Sonation in the male common snipe (*Capella gallinago gallinago* L.) is achieved by a flag-like fluttering of their tail feathers and consequent vortex shedding

A. van Casteren[1], J. R. Codd[1], J. D. Gardiner[1], H. McGhie[2] and A. R. Ennos[1,*]

[1]Faculty of Life Sciences, University of Manchester, Oxford Road, Manchester M13 9PT, UK and [2]Manchester Museum, Oxford Road, Manchester M13 9PL, UK

*Author for correspondence (r.ennos@manchester.ac.uk)

SUMMARY

Male common snipe (*Capella gallinago gallinago*) produce a 'drumming' sound with their outer tail feathers during their mating dives, but little is known about how this is achieved. We investigated the movements and sound producing capabilities of the outer tail feathers. Using a wind tunnel, we compared observations of the frequencies of sound produced with the predictions from aerodynamic theory. The feathers were also filmed in an air-flow with a high speed video camera, and subjected to morphological examination and biomechanical testing. We propose a mechanistic hypothesis of how the modified outer feathers of the male common snipe generate sound, and the adaptations that facilitate this. Video and audio analysis of the feather demonstrated that a fluttering of the trailing vane generated the sound. The flutter of the vane is facilitated by the rearward curvature of the feather shaft, reduced branching angles of the barbs in the trailing vane and the lack of hooks on the barbs along a hinge region, all of which increase its flexural compliance. Sound production occurred at the same frequency as the vane movements, at frequencies consistent with it being produced by a fluttering flag mechanism powered by vortex shedding.

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Key words: snipe, sonation, feather, aerodynamics, flutter.

INTRODUCTION

The acoustic communication of birds has received a great deal of attention and it is clear that audio communication plays vital roles in key behaviours of avian species. However, past research has concentrated mainly on vocalisations produced by the bird's syrinx; in comparison there has been little research into the other methods of acoustic communication (Alcock, 2005; Bostwick, 2006). Communication in birds can also be facilitated by non-vocally produced sounds that are generated by different parts of the bird, such as the wings, tail, bill and feet. These have been termed sonations in order to separate them from widely documented vocally produced sounds (Bostwick, 2006; Clark and Feo, 2008)

Sonations involving the bill or feet are comparatively simple, mostly involving percussive contact with body or substrate (Bostwick, 2006). Sonations produced by feathers, however, are more complex. Most birds make atonal sounds when they fly, due to the turbulence of the airflow around them. However, some species make tonal sounds in flight, many examples, including hummingbirds and snipe (Bahr, 1907; Carr-Lewty, 1943; Reddig, 1978; Sutton, 1981) being cited by Clark and Feo (Clark and Feo, 2008) and pigeons (Hingee and Magrath, 2009). The difficulty in observing these feather sonations has led to mainly descriptive, vague and speculative hypotheses being proposed on the mechanisms behind this form of acoustic communication. The sounds are often described as whistles, but the actual physics of the sound production has rarely been considered (Bostwick, 2006).

This is certainly true for the 'drumming' noise of male common snipe (*Capella gallinago gallinago*), that is produced during mating displays; the male rises to an altitude of around 50 m and then, with its outer two feathers of the tail held outwards, dives at an angle of

ca. 40 deg. When the airspeed of the dive reaches about $13\,\mathrm{m\,s^{-1}}$ these outer feathers produce an audible drumming sound (Carr-Lewty, 1943; Reddig, 1978; Sutton, 1981) and this continues until an air-speed of around $24\,\mathrm{m\,s^{-1}}$ is reached. This drumming usually lasts between 1 and 3 s. The intermittent nature of the sonation is commonly thought to be due to the action of the wings periodically obstructing the airflow (Headley, 1904; Carr-Lewty, 1943; Reddig, 1978; Clark, 2008), although it also occurs in feathers attached to arrows (Taylor, 1925).

