-1} on average: Jones and Rayner, 1989), and is also below the estimated flight speed for a minimum sink glide (4.0 m s^{-1}). When an animal is flying this slowly, it can improve its glide performance (reduce the glide angle and/or the rate of height loss) by *increasing* speed. For this reason glides in the wild may be longer, and may constitute a greater proportion of total flight time, than those we observed in the laboratory.

Even so, pipistrelles are unlikely to glide as much as ecologically 'similar' aerial feeding birds such as swallows and martins. The percentage of flying time spent flapping has been reported as 79% in the sand martin *Riparia riparia* and as 46% in the house martin *Delichon urbica* (Westerterp and Bryant, 1984). Glides forming such a large proportion ($20\text{--}55\%$) of total flight time would be obvious from visual observations of wild pipistrelles. Although the pipistrelle has a lower wing loading than both of these hirundines, it is smaller and has a lower aspect ratio (Norberg, 1986); when flying under natural conditions it is not observed to glide as extensively as do the birds. The larger flight cage was similar in dimensions to the space used by some pipistrelles patrolling foraging beats in the wild (G. Jones, unpublished observations), and it would be reasonable to expect that in the wild also this species might spend about 85% of its time in flapping flight.

During searching flight in microbats a single echolocation pulse is generally emitted on each wingbeat (Suthers *et al.* 1972; Schnitzler, 1971; Heblich, 1986)

and pulse emission is synchronized with the final phase of the upstroke (Heblich, 1986); at this time mechanical forces at the wing root are greatest and activity of the pectoralis major muscle depressing the wing is most intense (Rayner, 1986). Studies of echolocation in wild pipistrelles show that the distribution of interpulse intervals is bimodal, with a major peak corresponding to one wingbeat cycle [80 ms in *P. pipistrellus* (A. M. Hollyfield, unpublished results), 100 ms in *P. kuhli* (Schnitzler *et al.* 1987)], and a grouping of interpulse intervals around the time expected to complete two wingbeats (7.4 % of intervals in *P. pipistrellus*, about 25 % in *P. kuhli*). In view of the results presented here, we question the interpretation that these longer interpulse intervals represent wingbeats without sound emissions, with the implication that the bats flap their wings continuously (Schnitzler *et al.* 1987): we propose it is more probable that such longer intervals are associated with short glides during which no sound is emitted. In a gliding bat flight muscles do not contract and compress the thorax, and therefore presumably the respiratory cycle differs in timing and/or in airflow magnitude from that in flapping bats; it would therefore not be surprising if, while gliding, echolocation calls either cannot be emitted or are very much less intense than while flapping.

This may explain why glides are terminated by completion of an upstroke, and hence soon after by *depressing* pectoralis activity, with associated exhalation and the opportunity for pulse emission; if pulses are emitted on the upstrokes preceding and immediately following a glide, and if the glide duration is around 1.4 times the wingbeat period (as measured here), the interval between pulses will be close to the period of two wingbeats, as recorded in the field (above). Bats must echolocate at frequent intervals to obtain information about potential prey and obstacles around them, and they may be constrained from frequent gliding because of the close mechanical correlation between wingbeat and sound emission. Equally, the main perceptual sense of birds is vision, which is active continuously and is not constrained by wingbeat kinematics. The fact that microchiropteran bats apparently glide less frequently and for shorter periods than birds of similar size emphasizes how frequent pulse emission is a major constraint on flight activity in hunting bats.

The glides reported here were not steady. We cannot rule out the possibility that pipistrelles are capable of a sustained steady glide at or near the minimum sinking speed, but this was not observed. Rather, by holding the wings at a small dihedral angle, and possibly also by shortening the wings as suggested by Tucker (1987) (we could not distinguish from the video if this occurred), the bat reduced the mean lift/drag ratio, and descended rapidly, but still at a rather low flight speed. In addition to shortening the effective wingspan, the positive dihedral angle improves stability during the glide.

