

Mating in a viscous universe: the race is to the agile, not to the swift

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Charles Darwin's theory of natural selection has at its focal point the mating success of organisms. Among male animals, large body size is widely seen as the principal determinant of mating success. However, where mating takes place in a three-dimensional arena such as water, the arboreal habitat or air, small size with its concomitant aerobic advantages might be advantageous. Despite considerable interest, the relationship between aerobic ability and mating success has not yet been demonstrated in a single animal species. Here, we test the hypothesis that the known mating success of small male midges is due to their greater aerobic ability. To do this, male midges collected from leks in the wild were flown and their flight paths in free flight were recorded on high-speed cameras in the laboratory. Four flight parameters that would seem relevant to male mate acquisition in flight, i.e. acceleration, maximum speed, tortuosity and turn-rate, were analysed with respect to body size. We show that, while in terms of maximum speed there was no detectable difference between small and large males, small males outperformed larger ones with respect to acceleration, tortuosity and turn-rate. We conclude that the hypothesis that small males gain their mating advantage through aerobic superiority is consistent with the observations reported here.

Keywords: mating; aerobatics; midges

1. INTRODUCTION

A common target of natural selection is body size (Witfield 2001). Among male animals, large body size is widely seen as the principal determinant of mating success. By contrast, the expectation that small size in males ought to carry a mating advantage has been expressed repeatedly (Alexander *et al.* 1979; Thornhill & Alcock 1983; Andersson 1994; McLachlan & Neems 1995), but that it is small size *per se* that is responsible has not been demonstrated for a single animal species that mates on the wing. This is surprising in view of the intense interest and debate that male contests have attracted for over a hundred years (Cronin 1991). The failure may be due to difficulty in finding a suitable animal with which to test the hypothesis. This is the issue we take up here.

We adopt the common chironomid midge *Chironomus plumosus* L. as a test animal and confine our study to the male. There is good evidence that in this and several other chironomid species, small size correlates with mating success (McLachlan 1986*a*, 1997; McLachlan & Allen 1987; McLachlan & Neems 1989, 1996; Neems *et al.* 1990, 1992, 1998; McLachlan & Cant 1995). The mating system of this midge has proved suitable for investigations of the relationship between male traits and mating success. Males form large mating swarms, or leks, each evening in late spring, which attract patrolling females to seek a mate. Males with experimentally damaged wings had reduced mating success (McLachlan 1997). We therefore suspect that mating success is determined by flight performance. Competition appears to take the form of a scramble to be the first to grasp a female who may actively attempt to avoid capture. Such a system would seem to favour selection for aerobic performance. Males have a short lifespan

and do not need to feed as adults (Burt *et al.* 1986). In this they are like mayflies, mating being the sole function of flight in the male. The biomechanics of flight in the male must therefore have been shaped by sexual selection to meet the needs of mate acquisition.

At high Reynolds numbers (Re) it can be shown that acceleration is inversely proportional to body size (Vogel 1994). It follows therefore that larger animals should accelerate more slowly, have an increased turning moment and a reduced ability to vary velocity in flight. These are all measurable components of aerobic ability (Walker 1998), and can in principle be determined from a record of the flight path of individual midges. If the individual is later captured so that measurements of size can be made, conclusions can be drawn about the relationship between aerobatics and body size and by extrapolation, between aerobatics and mating success. We set out to test the hypothesis that small male midges are more aerobic than larger rivals. However, midges are very small flying devices and may experience air as a viscous medium, so expectations based on flight in an inertial universe may not hold. For readers interested in the biomechanics of flight we recommend the reviews by Ellington (1991) and Dudley (2000).

2. METHODS

(a) *Flight chamber*

Individual male *C. plumosus* midges were captured during dawn or dusk flight periods in the spring and summer of 2000 and maintained overnight in a 160 mm × 160 mm × 210 mm gauze-covered vivarium in the laboratory. Filter paper soaked in tap water, or raisin juice, was used to provide water and a carbohydrate source.

