

## TURNING FLIGHT OF BATS

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### SUMMARY

The turning flight of six microchiropteran bat species is described. The bats' abilities to turn tightly were determined by their abilities to fly slowly and to generate high lateral accelerations. *Rhinolophus ferrumequinum* developed high lateral accelerations by flapping its banked wings while flying at very low speed. *Plecotus auritus* turned at relatively low speed and at low lateral acceleration. The other species were all moving fast as they turned and generated lateral accelerations either by developing high bank angles or by flapping their wings with low bank angles. There was a significant correlation between wing loading and turning curvature, indicating that low wing loadings improve manoeuvrability.

### INTRODUCTION

Research on bat flight has concentrated on horizontal or hovering flight (e.g. Eisentraut, 1936; Norberg, 1976*a,b*; Altenbach, 1979; Aldridge, 1986), but for most bats a large portion of the time spent flying will be spent in pursuit of prey, avoiding obstacles and predators, and landing. Norberg (1976*c*) described manoeuvres in the bats *Nyctalus noctula* and *Otomops martiensseni*, while Altenbach (1979) described various manoeuvres in *Desmodus rotundus*. Rayner & Aldridge (1985) have described a turn performed by *Plecotus auritus*.

Pennycuik (1975) defined turning radius in gliding animals as:

$$r = 2W / \rho C_L S g \sin \theta, \quad (1)$$

where  $\rho$  is air density,  $C_L$  is lift coefficient,  $S$  is wing area,  $g$  is the acceleration due to gravity,  $W$  is weight and  $\theta$  is bank angle.

From equation 1 we can predict that, for any given lift coefficient, turning radius will be proportional to mass and wing loading; bats with low masses or wing loadings will turn tightly and have higher manoeuvrabilities. The aim of this study was to investigate the turning flight of six microchiropteran bat species, *Rhinolophus ferrumequinum* (Schreber), *R. hipposideros* (Bechstein) (Rhinolophidae), *Plecotus auritus* (L.), *Myotis mystacinus* (Kuhl), *M. daubentoni* (Kuhl) and *Pipistrellus*

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*pipistrellus* (Schreber) (Vespertilionidae), (1) to describe the mechanics of turning and (2) to elucidate the morphological parameters which are important in determining turning performance and therefore manoeuvrability and agility.

#### MATERIALS AND METHODS

##### *Morphological measurements*

The bats' relative sizes were defined by body mass ( $m$ ), while their wings were defined by two parameters, wing loading ( $Q_s$ ) and aspect ratio ( $R$ ) (Norberg, 1981) (Table 1).

##### *Training, photography and analysis*

The bats were trained to fly through an open-ended flight tunnel (2.0 m  $\times$  0.6 m  $\times$  0.6 m) (Aldridge, 1986). When they had mastered this simple procedure, a barrier was placed across the flight path forcing them to turn. For each individual several turns were photographed using the two-camera multiframe technique described by Rayner & Aldridge (1985). The number of turns photographed varied according to the species, but in no case were fewer than five recorded. For each turn six parameters were either measured or calculated; maximum curvature (curvature being the inverse of radius) achieved during the turn ( $k_{\max}$ ), the speed ( $V_k$ ) at  $k_{\max}$ , the maximum rate of change of curvature ( $\dot{k}_{\max}$ ), the lateral acceleration ( $a_l$ ) at  $k_{\max}$ , the vertical acceleration ( $a_v$ ) at  $k_{\max}$  and the maximum bank angle ( $\theta$ ). From the turns recorded for each bat, the ones with the greatest  $k_{\max}$  were chosen for further analysis.

The lift coefficients in Table 2 were calculated using equation 1 and are therefore the lift coefficients which would have been developed if the bats had been performing gliding turns. High values indicate a powered turn, the observed curvature not being possible at the observed speed unless the wings had been flapped.  $C_L$  values between 1 and 2 indicate that the observed turn could have been performed while the animal was gliding.