There have been several attempts to demonstrate the aerodynamic mechanisms responsible for the sound production of snipe. Many authors have noted the differences between the outer tail feathers and the inner ones: they are strong and stiff with a stout shaft; strong hooks or hamuli join the barbules of the rear vane, preventing it breaking at high wind speeds; and the barbs join the shaft at an acute angle (Headley, 1904; Carr-Lewty, 1943; Reddig, 1978). Reddig (Reddig, 1978) also placed the feathers in a wind tunnel and showed that the main frequency of the sound they generated rose from around 250 Hz at around $10\,\mathrm{m\,s^{-1}}$ to around 450 Hz at $20\,\mathrm{m\,s^{-1}}$. However, no observations have been made of the actual deformations of the feathers when they are producing the sounds, and previous authors have relied on speculation. Flying Officer Carr-Lewty, writing during the second world war (Carr-Lewty, 1943), suggested that the sound was produced by torsional fluttering of the entire feather, in which the shaft was twisted while the vane remained fairly flat, a suggestion that was endorsed without further evidence by Reddig.

Nowadays it is far easier to investigate high frequency vibrations by using high speed video and the physics of aeroelastic flutter is better understood. In this study, therefore, we first examined how

the tail feathers of snipe actually move when placed in a high speed air flow. We then carried out morphological investigations to determine how the movements were facilitated by the feather structure, and subjected the process to mechanical tests and aeroelastic analysis to determine how the movements were powered.

MATERIALS AND METHODS
Feather acquisition

Tail feathers of five common snipe (*Capella gallinago gallinago* L.) were acquired from museum specimens and from commercial game dealers. Each feather used was free from damage. If damage occurred during the experimental process the feather was discarded.

Preliminary investigations

To induce the feathers to produce the drumming sound we first attached an outer tail feather of a snipe to the end of a stick and waved it in a long smooth swing; this temporarily generated a musical rasping sound. To generate a continuous sound and allow observation of the feather during sonation a hairdryer was used to accelerate air, producing an outflow which was measured, using an Omega HHF92A digital anemometer (Bridgeport, NJ, USA), to be $7–10\,m\,s^{-1}$. Outer tail feathers held at the outflow with their shaft at right angles to flow and their chord parallel to it, made a similar noise to those moved through still air. On these occasions the trailing edge vane could be seen to be fluttering up and down along a hinge point approximately parallel to the feather shaft and along a line where there was a change from darker to lighter colouration (Fig. 1). When inner tail feathers of the snipe, or any tail feather of woodcock were swung or held in front of the hairdryer in the same way, only the next inmost snipe feather made a similar, though weaker, noise. The vanes of all the other feathers split apart readily at low wind speeds and none made any sound.

Footage and sound recordings of the feather during sonation were then acquired simultaneously. High-speed video images were acquired using a Trouble Shooter XR camera at 8000 frames per second (fps); the feather was lit using 1500 W halogen lights. The feather was filmed from an oblique angle looking from the base to the tip of the feather but about 15 deg. out of plane. This allowed a clear view of the vane movements. The frequency of oscillation was measured by counting the number of frames each flutter took. The sound produced by the feather was recorded at 48 kHz using a Sony XLR microphone. The sound was recorded, visualised and analysed using two programs: Raven Lite 1.0 and Audacity 1.2.5. Owing to the loud background noise produced by the hair dryer, a clear recording of the sonation of the feather was not possible. In order to obtain the frequency of the sound, therefore, recordings were made both with and without the feather. Audacity was then used to perform a fast Fourier transform, and plot sound amplitude against sound frequency, with a 1024 sample window, allowing the peak frequencies and their volume to be easily visualised. By comparing the baseline and the test amplitudes over a range of frequencies, it was clear at which frequencies the sound-producing feather was generating sound. The peak frequency was compared with the frequency of movement of the vane.

The movements of the vane were just as predicted by the preliminary examination; the rear of the trailing edge vane fluttered up and down along the hinge (supplementary material Movie 1) at a frequency of around 289 Hz, very similar to the peak sound frequency (275 Hz). This strongly suggested that the sound was produced by the fluttering of the rear vane.

Manipulations of the trailing edge vane of the outer tail feather showed that it could be pushed up or down with some ease, hinging
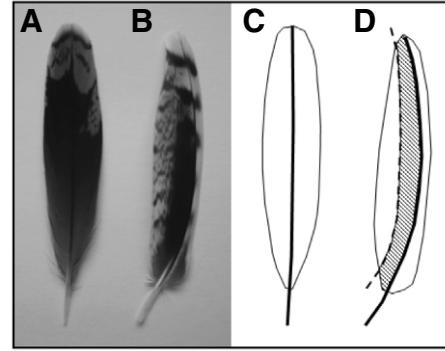

