work, as the standard methods for obtaining this information from diffusion profiles apply only to strictly binary systems[11].

Figure 2 shows the measured variation of $D(c)$ with concentration, based on profiles such as that in Fig. 1. A marked maximum in $D(c)$ towards the centre of the concentration range is apparent.

A prediction for the concentration dependence of $D(c)$ is provided by some recent analyses. As in the case of small molecules, the mutual diffusion coefficient may be written as the product of a mobility term and a thermodynamic term expressing the departure from ideality of mixing[12]. The thermodynamic term may be evaluated using the Flory-Huggins theory for the free energy of mixing of a polymer blend; for polymers of identical chain lengths this gives[6-8]

$$D(c) = D_0[1 - 2\chi Nc(1-c)] \quad (1)$$

where c is the volume fraction of one polymer, D_0 is a coefficient expressing the mobility of the components (if the two materials have identical mobilities this would correspond to their self-diffusion coefficient), and χ is an interaction parameter (for polymers to be miscible χ must be $<1/2\ N$). For this sytem χ has been estimated by melting-point depression, and is expressed per monomer unit of PCL ($\chi = -0.38$)[13]. The presence of the polymerization index N ensures that the second term in equation (1) dominates for all but the smallest concentrations; that is, the diffusion is driven by enthalpy rather than by entropy. It is this that leads to the characteristic observed concentration dependence. For polymers with differing molecular masses the thermodynamic term is slightly different[8]; this introduces a skewing of the curve towards the region rich in the longer polymer.

The measured concentration dependence in the system we have studied is rather stronger than the simple quadratic relation given in equation (1) (compare with broken line in Fig. 2). Quantitative agreement with this result is not to be expected, because of the simplifications in the model used. In particular, no microscopic theory exists for the average mobility term D_0 when the polymers have different mobilities. In this system it is clear that there are large differences between the mobilities of the pure components; this is reflected in the large variation of glass transition temperature with composition[14]. Nonetheless, the present study shows directly for the first time that in a miscible polymer blend the mutual diffusion coefficient does indeed vary strongly with blend composition; a maximum is indicated near the middle of the blend composition range, in qualitative agreement with recent theoretical treatments.

We thank Dr F. Brochard, Professor E. J. Kramer and Dr R. C. Ball for useful discussions. R.A.L.J. holds an SERC CASE studentship with ICI PLC.

Received 30 December 1985; accepted 27 February 1986.

1. de Gennes, P. G. *J. chem. Phys.* **55**, 572-579 (1971).
2. Doi, M. & Edwards, S. F. *JCS Faraday Trans. II* **74**, 1789-1801 (1978).
3. Klein, J. *Nature* **271**, 143-145 (1978).
4. Tirrell, M. *Rubber Chem. Technol.* **57**, 523-548 (1984).
5. de Gennes, P. G. *C. r. hebd. Séanc. Acad. Sci., Paris* **292**, 1505-1508 (1981).
6. Brochard, F., Jouffroy, J. & Levinson, P. *Macromolecules* **16**, 1638-1643 (1983).
7. Kramer, E. J., Green, P. F. & Palmstrom, C. J. *Polymer* **25**, 473-479 (1984).
8. Sillescu, H. Die Makromolekulare Chemie, Rapid Communications **5**, 599-603 (1984).
9. Price, F. P., Gilmore, P. T., Thomas, E. L. & Laurence, R. L. *J. Polym. Sci. Polym. Symp.* **63**, 33-44 (1978); *Macromolecules* **13**, 880-886 (1980).
10. Chalykh, A. Ye., Sapozhnikova, I. N. & Aliyev, A. D. *Polymer. Sci. USSR* **21**, 1835-1840 (1980).
11. Crank, J. *Mathematics of Diffusion* 2nd edn (Oxford University Press, 1975).
12. Prigogine, I. *Thermodynamics of Irreversible Processes*, 3rd Edn (Wiley, New York, 1967).
13. Woo, E. M., Barlow, J. W. & Paul, D. R. *Polymer* **26**, 763-774 (1985).
14. Koleske, J. V. & Lundberg, R. D. *J. Polym. Sci.* Pt A-2 **7**, 795-807 (1969).