Table 1. *Morphological parameters for individuals of seven microchiropteran bat species*

Species	$m$ (kg)	$b$ (m)	$S$ (m <sup>2</sup> )	$Q_s$ (N m <sup>-2</sup> )	$R$
<i>Rhinolophus ferrumequinum</i>	0.0215	0.36	0.0223	9.45	5.8
<i>R. hipposideros</i>	0.0065	0.24	0.0094	6.78	5.9
<i>Plecotus auritus</i>	0.0095	0.26	0.0128	7.28	5.1
<i>Myotis mystacinus</i>	0.0059	0.23	0.0080	7.23	6.6
<i>M. daubentoni</i>	0.0095	0.24	0.0107	8.71	5.4
<i>Pipistrellus pipistrellus</i>	0.0060	0.21	0.0069	8.53	6.5

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

Table 2. The best turning performance parameters for individuals of seven microchiropteran bat species

Species	$k_{\max}$ ( $\text{m}^{-1}$ )	$V_k$ ( $\text{m s}^{-1}$ )	$\dot{k}_{\max}$ ( $\text{m}^{-1} \text{s}^{-1}$ )	$a_v$ ( $\text{m s}^{-2}$ )	$a_l$ ( $\text{m s}^{-2}$ )	$\theta$ (degrees)	$C_L$
<i>Rhinolophus ferrumequinum</i>	115.0	0.29	478.0	2.27	9.55	51.7	22.90
<i>R. hipposideros</i>	52.3	0.58	326.2	8.53	17.56	89.5	5.75
<i>Plecotus auritus</i>	52.2	0.24	273.2	1.49	2.99	51.9	1.57
<i>Myotis mystacinus</i>	36.8	0.51	247.2	6.18	9.67	75.0	4.77
<i>M. daubentoni</i>	28.8	0.54	173.2	4.36	8.57	57.5	4.58
<i>Pipistrellus pipistrellus</i>	18.5	0.71	138.8	2.42	9.12	51.9	3.30

Theoretical values for lift coefficient ( $C_L$ ) during the turns were calculated using equation 1 and therefore imply that the bats turn without beating their wings.

$k_{\max}$ , maximum curvature during the turn;  $V_k$ , speed at  $k_{\max}$ ;  $\dot{k}_{\max}$ , maximum rate of change of curvature;  $a_v$ , vertical acceleration at  $k_{\max}$ ;  $a_l$ , lateral acceleration at  $k_{\max}$ ;  $\theta$ , maximum bank angle.

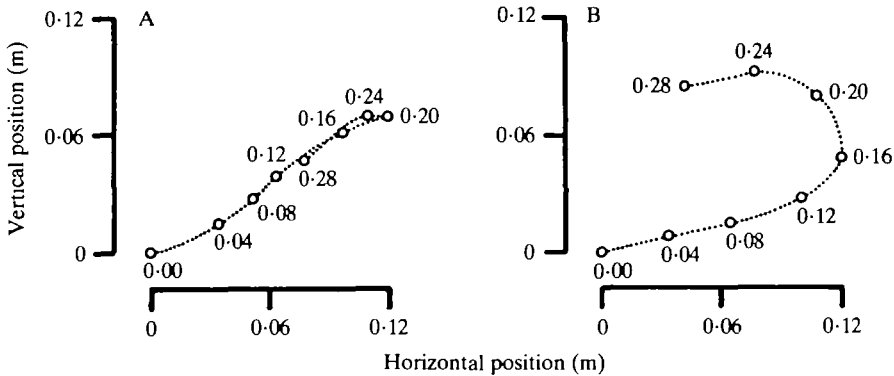


Fig. 1. (A) Lateral and (B) dorsal projections of the flight path of a turning bat, *Myotis mystacinus*. Numbers by each point give time (s) after start of observations.

## RESULTS

All the turns recorded in this study were essentially similar to the turn described for *P. auritus* by Rayner & Aldridge (1985). The bats initiated their turns by flying upwards and losing speed (Figs 1, 2). Curvature increased gradually, reaching a maximum as lateral acceleration reached a maximum, and speed and vertical acceleration a minimum (Figs 2, 3). When  $k_{\max}$  was reached, the bats began to lose height with increasing speed as a result (Figs 1, 2). In *M. mystacinus*, vertical and lateral accelerations remained almost constant as curvature decreased (Fig. 2). In the turn described for *P. auritus* by Rayner & Aldridge (1985), the increase in speed was accompanied by an increase in vertical acceleration and a decrease in lateral acceleration, which may be a more normal situation.