Fig. 1. Photographs and simplified diagrams of inner tail feather (A,C) and the outer tail feather of a snipe (B,D). The shaded area in D indicates the basal black area of the outer tail feather and the dashed line indicates the suggested flexion line along which flutter occurs.

for the most part, along the line seen when sounds were being produced. Initial morphological examination of the outer tail feathers (Fig. 1) suggested that they differed from other feathers in having a rearwards-curved shaft and barbs that diverged at a very low angle to the shaft; together these orientated the barbs almost parallel to the shaft and would facilitate out-of-plane movements of the rear vane (Ennos et al., 1995). These observations therefore suggested that the flutter was facilitated by a morphological mechanism that allowed the rear vane to swing readily up and down at a fairly localised 'hinge'.

Subsequent experimental work was therefore carried out to qualitatively and quantitatively investigate the mechanical design of the rear feather vane, to explain why it hinged up and down at the 'hinge'. The effects of air velocity on the frequency of sound production were also investigated, as this could be compared with the predictions made by different aeroelastic models of sound production.

Morphology

In order to quantify the barb angles in different feathers, a Leica® MZ9s stereo light dissecting microscope was used. Using Leica® Application Suite, images were obtained and the barb branching angles were then recorded. This was done at intervals of 10% of length from the base of the feather to the tip. and the mean barb angle was determined at each point. This process was repeated for eight sound-producing tail feathers from four birds, twelve non-sound producing tail feathers from a single bird, and three outer feathers from two woodcock (*Scolopax rusticola*) a species that is similar to the snipe but that does not generate the 'drumming' sound.

Earlier work has demonstrated that the in-plane and out-of-plane behaviour of feather vanes is strongly influenced not only by the barb angle but also by the arrangement of the barbules (Ennos et al., 1995); hooked distal barbules prevent breaking between, and relative movement of, barbs by their attachment into the grooved proximal barbules of adjacent barbs. In order to observe the feathers under higher magnification and to locate any morphological adaptation that may account for the sound-producing qualities of the trailing edge, an environmental scanning electron microscope (ESEM) was used. The ESEM allows uncoated biological samples to be observed at a high magnification and resolution. Owing to the small chamber size, whole feathers could not be inserted into the ESEM so sections were cut and mounted. These included the leading vane, rachis and trailing vane; markers were used to distinguish

where colour changes occurred on the feather as the ESEM only produces pictures in black and white. Images were then taken along the width of the trailing edge and any morphological adaptations noted.

Sound production and airspeed

The sound production of four outer tail feathers was investigated in a closed-circuit wind tunnel (working area ca. 30 cm× 30 cm×100 cm) at the University of Sheffield Experimental Aerodynamics Laboratory, working at a variety of speeds ranging from $12\,\mathrm{m\,s^{-1}}$ to $26\,\mathrm{m\,s^{-1}}$. A pitot tube was used to record airspeed in all wind tunnel experiments.

The noise of the tunnel was recorded at wind speeds from 6 to $26\,\mathrm{m\,s^{-1}}$ at increments of $2\,\mathrm{m\,s^{-1}}$ without feathers to generate a baseline of background noise produced by the airflow and workings of the wind tunnel. This is the range of speeds that previous studies have shown to be achieved during the common snipe's mating dives (Carr-Lewty, 1943; Reddig, 1978; Sutton, 1981). The experiment was then run again with one of the four sound-producing feathers or with a central tail feather (non sound producing) at the same wind speeds as the baseline experiments. The sound produced by the feathers was determined by the same process as used for the preliminary investigations: finding the difference between the Fourier transforms of the noise produced with and without feathers.

RESULTS
Morphology

The measurements for the angle of the barbs to the rachis are shown in Fig. 2A,B. The sound-producing outer feathers had lower barb angles than the other non-sound-producing feathers of the snipe (Fig. 2A). Together with the rearward curvature of the shaft, this placed the orientation of the barbs in the sound-producing feathers in a more parallel position to the rachis. In the second-most outer feathers the branching angles were also relatively low, which correlates with the ability of this feather to generate sound, albeit not as well as the outer feathers. Comparison of the sound-producing feathers of the snipe with the non-sound-producing feathers of the woodcock (Fig. 2B), show that the woodcock feathers also had a larger angle between the barb and the rachis than snipe feathers. It would appear that the ability to generate the sound necessitates the low angle arrangement of the barbs shown in the sound-producing feathers.