Vortex flow visualizations reveal change in upstroke function with flight speed in bats

Jeremy M. V. Rayner, Gareth Jones & Adrian Thomas

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

The flapping wings of flying birds and bats generate complex, unsteady air movements. These consist of well-defined vortex structures which are a necessary result of the aerofoil action of the wings, and which transport momentum below and behind the animal in reaction to the lift force which both balances weight and provides thrust[1]. Visualization of the vortex patterns enables the aerodynamic function of the flapping wings to be determined[2-6]. Here we present the results of experiments with small vespertilionids which allow the first description of the vortex wake of bats. The aerodynamics of flapping flight is similar between birds and bats: thrust is always generated during the downstroke, but wingbeat gait (the cyclic pattern of wing movements) and the mechanical function of the upstroke are determined by wing morphology. We present the first evidence from aerodynamic experiments that in an individual bat or bat species, upstroke function and wingbeat gait also vary with flight speed, with aerodynamic lift being generated during the upstroke at high speeds but not during slow flight. This result confirms that flapping gaits are not species-specific, but are selected according to the mechanical conditions experienced by the animal.

We trained long-eared bats (*Plecotus auritus* L.) and noctules (*Nyctalus noctula* L.) to fly through a cloud of neutrally buoyant helium-filled soap bubbles, and recorded wake airflows by photographing the movements of the bubbles in stereo; illumination by four electronic flash guns fired successively at short intervals (8-12 ms) enabled vortex-induced air speeds to be determined, since speed is proportional to the distance between bubble images. Discrete vortices are identified by localized high flow velocities and pronounced rotational flows. This method has been applied to various species of birds[3,4,6], but has not been used previously with bats. Figures 1-3 show typical photographs from a total of about 250 of the two species, together with sketches, drawn from stereo pairs, of the associated discrete vortex patterns.

Wake photographs should be interpreted in relation to the balance of forces on the flying animal. The lift on the flapping wings acts horizontally as a thrust as well as vertically supporting the weight. If weight support alone were required the wings would not need to be flapped (a fixed gliding wing can generate sufficient lift to equal weight), but flapping of the wings must serve also to balance frictional and vortex drag forces: in gliding flight drag is uncompensated, and the animal has no alternative but to descend or decelerate relative to the air. The wake vortices transport momentum, the mean reaction of which in flapping flight is experienced as a lift force acting on the wings and providing *both* thrust and weight support. In the downstroke the wings move forwards and downwards relative to the air, and lift has the required forwards and upwards action[1,5,7,8]. In the upstroke, however, the wings move primarily upwards; at high flight speeds they also travel forwards, the air flow meets the ventral side of the wing as in the downstroke, and if lift is to contribute to weight support it cannot also give thrust, but must retard the animal[5-7]. In slow flight the wings may move slightly backwards relative to the air; lift forces are likely to be small or absent[1,7], but it has been suggested that if in bats the air flow strikes the dorsal surface of the wing, the resulting weak lift may act as both thrust and weight support[5,7,8].

Thus, upstroke function is the main mechanism of differentiation between flapping flight gaits in flying vertebrates, and the upstroke may be expected to act in different ways at different flight speeds. Experiments with birds have confirmed that gaits are constrained by wing morphology[2-6]: an active, lifting

