Aerodynamic constraints on flight ontogeny in free-living greater horseshoe bats, *Rhinolophus ferrumequinum*

Patricia M. HUGHES & Roger D. RANSOME*, Gareth JONES

Department of Zoology, University of Bristol, Woodland Road, Bristol BS8 1UG, UK

*Moorings, 14B Dursley Road, Dursley, Gloucestershire GL11 6PP, UK

Abstract: Changes in wingshape and wingsize during development were recorded by using a photographic technique at a wild colony of the greater horseshoe bat, *Rhinolophus ferrumequinum*. Analyses of these changes were used to draw conclusions about the ontogeny of flight, in particular concerning their relevance to the time of the first flight.

Introduction

The first few weeks in the life of a bat see profound changes in the animal, most obviously in the structure of the wings and in the ability to echolocate. The time at which the bat first starts to flutter around in the roost varies according to species, with wing stretching occurring much earlier and the initial flights outside the roost following perhaps a week or so later. In the case of the greater horseshoe bat, the juveniles are able to fly 15 days after birth, and regularly leave the roost from the age of around 24 days onwards (Ransome, unpublished observations).

Paralleling these changes in flying ability are changes in echolocation calls, and in lower frequency vocalisations. Many baby bats emit distress or identification calls which enable the mother to identify her offspring from a cluster of other juveniles (see, for example, Thomson *et al*, 1984; Matsumura, 1981). As the need for acoustic orientation arises with the onset of flight in the bat, echolocation calls become more refined and adult-like in structure. Konstan-

---

REFERENCES

Brown, P. E., T. W. Brown & A. D. Grinnell, 1983: Echolocation, development and vocal communication in the lesser bulldog bat, *Noctilio albiventris*. *Behav. Ecol. Sociobiol.* 13: 287—292.

Buchler, E. R., 1980: The development of flight, foraging and echolocation in the little brown bat, *Myotis lucifugus*. *Behav. Ecol. Sociobiol.* 6: 211—218.

Jones, C., 1967: Growth, development and wing loading in the evening bat, *Nycticeius humeralis* (Rafinesque). *J. Mamm.* 48 (1): 1—19.

Konstantinov, A. I., 1973: Development of echolocation in bats in postnatal ontogenesis. *Period. Biol.* 75: 13—19.

Krátký, J., 1981: Postnatale Entwicklung der Wasserfledermaus, *Myotis daubentoni* Kuhl, und bisherige Kenntnis dieser Problematik im Rahmen der Unterordnung Microchiroptera (Mammalia: Chiroptera). *Fol. Mus. Rer. Natur. Bohem. Occident. Pizen, Zool.* 16: 3—34.

Matsumura, S., 1981: Mother—infant communication in a horseshoe bat (*Rhinolophus ferrumequinum nippon*): vocal communication in three-week-old infants. *J. Mamm.,* 62 (1): 20—28.

Mohr, E., 1932: Haltung und Aufzucht des Abendseglers (*Nyctalus noctula* Schreb.). *Zool. Garten* 5: 106—120.

Norberg, U. & J. M. V. Rayner, 1987: Ecological morphology and flight in bats (Mammalia: Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Phil. Trans. R. Soc. Lond.* B (316): 335—427.

O'Farrell, M. J. & E. H. Studier, 1973: Reproduction, growth and development in *Myotis thysanodes* and *M. lucifugus* (Chiroptera: Vespertilionidae). *Ecology* 54: 18—30.

Pagels, J. F. & C. Jones, 1974: Growth and development of the Freetailed bat, *Tadaria brasiliensis cynocephala* (Le Conte). *Southwest. Nat,* 19 (3): 267—276.

Ransome, R. D., 1971: The effect of ambient temperature on the arousal frequency of the hibernating Greater horseshoe bat, *Rhinolophus ferrumequinum* in relation to site selection and the hibernation state. *J. Zool, Lond.* 164: 353—371.

Ransome, R. D., 1973: Factors affecting the timing of births of the greater horseshoe bat (*Rhinolophus ferrumequinum*). *Period. Biol.* 75: 169—175.