The images from the ESEM of the outer feather revealed that there was also a difference in the barbule morphology in the hind vane depending on the distance back from the rachis. When close to the rachis the distal barbules possessed the classic hooks that attach to the grooved proximal barbules (Ennos et al., 1995) and so hold the feather vane intact (Fig. 3). However, further away from the rachis at the 'hinge' region the barbules were straighter and lacked hooks; this would allow easier relative movement between barbules (Fig. 3). The barbs close to the trailing edge also had hooked barbules. In both feathers the hinge barbules appeared to have a spatula type structure (Fig. 3); the function of this structure is unknown but may be there to resist splitting apart of barbs while allowing bending of the vane.

Sound production and airspeed

In the wind tunnel, the flutter of the trailing edge began at around $6\,\mathrm{m\,s^{-1}}$ and rose in amplitude with wind speed until the trailing edge broke up at around $26\,\mathrm{m\,s^{-1}}$. Audible sound was only picked up at higher air speeds, beginning at $12\,\mathrm{m\,s^{-1}}$, after which the volume
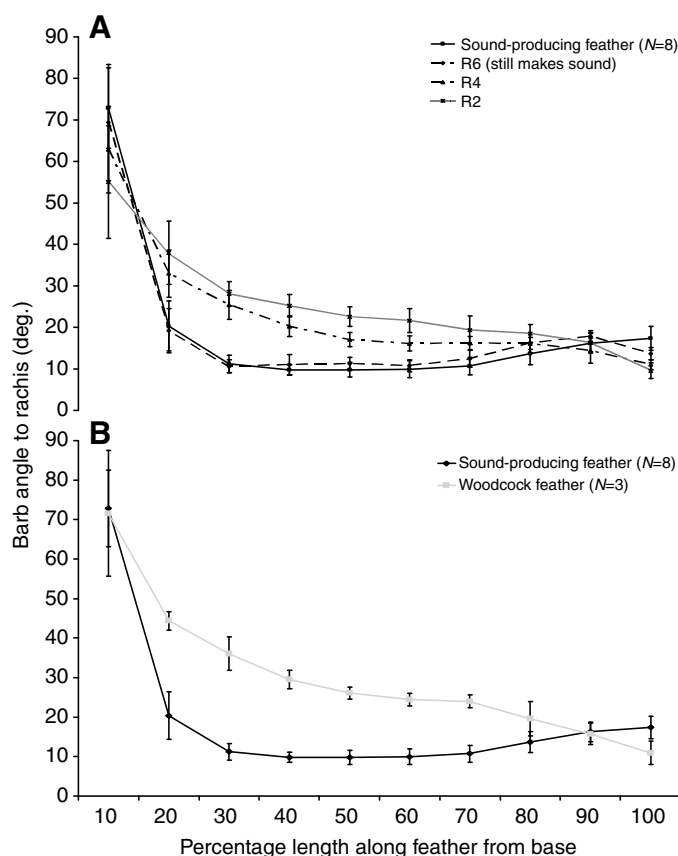

Fig. 2. (A) The mean (N=2 for each feather) barb angles plotted against percentage feather length (from the base of the feather) for all the inner retrices of the common snipe (*Capella gallinago gallinago*). (B) The mean barb angles plotted against percentage feather length from the base of the feather for the outer rectrices of common snipe and the woodcock (*Scolopax rusticola*). Error bars indicate the standard deviation.

continued to rise until around $26\,\mathrm{m\,s^{-1}}$ when a decrease in volume was noted. Fig. 4 shows a typical Fourier analysis of the sound with and without a feather (Fig. 4A), and the difference between them (Fig. 4B). There is a clear peak frequency and little obvious sign of higher harmonics. Sounds produced by feathers in the wind tunnel rose in frequency as wind speed increased, from around 300 to 600 Hz. Fig. 5 shows how the frequency of the sound produced by the four feathers changed with airspeed. For all the feathers tested the frequency increase was roughly linear (Fig. 6), although the frequency was not directly proportional to speed since in all cases the intercept of the regression line between the points was greater than zero. The mean frequency (*f*) of all the feathers, calculated by linear regression followed the equation:

$$f = 179 + 13.5\mathbf{v}\,,\qquad(1)$$

where **v** is velocity.