$k_{\max}$  was significantly correlated with mass ( $r = 0.78$ ,  $P < 0.05$ ,  $b = 0.98$ ) but not with wing loading ( $r = 0.11$ ,  $P > 0.05$ ,  $b = 0.52$ ) when all species were considered. However, if *R. ferrumequinum* was excluded from the analysis the correlation

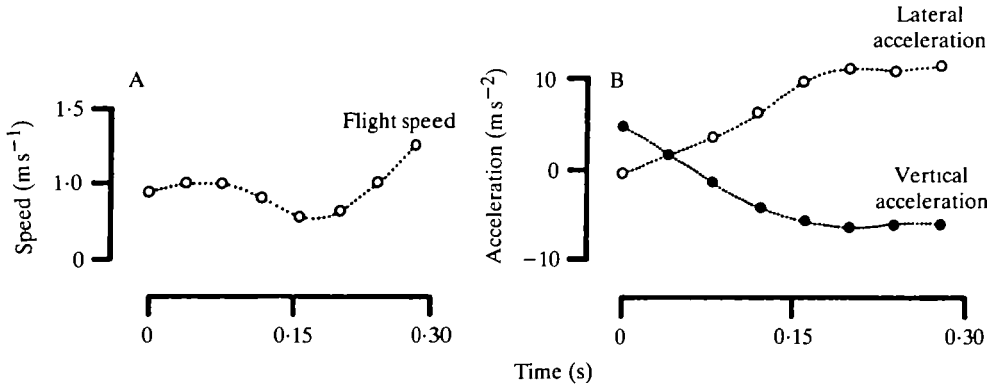


Fig. 2. (A) Speed and (B) lateral (open circles) and vertical accelerations (closed circles) for the turning bat *Myotis mystacinus*.

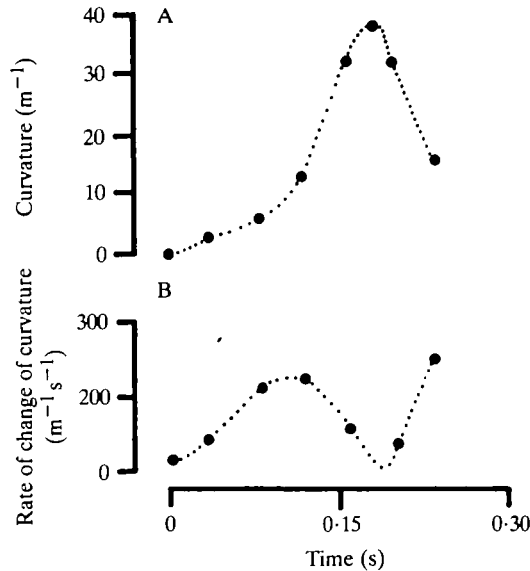


Fig. 3. (A) Curvature ( $1/r$ ) and (B) rate of change of curvature for a turning bat, *Myotis mystacinus*.

between curvature and wing loading became significant ( $r = -0.86$ ,  $P < 0.01$ ,  $b = 0.52$ ) (Fig. 3), although the slope of the line is lower than that predicted from equation 1 (Fig. 4).  $\dot{k}_{\max}$  was significantly correlated with wing span ( $r = 0.84$ ,  $P < 0.01$ ,  $b = 1.99$ ) (Fig. 4B).

#### DISCUSSION

*R. ferrumequinum* turned in a manner mechanically similar to that employed by helicopters. The bat reduced its flight speed almost to zero before  $k_{\max}$  was reached,