Rayner, J. M. V., 1986: Vertebrate flapping flight mechanics and aerodynamics and the evolution of flight in bats. *Biona-report* 5: 27—74.

Smith, J. D., 1977: Comment on flight and the evolution of bats. *In*: Major problems in vertebrate evolution. *Ed.*: M. K. Hecht, P. C. Goody and M. Hecht, pp. 427—437. Plenum Press.

Thomson, C. E., M. B. Fenton and R. M. R. Barclay, 1984: The role of infant-isolation calls in mother—infant reunions in the little brown bat, *Myotis lucifugus*. *Can. J. Zool.* 63: 1982—1988.

Yokoyama, K. & T. A. Uchida, 1979: Ultrastructure of Postembryonic development of the Pectoral Muscles in the Japanese Lesser Horseshoe Bat, *Rhinolophus cornutus cornutus* from the Standpoint of Adaptation for Flight. *J. Fac. Agr. Kyushu Univ.* 24 (1): 49—63.

Yokoyama, K., R. Ohtsu & T. A. Uchida, 1979: Growth and LDH isozyme patterns in the pectoral and cardiac muscles of the Japanese Lesser horseshoe bat, *Rhinolophus cornutus cornutus,* from the standpoint of adaptation for flight. *J. Zool, Lond.* 187: 85—96.

tinov (1973) described the development of echolocation in the greater horseshoe bat, particularly the transition from predominantly oral to nasal emission.

By careful measurement of various wing parameters and other values, together with description of individual calls, it is possible to assess the extent to which wing morphology, the ability to echolocate and mechanical requirements constrain the development of the young bat. It is necessary to know the precise ages of the study animals, and preferable to use a wild colony, since development of bats has been shown to be altered in captivity (e.g. Buchler, 1980, Brown et al., 1983). Both these criteria have been met in this study, in which the development of the greater horseshoe bat is described from the date of birth to the age of 23 days.

Methods

Visits to the study site, a large, derelict house in Gloucestershire, were made between 8th and 27th of July 1987. The house is used by bats as a hibernaculum and a breeding site (Ransome, 1973). At the time of the present work, approximately 25 females were breeding. The colony is very well established, and has been observed for the past 28 years, with a ringing programme of the babies being conducted more recently, making this an ideal and unique study colony.

Juveniles were removed from the breeding attic immediately after all of the adult bats had been counted out as they exited to feed at dusk. The ring number of each juvenile was noted, and one wing extended and photographed against a scaled background. The bat was then held close to a Racal Store-4DS instrumentation recorder linked to a QMC S-200 bat detector until several calls were emitted. Simultaneously, other bats were being weighed, and forearm measurements taken, with newly-borns also being ringed. Once all the bats captured had passed through these processes, they were returned to the attic to await the return of the adults, the entire procedure thus lasting less than 40 minutes.

On development of the film, wing outlines were taken for each individual by tracing projections of the negatives. These were then digitised by using a Summagraphics Bit Pad One linked to a BBC Master microcomputer, and direct measurements taken, to give the wing parameters defined by, for instance, Norberg & Rayner (1987) (see below).

The recordings of echolocation calls were analysed by playing them via a QMC period-pitch-frequency meter into a Tektronix 5103N oscilloscope, with a signal generator to provide frequency calibration. The frequency and duration of the calls could then be recorded from the screen.

Results

CHANGES IN WING FORM.

Changes in the shape of the growing wing (fig. 1) are better described in terms of the specific parameters generally used to define bat wings. In all figures, the time of the first flight is denoted by 'f', that of first flights outside the roost by 's', and the value for the adult bat by 'a', with standard deviation bars. Table 1 shows the regression equations obtained for the relations between the parameters and age together with correlation coefficients, probabilities, and