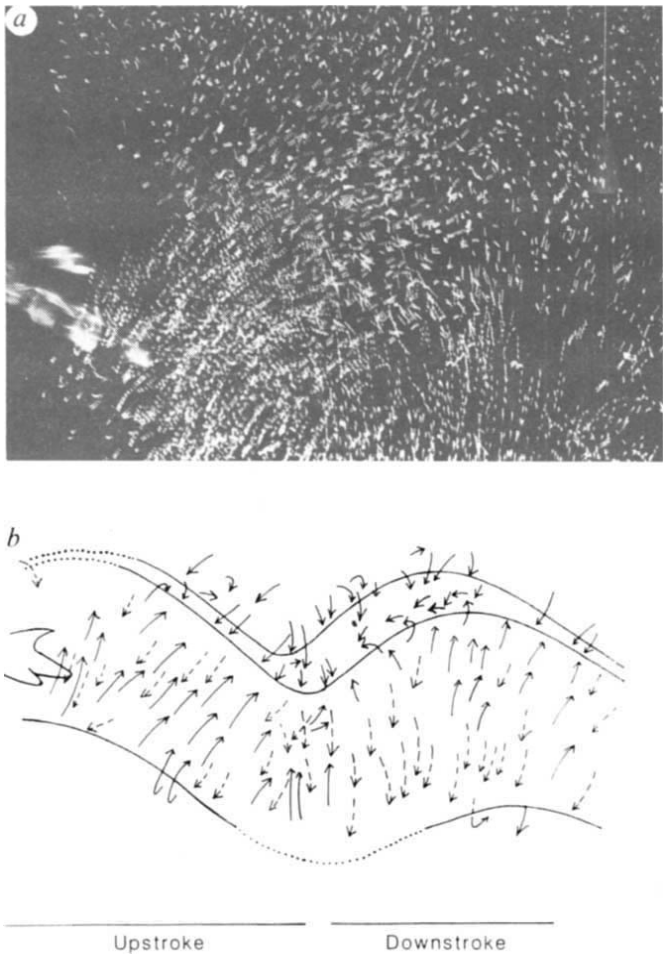


Fig. 1 Flow visualization for the noctule *N. noctula* in steady forward flight at ~7.5 m s^{-1}. *a*, Flow visualization photograph (one half of a stereo pair). *b*, The wake vortices and induced air movements as drawn from stereo pairs. (Bubble direction can be inferred from the photographs as the light intensity is not constant during each flash[3,4]; broken arrows indicate air movements between the vortex cores.) The wake is formed from a pair of continuous vortex tubes which follow the path of the wings; the spacing of the core centres is ~75% of the distance between the wingtips. The cross-sectional diameter of the cores is greater than that commonly seen in birds[2-4] owing to the relatively small size of the bat. The bat is climbing slightly, but this does not substantially distort wingbeat action compared with level flight. Flash interval 10 ms.

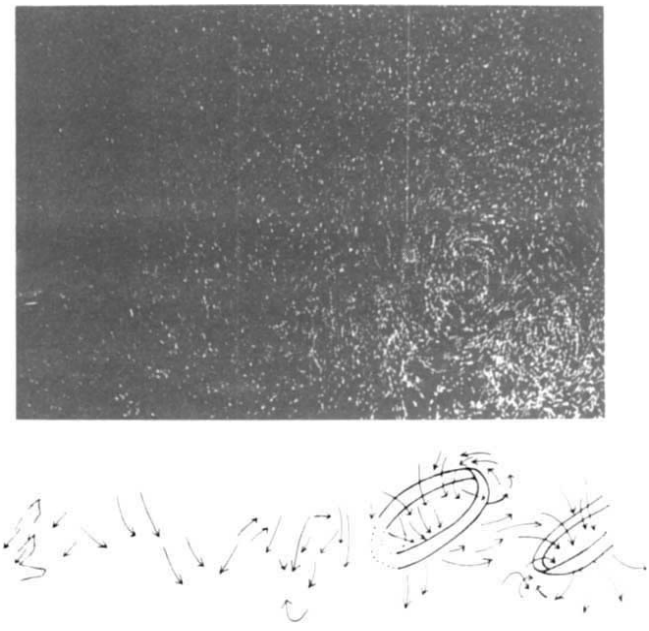
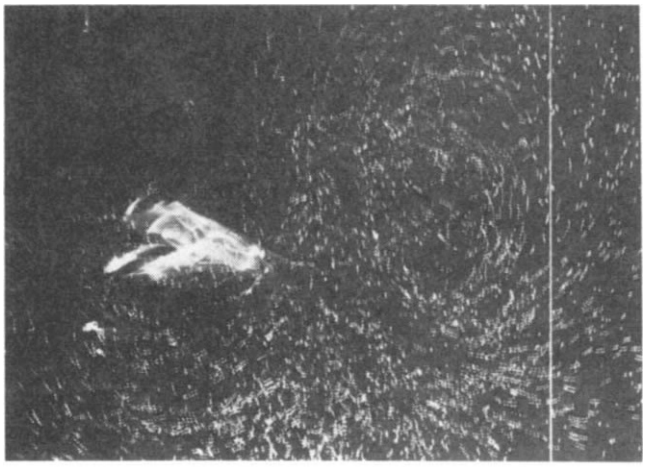


Fig. 2 Flow visualization for noctule in slow flight (3 m s^{-1}), together with the transition to faster flight as the bat accelerates. Two vortex rings are visible to the right; no trailing vorticity is shed during the upstroke, and there is a strong momentum-transporting flux of air through the centres of the rings. These are followed by a weak, continuous tube vortex closer to the bat. Flash interval 10 ms; only three flash guns were used in taking this photograph.

upstroke is more common in long-winged species (typically in fast flight at ~8 m s^{-1} in the kestrel *Falco tinnunculus*[3,6], with above-average aspect ratio and pointed wings), but is absent in small finches[2], which have shorter, rounded wings. During an active upstroke (that is, with aerofoil action generating a lift force) the effective wingspan must be reduced by flexing or sweeping back the wing to reduce retardation from lift and so ensure a mean positive thrust. Theoretical models predict that in an individual animal the upstroke should be active at higher flight speeds, while in slow flight it should be inactive and the wingtips should be brought close to the body to minimize friction drag and inertial forces[1,5,7]. The experiments reported here provide the first direct aerodynamic evidence for such changes in upstroke function.