Flights (figure 1) were recorded in a periscopic chamber, 50 mm × 50 mm × 180 mm. The size of the chamber was determined as a trade-off between space for flight and resolution

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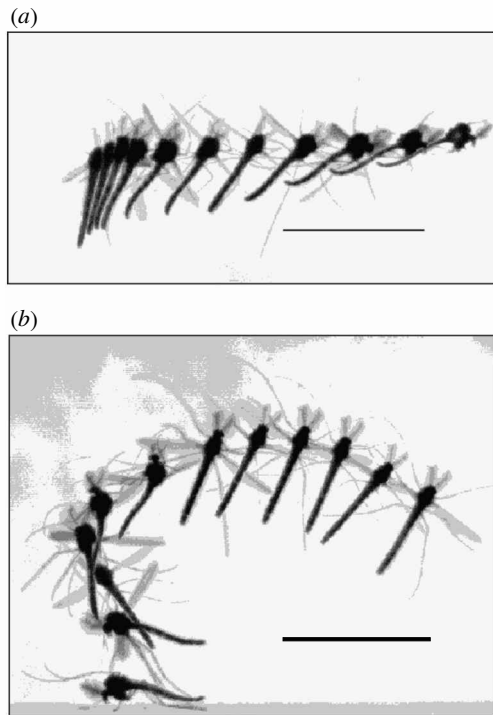


Figure 1. Multiple exposures of the same midge, at the same orientation relative to the camera, performing two types of flight. (a) Straight-line flight just after take-off and (b) curved flight. The actual point of take-off is seen here. (Scale bars, 10 mm).

of image. A mirror fixed at 45° to the top rear edge of the chamber enabled simultaneous plan (to give x -, y -coordinates) and elevation (to give x -, z -coordinates) views to be recorded on each frame, hence permitting three-dimensional (3D) analyses using a single camera (Pitcher 1975; Dudley 2000, p. 233). Lens to chamber distance was 3.0 m, reducing parallax and perspective errors while maintaining resolution. Midges were stimulated to fly by gentle touches on a prothoracic leg. Temperature was kept at $22 \pm 1^\circ\text{C}$.

(b) Video technology

A digital high-speed video camera (Roper Fastcam 10K with 8–80 mm lens), was used to record flights. To minimize total sampling error (Harper & Blake 1989) flights were filmed at 250 Hz. After a number of trials, this rate was chosen as a trade-off between camera resolution, introduction of jitter and over-smoothing of the data (figure 2). The first 0.2 s of each flight was tracked using VIDEOPOINT 2.1 software with the midge thorax used as the centre of gravity. Coordinates (x , y and z) were corrected for perspective error, distance travelled in 3D was calculated using Pythagoras' rule, and angles turned in 3D using the cosine rule (Tapson 1996).

(c) Calibration

Measurement error introduced by image capture was determined by filming a static, carefully calibrated object. The 3D right-angle object ($45\text{ mm} \times 45\text{ mm} \times 60\text{ mm}$) was constructed from aluminium sheeting to test the corrections for perspective error. Pin-holes (maximum diameter 0.15 mm) were made through the aluminium on x , y and z planes. The object was filmed in the flight chamber and two frames were analysed. Distances between 11 pairs of holes were measured using vernier

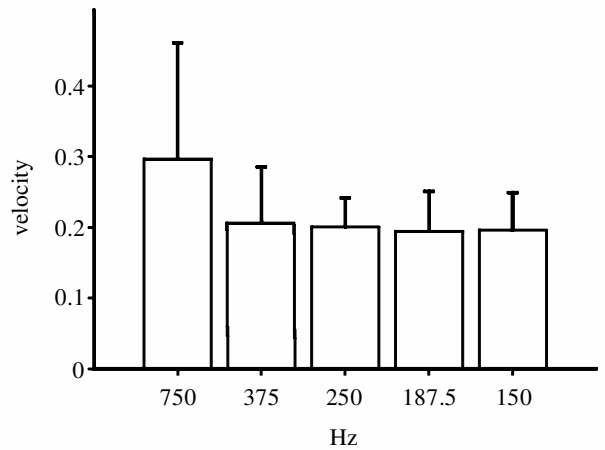


Figure 2. Analysis of single flight track filmed at 750 Hz and re-analysed at successively lower rates in VIDEOPOINT. Mean velocities and standard errors are shown. Reading from left to right, the number of coordinates describing the trajectory are 50, 25, 16, 8 and 4.

callipers ($\pm 0.05\text{ mm}$) on the object and in the images as above. Measurement error was calculated as the difference between pairs of holes measured by vernier and those obtained through the software routine described above. The mean distance between holes was 50 mm and the mean error 0.78 mm.