Fig. 1. Diagram to show the changes in the wing shape during development. Wing outlines are shown for the ages of 1, 5, 15 and 22 days, together with an adult wing. Various wing parameters are also shown; the hatched area on the 1 day old bat represents 1/2 wing area, and on the adult outline, handwing (HW) and armwing (AW) areas. Hand-wing and armwing length are indicated, together with 1/2 span. Note the increase of handwing area and length relative to those of the armwing.
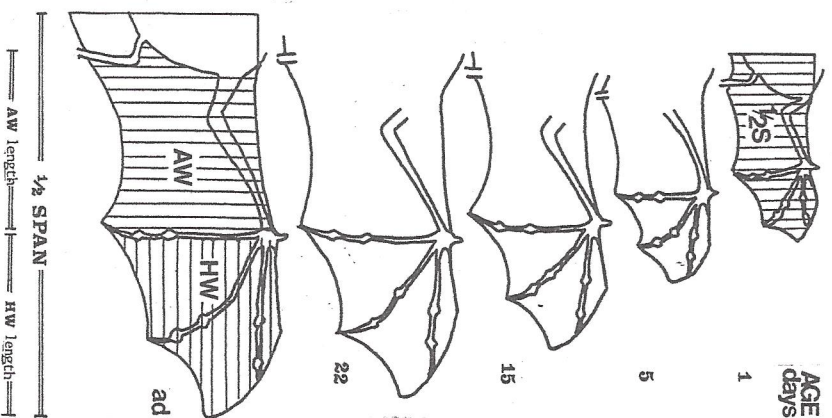
numbers of observations: most relations are approximately linear and are treated as such here.
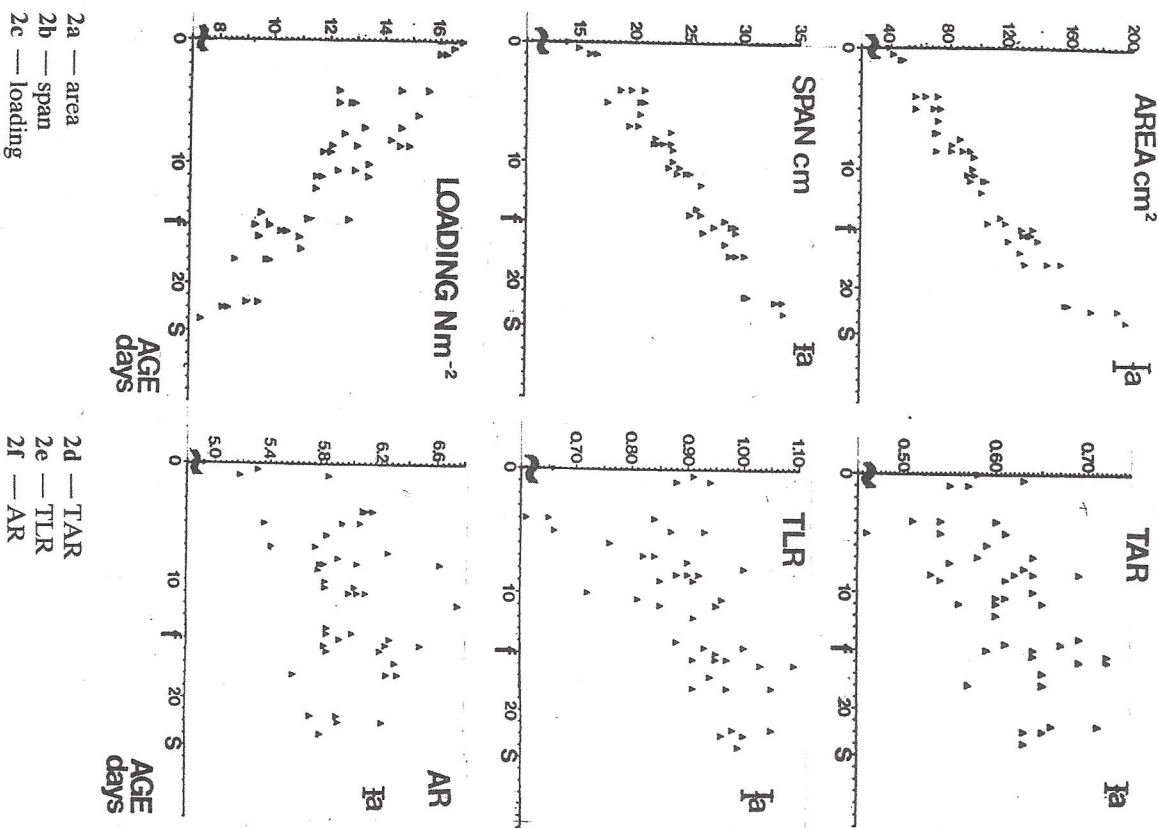
Wing area (S)

All surfaces used in the production of lift are included in wing area; the tail membrane, and also the area of the body between the wings, excluding the head. At birth, wing area is approximately 35 cm², the regression equation for fig. 2a being shown in table 1. The graph shows a tendency to be curvilinear, with the rate of increase of area accelerating as the bat grows.