The wakes of flying microbats have much in common with those of birds. When the wings are actively generating lift, the vortex sheets shed from the trailing edges roll rapidly into a pair of discrete vortex lines or tubes behind the wingtips. In fast flight (7–9 m s^{-1}—normal cruising speeds) the noctule's wake is a continuous, undulating vortex pair (Fig. 1); this indicates that the upstroke is active in the way described above, and confirms an earlier prediction[5] based on wingbeat kinematics. The vortex structure is similar to that seen for the kestrel[3,6]. The marked absence of transverse vorticity leads to the remarkable conclusion that in both animals the strength (circulation) of the bound wing vortex does not vary during the wingstroke; this conveys certain mechanical advantages[5,7]. Both noctule and kestrel have wings of above-average aspect ratio, and use similar wingbeat kinematics which are fully consistent with this form of wake[5]. The wingtip is swept back in the bird, while the arm wing is flexed in the bat; but, in both, the wingtip moves towards the body during the upstroke.

At lower speeds (3 m s^{-1}) the noctule wake is rather different (Fig. 2): prominent transverse vortices are shed at the top and bottom of the downstroke, and the upstroke is flexed and inactive. Circulation can no longer remain constant, although it may be nearly so during the downstroke. This 'vortex ring' wake is similar to that of small finches[2] and slow-flying pigeons[3,4,6]. Noctules are fast-flying bats which rarely fly sufficiently slowly to show an inactive upstroke, but together our results (as illustrated by Figs 1 and 2) provide the first evidence that upstroke function is variable and is not in general species-specific; moreover, an individual animal changes its gait optimally as flight speed increases. In slow flight (1–2 m s^{-1}) in the long-eared bat (which has rather large wings of low aspect ratio) the wake is similar to that of the slow-flying noctule (Fig. 3), with a clear vortex ring corresponding to aerodynamic lift during the downstroke. Our flow visualizations provide no evidence that the upstroke is active in *P. auritus* at any speed, although Norberg concluded from wingbeat photography that in this species at low speeds a weak lift acts as thrust[8]. In slow flight the wingbeat kinematics of both species show considerable flexure and twisting of the wings during the upstroke[5,7-10], and any lift generated then is weak. It has been suggested[5,8,9] that the rapid 'flick' phase at the top of the upstroke in this and similar bats[8-10] may



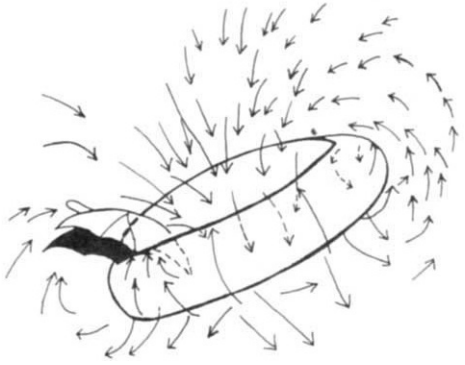


Fig. 3 Flow visualization for long-eared bat *P. auritus* in slow flight (1.5 m s^{-1}). Intense rotational flows induced by a vortex ring generated during the downstroke are visible; at the time of the photograph the wings were at the bottom of the downstroke, and ring generation was still in progress. No vorticity had been shed during the predeeding upstroke, but a similar ring was generated by the preceeding downstroke. The wake in this species is similar to that recorded previously in finches[2] and pigeons[3,4]. Flash interval 8 ms. The matching stereo pair of this photograph is shown on the front cover.

generate thrust; this would entail generation of a concentratated transverse vortex at the start of the flick, approximately midway through the upstroke. We found no trace of such vortices in any of our photographs, although as any lift would necessarily be small, they might have been obscured by the more dominant forces and vortices associated with the downstroke. Although unsupported by the present experimental evidence, we cannot exclude the possibility of weak upstroke lift in at least some bat species.