(d) Measuring aerobic ability

From the 3D trajectories we calculated maxima of velocity (m s^{-1}), acceleration (m s^{-2}), tortuosity (deg mm^{-1}) and turn-rate (deg ms^{-1}). Turn-rate is a measure of how quickly a turn is made and tortuosity is a measure of the tightness of a turn. Only flights with a positive slope and with forward movement were used. The median sinuosity value, calculated as the ratio between the straight line distance and the total distance travelled ($= 0.938$), was used to differentiate between 'straight' and 'curved' flights. Straight flights were used to quantify acceleration and maximum velocity, and curved flights were used for tortuosity and turn-rate. Maximum velocity was recorded only when this was achieved before the final frame. We took a leveling of, or drop in, velocity to indicate that the maximum value had been recorded. This invariably occurred within the first 0.2 s of flight and hence our choice of this as optimum length of flight (see § 2b).

(e) Estimating Reynolds number

Lateral images of midge bodies were recorded at $\times 6$ magnification as above, and body length measured from anterior of the pronotum to the tip of the abdominal claspers. Reynolds number (Re) was calculated according to Vogel (1994, p. 85; i.e. $Re = ul/kv$, where u is flight speed, l is body length and kv is kinematic viscosity). Velocities were the maxima obtained during straight positively sloped flight. Kinematic viscosity was taken to be $1.57 \times 10^{-5}\text{ m}^2\text{ s}^{-1}$ at 22°C .

(f) Statistical analysis

Ninety-three midges collected in the wild were used in the study, with each midge being flown for a maximum of five flights, and a total of 149 flights were analysed. From these flights a single maximum value for each parameter derived from straight-line flight or curved flight was chosen for each midge. Thus, hereafter n is the number of points describing the trajectory in each analysis. Wing length is a strong predictor of

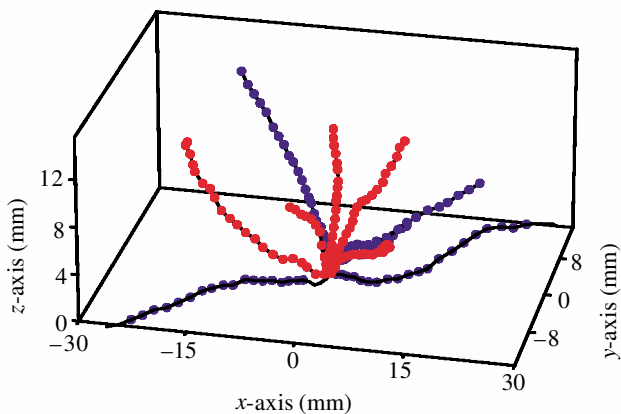


Figure 3. A 3D plot of representative flight paths of five straight (blue) and five curved flights (red). See also figure 4.

body size in insects (Greenewalt 1962) and in chironomids in particular (McLachlan 1986*b*). Wing images were obtained using the Fastcam 10K mounted on a Wild Heerbrugg binocular microscope. Calibrated images at $\times 12$ magnification were analysed using IMAGE TOOL v. 2. Statistical relationships between body size and our four measures of aerobic ability were conducted using MINITAB v. 12.

3. RESULTS

(a) Morphology of *Chironomus plumosus*

Wing length is readily measured and hence, except in the calculation of Re , it is used throughout as the measure of body size. There was a strong relationship between wing length and body mass ($r^2 = 0.86$, $F = 101.1$, $p < 0.001$, $n = 99$). Mean \pm s.e. wing length = 4.19 ± 0.03 mm, body length = 4.86 ± 0.05 mm, and dry weight = 483.8 ± 22.32 μg ; $n = 50$ in each case.