Wingspan

The wingspan is the distance between the extended wingtips; it is approximately 16 cm at birth. The relation with age is more linear than that for area, as seen in fig. 2b and table 1.

Wing loading

Wing loading is the weight carried per unit area of wing, and an important factor in determining flight speed and power requirements for flying. Newly-

AREA cm² — 2a

SPAN cm — 2b

LOADING Nm⁻² — 2c

TAR — 2d

TLR — 2e

AR — 2f

AGE days

2a — area
2b — span
2c — loading
2d — TAR
2e — TLR
2f — AR

Figs. 2a—2f. Graphs of the relations of wing parameters with age. Time of first flight (f) and first sustained flight (s) are shown, together with the values for adult bats (a), with standard deviation bars. The relations are discussed in the text.

-born bats had a high wing loading, of around 16 Nm^{-2}, and there was a negative correlation with age (fig. 2c).

Tip area ratio (TAR)

The tip area ratio is defined as the area of the handwing (the area of wing membrane supported by the digits and therefore distal to the fifth digit), divided by the area of the armwing (proximal to the fifth digit, bounded by it, the leg, and the body). The TAR at birth was relatively high, at around 0.56. Although there is considerable scatter in fig. 2d, which was not reflected in the graphs of hand-wing and armwing growth (not published), TAR has been used for ease of interpretation. The linear increase of TAR with age tends to cease after approximately 15 days.

Tip length ratio (TLR)

Tip length ratio is defined as the length of the handwing (measured from the wingtip to thumb) to that of the armwing (from thumb to shoulder). The TLR at birth is approximately 0.77, and fig. 2e shows a similar pattern to the graph for TAR, with a marked drop in the rate of increase with age after around 15 days.

Aspect ratio (AR)

Aspect ratio is dimensionless, being the square of the wingspan divided by the wing area. The variation shown in fig. 2f is best described by a curvilinear relation, peaking at around 15 days, and falling thereafter, although there is a good deal of scatter.

TABLE 1 — *Relation of wing parameters with age (t, days). This table shows regression equations for the graphs in fig. 2, with their correlation coefficients and probabilities. Typical values for the adult bats are also given. (All cases n = 47, except adult values n = 10.)*

	Area (S, cm²)	Span (B, cm)	Loading (L, Nm^{-2})	TAR	TLR	Aspect ratio (AR)
regression equation	S = 35.0 + 6.03 t	B = 15.7 + 0.76 t	L = 16.0 − 0.35 t	TAR = 0.57 + 0.005 t	TLR = 0.77 + 0.01 t	—
correlation coefficient (r)	0.974	0.974	−0.910	0.574	0.668	—
probability (p)	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	—
adult values	203.32 ± 9.29	35.35 ± 1.01	—	0.73 ± 0.04	1.01 ± 0.06	6.15 ± 0.46

ECHOLOCATION ANALYSIS.

A brief analysis of the recordings made of the growing bats showed that the calls of juveniles differed from those of adults in both frequency and duration.

Initially, young bats emit calls both orally and nasally. The typical frequency of nasal call increased steadily, to a value of around 79.52 ± 0.89 kHz (n = 6) by the age of 15 days. The usual frequency of the adult greater horseshoe of 83 kHz was produced by the age of around 22 days. In addition to this, the duration of call increased steadily, with calls of hand-held bats lasting 40 to 50 ms by the age of 19 days. It is hoped that a more complete picture of the relation between echolocation and age will be published in the future.