We propose three linked hypotheses for the relative steepness of the glides.

First, there is no reason to expect steady glides during undulating flight: the energetic advantage of this mode of flight is based on periodic interchange between kinetic and potential energy (Rayner, 1985), and larger and more rapid potential/kinetic energy transfers may increase the energy savings attainable.

Second, non-steady glides may permit a more gradual transition between ascending flapping (increasing potential and decreasing kinetic energy) and descending gliding (decreasing potential and increasing kinetic energy) phases. On the basis of the above two hypotheses we would predict similar steeper and unsteady gliding behaviour in birds.

Third, the pipistrelles in the flight cages are flying at speeds appreciably below the minimum sink speed. In the wild (Norberg and Rayner, 1987) low speeds enable the bat to turn without stalling, and to maximize the chance of locating and catching flying prey. At the theoretical minimum sink speed (4.0 m s^{-1}) the lift coefficient in the shallowest glide (5.2°) is 0.84; at 3 m s^{-1} the shallowest glide angle is 8.6° , but the lift coefficient of 1.49 is much higher. Thus, very shallow glides at low speeds are feasible but may demand very high lift coefficients, and therefore risk of stall and loss of manoeuvrability. A steeper glide may be preferable because it permits air speed to remain low without risk of stall; however, since the bat accelerates during the steep glide the gliding phase must be brief.

Further support for the third hypothesis can be deduced from turning behaviour: we noted that the pipistrelles sometimes glided while turning. This contrasts with the situation in other microbats (*Plecotus auritus*, Rayner and Aldridge, 1985; *Myotis daubentoni*, Jones and Rayner, 1988; various species, including *P. pipistrellus*, Aldridge, 1987a), in which the bats usually flapped their wings throughout the turn. [Aldridge may not have seen gliding turns in *P. pipistrellus* because his flight cage was relatively small (0.6 m cross-section).] The feeding habits of most aerial-feeding microchiropteran bats place an emphasis on manoeuvrability (small turning circle), and most of their prey is caught on or close to surfaces, and the bats habitually fly in confined spaces. In contrast to the other species in which turns have been studied, pipistrelles feed on free-flying insects away from clutter in more open habitats, and this habit requires agility (the ability to turn quickly) rather than manoeuvrability; compared with microbats of similar size, pipistrelles achieve improved agility by their comparatively high aspect ratio and wing loading (Norberg and Rayner, 1987). Their turning circle is therefore relatively broad, but they can turn without significant loss of height and speed (cf. *Plecotus auritus*, with lower aspect ratio and wing loading; Rayner and Aldridge, 1985; Aldridge, 1987a).

In pipistrelles, rapid turns require the animal to bank steeply, and impose high aerodynamic forces on the wings. In one turn studied the bat banked at approximately 60° , and during the turn would have experienced a steady lateral acceleration of approximately $2g$ (where $g=9.81 \text{ m s}^{-2}$ is the acceleration due to gravity). At a bank angle of 80° in a sharper turn this acceleration would be increased to approximately $6g$. Gliding in turns may be a response to these dramatic increases in forces on the wings, removing the additional large dynamic forces which would be generated by flapping. Bats with larger wings (lower wing loading), such as the other microbats studied, can turn more sharply while maintaining lower angles of bank and, owing to their larger wing area, are mor

likely to be able to accommodate the transient aerodynamic forces of a flapping turn. We therefore predict that adaptations for agility, such as reduction in relative wing size, will be associated with an increasing tendency to glide when turning.

Undulating flight has been shown to be capable of reducing the cost of flight significantly (Rayner, 1985). One explanation for the flight behaviour reported here is reduction of the energy cost of foraging in the pipistrelle bat. Gliding – and therefore undulating flight – may be less important to other British microbats which have relatively larger wings, and hence lower mechanical power in flight, and less opportunity for energy saving. Gliding may also be less attractive in other bats with lower aspect ratio, and therefore poorer gliding performance.

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