(b) Aerobatics of *C. plumosus*

A 3D plot of some selected flight paths is shown in figure 3. Curved flights showed most angular deviation during the first 50 ms after take-off, with straight flights showing little deviation. Acceleration was very variable between frames, indicative of a viscous medium, and velocity increased steadily throughout flight (figure 4). Velocities ranged from 0.25 to 1.1 m s^{-1} but there were no significant relationships between maximum velocity reached and body size ($r^2 = 0.04$, $F_{1,59} = 2.71$, $p > 0.05$). As the competition for females within swarms is undertaken over a short distance, a reasonable assumption is that males capable of greater acceleration, tortuosity and turning ability than conspecifics will be the first to reach and pair with a female. There is a strong linear relationship between size and acceleration (acceleration = $72.9 - 14.2$ wing length; $r^2 = 0.43$, $F_{1,72} = 54.8$, $p < 0.001$; figure 5), with smaller midges accelerating more than 1.5 times faster than their larger conspecifics. In curved flight, smaller males produce quicker turns measured as either turn rate of tortuosity (turn-rate = $105.2 - 14.0$ wing length; $r^2 = 0.19$, $F_{1,73} = 17.50$, $p < 0.001$; tortuosity = $17.7 - 2.27$ wing length; $r^2 = 0.05$, $F_{1,73} = 4.15$, $p = 0.045$; figure 5). Data for tortuosity are only just significant and given the low r^2 should be interpreted with caution. If males compete for a female that is not directly in front of them, a degree of turning ability would seem advantageous.