Discussion

The bat is first capable of flight at the age of about fifteen days, and of more sustained flight at over 24 days of age; lactation continues for at least 45 days (Ransome, unpublished). The wings at these stages are therefore likely to possess properties that are more conducive to efficient flight than at those stages preceeding. In addition, it is logical to assume that the echolocation system is likewise improving.

Obviously, the wing is constantly increasing in area as the bat ages, giving a greater lifting surface, but to analyse this more subtly it is useful to consider TAR and TLR. Both increase as the bat grows, meaning that in effect the handwing is increasing relative in size to the armwing. Indeed, in some cases the TLR becomes greater than unity, when the handwing is longer than the armwing. The significance of this is that the handwing is used to produce the bulk of the thrust generated during the downstroke. Its size is therefore of greater importance as the need for flight arises.

Another parameter directly associated with wing area is wing loading. Despite the fact that the bat increases in weight as it grows, the wing loading decreases steadily and substantially. This means that the wing area increases in magnitude at a greater rate with age than does weight. At 15 days, the loading is 67 % of that at birth, and at 21 days merely 54 %, decreasing the power needed for flight, which is in the interest of the animal favouring the ability to forage efficiently as early as possible.

Flight performance is also influenced by aspect ratio. This value, as shown above, is determined by the wing area and the wing span. Both of these increase steadily with age. Aspect ratio, which is dimensionless, might therefore not be expected to change particularly with age. However, fig. 2f shows an initial increase up until the age of 12—15 days, and a subsequent decline. The changes in aspect ratio prior to flight are probably unimportant, and after the age of 15 days the mechanical and ecological pressures operating on the animal could well cause conformation to the aspect ratio of the adult.

The general trends quoted above are in agreement with those observed in other bats, for instance, the evening bat, Nycticeius humeralis, (Jones, 1967),

noctule Nyctalus noctula, (Mohr, 1932), and Daubenton's bat, Myotis daubentoni, (Krátký, 1981). In order to fly, it seems necessary for the TAR and TLR to have increased in value sufficiently for the handwing to provide the necessary thrust, and for the wing loading to have decreased to a value whereby flight is not too energy-expensive. These objectives are achieved during the first few weeks of development, when in addition to simple growth, preparations are being made for efficient flight, which go hand in hand with refinement of the echolocation system.

The wing parameters at various stages of this development can be briefly compared to those of the adult bat. Wing area is 17.2 % of the mean adult value at birth, rising to 61.7 % at the age of 15 days, and 88.4 % at the age of 24 days. These same values for wing span are 44.4, 76.7 and 98.0, for tip area ratio 78.0, 88.4 and 94.5, and for tip length ratio 76, 91.1 and 100 % respectively. The same comparisons cannot be made for wing loading, because the adult value varies so widely according to, for instance, time of year and body condition, nor for aspect ratio, because of the complex nature of the relation with age. Wing loading of wild adult females is observed to range between $8.7-16.6$ Nm^{-2} (Ransome, unpublished data).

Although not a mechanical limitation, the ability to echolocate is certainly necessary for practical flight. The calls produced by the baby bat are primarily social, acting as attractive calls to adult females. The echolocation calls develop gradually, and it is not until the age of 22 days that they are emitted at a similar frequency to that of the adults.

By the age of the first sustained flight, the bat is therefore presumably capable of producing echolocation calls that can be used in navigation: it would be interesting to know if they were also capable of prey capture. Associated neurological processes would not necessarily be fully functional. Mechanical constraints are also likely to be becoming less restrictive by this time, although if the phalanges and metacarpels are still lengthening, incomplete ossification may act as a mechanical. However, this study has not taken account of the changes in muscle physiology accompanying the onset of flight, as described, for instance, in the Japanese lesser horseshoe Rhinolophus cornutus cornutus by Yokoyama & Uchida (1979), also Yokoyama, Ohtsu & Uchida (1979).

The changes in wing shape that occur during the development of flight in the bat can be seen to be reminiscent of those envisaged during the evolution of bat flight (see, for instance, Smith 1977, Rayner 1986). This has far-reaching implications, and would merit further work in this, and other, species, to see how far the relation held, and whether it extends to other aspects of bat ontogeny.