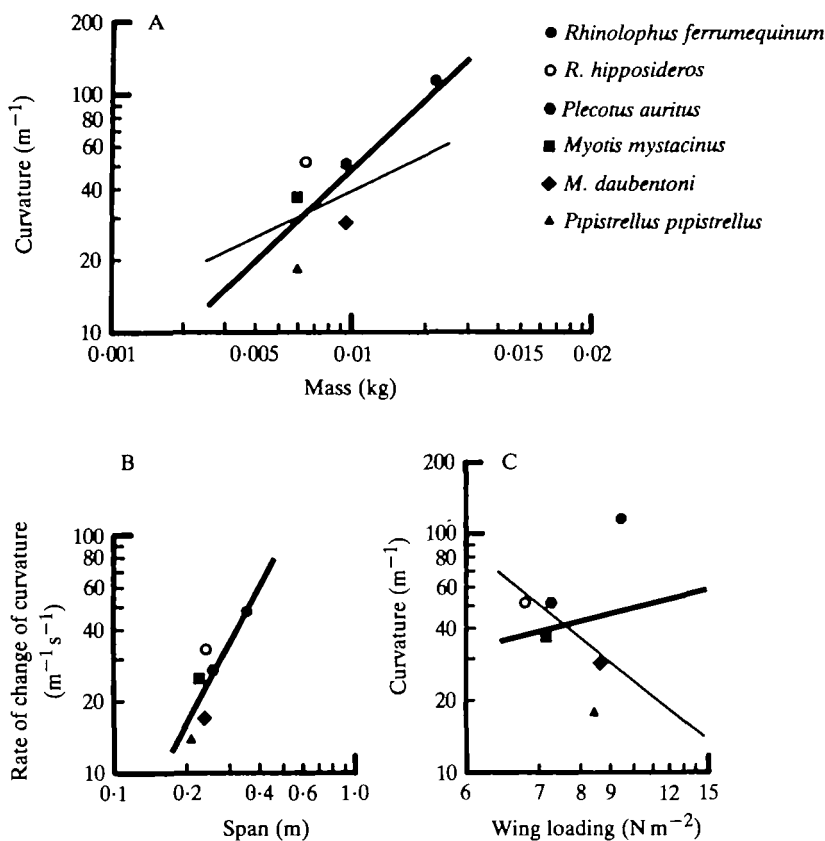


Fig. 4. Double log plots showing (A) maximum curvature against mass, (B) rate of change of curvature against wing span and (C) maximum curvature against wing loading. Thick lines are the regression lines for all species and thin lines are the regression lines excluding *Rhinolophus ferrumequinum*.

and by flapping its banked wings generated weight support and a high enough centripetal force to turn tightly. After achieving  $k_{max}$  the bat accelerated by losing height, thus converting its potential energy into kinetic energy. This bat's high  $C_L$  value indicates that a gliding turn of the observed curvature and speed could not have been performed. The combination of low flight speed and relatively high lateral acceleration permitted *R. ferrumequinum* to turn more tightly than any of the other species.

The lift coefficient for *P. auritus* was 1.57 indicating that this bat could probably perform a gliding turn of the observed curvature and speed. This suggests that *P. auritus* did not have to increase wing angular velocity when turning to generate the lift necessary to support its weight and to develop a centripetal force. *P. auritus* is essentially performing an unpowered turn, mechanically equivalent to a gliding turn to which equation 1 applies.

*R. hipposideros*, *M. mystacinus*, *M. daubentoni* and *P. pipistrellus* all approach the obstacle at quite high speeds. To make the turn within the space available

*R. hipposideros* and *M. mystacinus* generate relatively high lateral accelerations by banking and beating their wings. This procedure produces the desired centripetal forces, but at the expense of weight support, as indicated by their high downward accelerations. *M. daubentoni* and *P. pipistrellus*, however, do not develop high bank angles to generate high centripetal forces, nor do they perform high-powered turns similar to that performed by *R. ferrumequinum*, and as a result they do not turn particularly tightly. They both have relatively high lift coefficients, indicating that they had to flap their wings to perform the observed turns.

It is clear that the bats, with the possible exception of *P. auritus*, were performing powered turns. Therefore we would not expect there to be a clear relationship between morphology and turning performance (as predicted from equation 1). By flapping their wings at different angular velocities these bats can modify the lift generated to enable them to turn tightly. Nevertheless, the exclusion of *R. ferrumequinum* showed that there was a relationship between wing loading and curvature as predicted. The exclusion of *R. ferrumequinum* is justifiable on the grounds that it is employing a different method of turning, which allows it to turn tightly and overcome some of the morphological limitations predicted by equation 1. For the other species the results suggest that, even if the bats perform powered turns, those with low wing loadings will be able to perform tighter manoeuvres at lower energetic cost than bats with high loadings. This difference might have important implications for foraging habitat selection. Although bats like *R. ferrumequinum* can perform tight turns, the results suggest that these turns will be energetically more expensive than tight turns performed by bats such as *P. auritus*. If foraging bats attempt to optimize net energy gain, we might predict that *P. auritus* could afford to forage where tight manoeuvres are more often required than could *R. ferrumequinum*, even though *R. ferrumequinum* seems the more manoeuvrable.

Agility can be defined as the ability to carry out manoeuvres quickly.  $\dot{k}_{\max}$  is a possible measure of this performance parameter, as it represents a bat's ability to initiate a turn. On this basis, *R. ferrumequinum* is the most agile and *P. pipistrellus* the least agile of the species in this group.

To initiate a turn a bat has to generate a moment about its longitudinal axis. This moment will be larger in animals with long wings, thus explaining why  $\dot{k}_{\max}$  is significantly correlated with wing span. It has been suggested that long wing span will tend to reduce  $\dot{k}_{\max}$ , long wings having higher moments of inertia than short wings, thus making roll initiation more difficult. In this group there is a highly significant positive correlation between wing span and wing area, and I would suggest that the high aerodynamic roll moments generated by large wings more than compensate for the high moments of inertia associated with long wings. In general, however, long wings are probably not good adaptations for agility, explaining why bats thought of as agile (e.g. some molossids) have relatively short wings (Norberg, 1981, 1986).

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