Despite obvious morphological differences, the flapping-wing aerodynamics of birds and bats show considerable similarities. In both groups gaits are defined by upstroke function, which has been shown to vary with wing morphology. Gait changes with flight speed similar to those reported here in bats have been inferred in birds from analysis of wingbeat kinematics[1,5]; similarly, in bats these changes are likely to be reflected in generation of upstroke lift and the structure of the wake vortices.

We thank H. D. J. N. Aldridge, M. A. Rezende and G. R. Spedding for advice, and U. M. Norberg for comments on the manuscript. This work was supported by grants from the Royal Society, NERC and SERC.

Received 6 February; accepted 20 March 1986.

1. Rayner, J. M. V. *J. exp. Biol.* **80**, 17–54 (1979).
2. Kokshaysky, N. V. *Nature* **279**, 146–148 (1979).
3. Spedding, G. R. Thesis, Univ. Bristol (1982).
4. Spedding, G. R., Rayner, J. M. V. & Pennycuick, C. J. *J. exp. Biol.* **111**, 81–102 (1984).
5. Rayner, J. M. V. in *Biona Report 5* (ed. Nachtigall, W.) 27–74 (Gustav Fischer, **Stuttgart**, in the press).
6. Rayner, J. M. V. in *Konstruktionsprinzipien lebender und ausgestorbener Reptilien. Konzepte SFB 230 4* (eds Riess, J. & Frey, E.) 89–118 (University of Tübingen, 1985).
7. Rayner, J. M. V. in *Recent Advances in the Study of Bats* (eds Fenton, M. B., Racey, P. A. & Rayner, J. M. V.) (Cambridge University Press, in the press).
8. Norberg, U. M. *J. exp. Biol.* **65**, 179–212 (1976).
9. Eisentraut, M. *Z. wiss. Zool.* **148**, 159–188 (1936).
10. Aldridge, H. D. J. N. Thesis, Univ. Bristol (1985).

Genetics and evolution of female choice

M. E. N. Majerus, P. O'Donald, P. W. E. Kearns & H. Ireland

Department of Genetics, University of Cambridge, Downing Street, Cambridge CB2 3EH, UK

Fisher's theory of the evolution of sexual selection by female choice depends crucially on the premise that the preference of females to mate with males of a specific genotype is itself genetic[1]. In the polymorphic ladybird *Adalia bipunctata*, a genetically determined, non-assortative female preference for melanic males has been demonstrated[2]. Models of the evolution of female choice show that the rate of evolution and the final outcome of this selection depend critically on the exact mode of inheritance of both the preferred character and the preference[3]. Here we describe experiments in which the level of preference has been raised by artificial selection over 14 generations. Resultant estimates of heritability are consistent with models in which one or a small number of genes control the preference. Analysis of the levels of preference in isofemale lines derived from the high preference stock shows a quadrimodal distribution in preference. These results are entirely consistent with the deduction that a single dominant gene controls female choice. We conclude that this complex behavioural strategy is based on simple genetics. Furthermore, the demonstration of a simple genetic basis to female mating preferences in *A. bipunctata* implies that sexual selection by female choice is not only important in the evolution of male sexual adornments in sexually dimorphic species, but may also maintain polymorphisms that are not sex-limited.

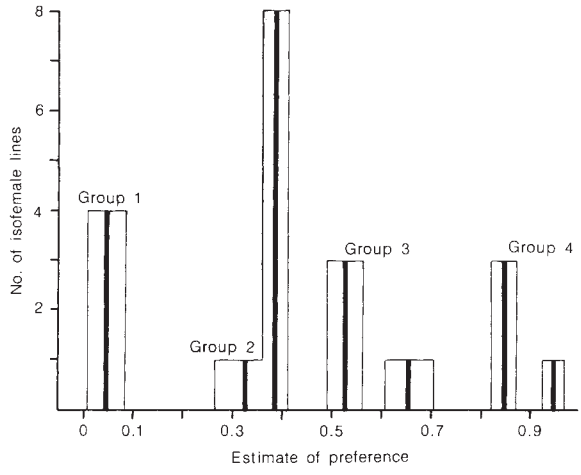


Fig. 1 Isofemale lines shown divided into four distinct groups. The solid black bar shows the position of the estimated preference in the given number of lines, open bars, the standard error. In groups 2, 3 and 4, the preference is also shown for the line most divergent from the others in the group. When groups are considered separately, each of groups 1, 2 and 3 is found to be statistically homogeneous. Group 4 is heterogeneous, with line Z35 having a significantly higher preference. In later population cage experiments, however, Z35 did not show a higher preference. The total χ^2 for heterogeneity within all groups is not significant (Table 2).