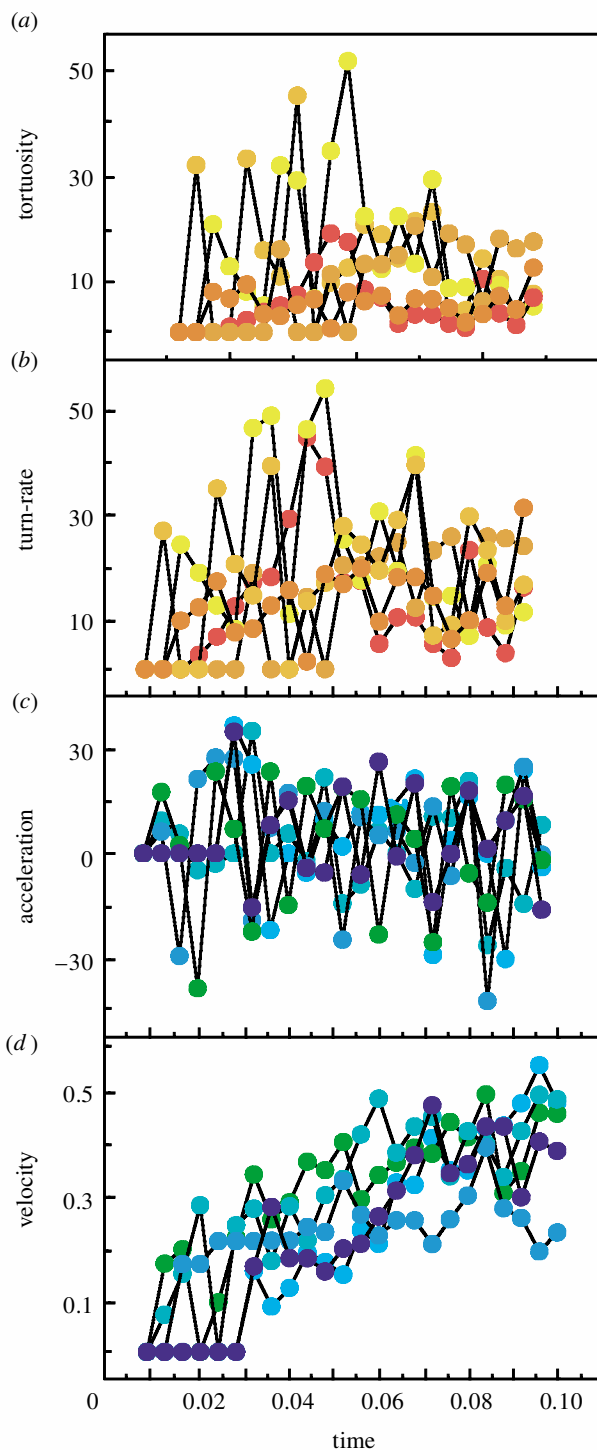


Figure 4. Data from the curved flights (red), showing (a) tortuosity (deg mm^{-1}) and (b) turn-rate (deg ms^{-1}). Data from straight flights (blue) showing (c) acceleration (m s^{-2}) and (d) velocity (m s^{-1}). See also figure 3.

Furthermore, if all individuals are constrained to the same speed and accelerations during a turn, individuals capable of the quickest turn are free to accelerate at a greater rate in a straight line, thus reaching the female first. The mean Re of midges in straight positively sloped flight was 272.2 ± 66.8 , and ranged from 125 to 473. Such small Re values lend support to the assumption that midges fly in relatively viscous medium.

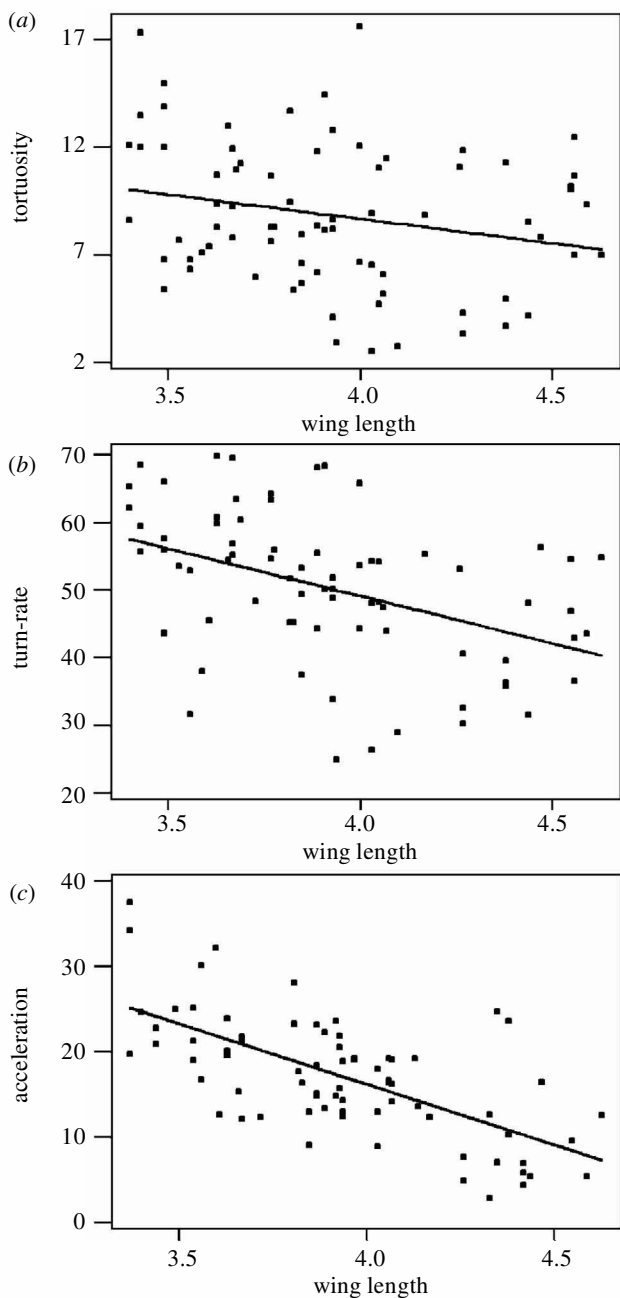


Figure 5. The relationship between body size and aerobics measured as (a) tortuosity (deg mm^{-1}), (b) turn-rate (deg ms^{-1}) and (c) acceleration (m s^{-2}).

4. DISCUSSION

We used high-speed digital video technology to test the hypothesis that aerobic ability is inversely related to body size in a very small flying insect. This is a technique that is transforming the interface between biomechanics and evolutionary biology (for review see Dalton (2002) and references therein). We found that small males accelerate quicker and also produce significantly faster and tighter turns. It has already been demonstrated that small males outcompete larger rivals for access to females (see McLachlan & Neems (1995) for review). By inference we arrive at the conclusion that it is through their superior aerobic ability that small males achieve this success. There are costs to small size that lead to stabilizing selection for body size in males (Neems *et al.* 1998). The small

size advantage has been demonstrated earlier for the males of several other species of midges (McLachlan & Neems 1995). This conclusion might therefore be widely applicable to chironomid midges and probably also to a variety of other insects where there is an untested assumption of aerobics as the explanation for an observed small size mating advantage (Alcock & Pyle 1979; Litte 1979; Thornhill & Alcock 1983). Indeed, an aerobic advantage to small size may be as common as the advantage to large size recognized by Charles Darwin (1871) and many others since. It seems likely that large size and the concomitant larger mass is favoured by sexual selection principally in cases where mating involves fighting, as between stags (Krebs & Davies 1993). Where mating appears to involve agility rather than strength, as possibly in apes, some birds, most fishes and many insects, it is small size and the associated acrobatic advantage that should be favoured (Alexander *et al.* 1979; Thornhill & Alcock 1983; Andersson 1994; McLachlan & Neems 1995). As far as we are aware, agility as a fitness component in the mating success of small males has previously been demonstrated directly in only a single case, *Drosophila*. This does not mate on the wing but on a solid surface, success for the male depending on agility in the nuptial dance (Steel & Partridge 1988).

To compare midges with other animals, account must be taken of the viscosity of the medium through which the animal moves and the effect of viscosity is determined by speed and body size. *Chironomus plumosus* is among the smallest 0.2% of all flying animals (McLachlan & Neems 1996) and when in flight may therefore encounter air as a viscous medium. The extremely rapid changes in velocity seen in figure 4 might be expected of locomotion in a viscous medium. These data suggest that cessation of wing beats results in a rapid full stop, while resumption of powered wing beats results in an almost equally rapid acceleration. Re is a measure of inertial over viscous forces. Estimates of Re for midge-sized animals differ widely depending upon method of measurement. It is thus difficult to make meaningful comparisons between *C. plumosus* and other flying animals of similar size. The comparisons below are thus uncertain. For mosquitoes Re is thought to lie between 10 and 100 (Kuethe 1974; Wilkin 1985). For *C. plumosus*, an animal of closely comparable size, architecture and flight behaviour, a value of *ca.* 12 has been estimated (McLachlan & Neems 1995). Here, based on improved methods of determining velocity we arrive at Re *ca.* 300 for *C. plumosus*, which is closer to the upper value for mosquitoes. For a large dragonfly, a relatively gigantic insect and flying at 4 m s^{-1} , the Re is 10^4 (Vogel 1994, p. 86). At Re *ca.* 300, *C. plumosus* may encounter air as a viscous medium. Just how viscous, though, is not clear. Taking a midge to be essentially an elongated cylinder puts *C. plumosus* in a place where viscous and inertial forces overlap (see Vogel 1994, p. 92 figs. 5.2 and 5.4). Flying animals of this size therefore provide an especially interesting challenge for biologists.

Another way of comparing the flight performance of animals involves determining the ratio of flight muscle mass to body mass (flight muscle ratio (FMR)). This indirect measure is favoured by some as a reliable indicator of flight performance (Marden 1987; Ellington 1991). The FMR of *C. plumosus* appears to exceed that of

any other animal thus far examined (McLachlan & Neems 1995). The rigours of swarming in a moving viscous medium may account for the extraordinary powers of flight in male midges suggested by this FMR.

We have demonstrated that for several key criteria of aerobatics, small male midges are potentially able to outmanoeuvre larger rivals in the mating swarm. We infer that superior aerobatics provide a plausible explanation for the greater mating success of small midges.

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