DISCUSSION

Observation of the vanes and examination of the frequency of sound produced together provide strong evidence that the sound produced by the outer pair of tail feathers in the common snipe is generated by flutter of the rear part of the trailing vane. The rear of the trailing vane swings upwards and downwards with its flexion localised to a large extent at a hinge region. This contrasts with the suggestion
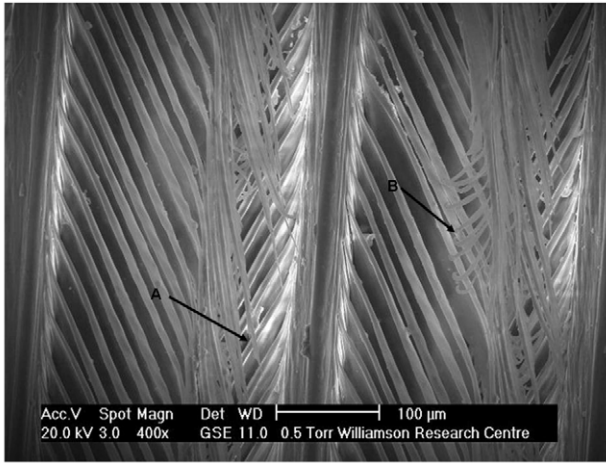
Fig. 3. An image taken using an environmental scanning electron microscope that demonstrates the transition from hooked distal barbules (B) to a straighter barbule morphology (A).

(Carr-Lewty, 1943) that the whole feather twists. The sound frequency produced is also almost equal to the frequency of oscillation of the rear vane seen in the high speed video. The small differences between peak sound and the flutter frequency movement may have occurred because they were not measured at precisely the same time, so the wind speed produced by the hairdryer may not have been identical.

The key to the ability of the feather to flutter and hence make a noise appears to be the great ease with which the rear part of the hind vane flexes up and down. In normal feathers this is prevented by the flexural rigidity of the rear-pointing barbs and the strength of the barbule-to-barbule hook connections (Ennos et al., 1995). The flexibility of the rear of the hind vane is due to two things. First, the rearward curvature of the shaft and the low divergence angle of the barbs, means that the barbs are oriented virtually parallel to the rear of the black region. This means that flexing of the vane can be performed readily merely by slight reorientation of the barbs

rather than having to bend them sharply. Second, the lack of any connecting barbule hooks around the middle of the vane, will allow the barbs to reorientate easily relative to each other, and so form the hinge. It is ironic that many previous authors concentrated on the strength of the barbule hooks (Bahr, 1907; Carr-Lewty, 1943; Reddig, 1978) as a possible cause for the sonations, while missing the fact that there was a region with no such hooks. There may also be changes to the keratin itself at the hinge. The black front part of the hind vane is probably stiffened by the inclusion of melanin, which acts as a filler in the composite material (Voitkevich, 1966; Videler, 2005; Bonser, 1995) while keratin in the lighter rear part is more compliant.

But if the flexibility of the vane facilitates the fluttering, how are the movements powered? Wind tunnel tests on flat plates moving parallel to flow show that at Reynolds numbers above about 700 (corresponding to airspeeds of the feathers of around $0.7\,\mathrm{m\,s^{-1}}$) they shed a stream of alternating vortices (Taneda, 1958). The frequency of vortex shedding, f_V, is then given by the equation:

$$f_V = \frac{St\mathbf{v}}{d} \,, \qquad (2)$$

where $\mathbf{v}$ is the airspeed, d the chord length of the plate, and St is the Strouhal number, which for plates parallel to flow is approximately 0.8 (Chen and Fang, 1996). For our feathers, with their mean chord of 14.7 mm, at the speed of $12\,\mathrm{m\,s^{-1}}$ when the feather is just starting to flutter, vortices would therefore be shed at around 650 Hz. These alternating vortices would cause the feather to flutter and produce sound at precisely half this frequency, 325 Hz. This is strikingly similar to the actual mean frequency of sound produced at $12\,\mathrm{m\,s^{-1}}$, which is 341 Hz.

One might then expect the frequency of oscillation to rise in direct proportion to the velocity. However, as the velocity increases, and as the feather begins to flutter as a result of the forces induced by the shedding of vortices, it will produce a wider wake. It has been found that the frequency of vortex shedding with wake w is given by the expression:

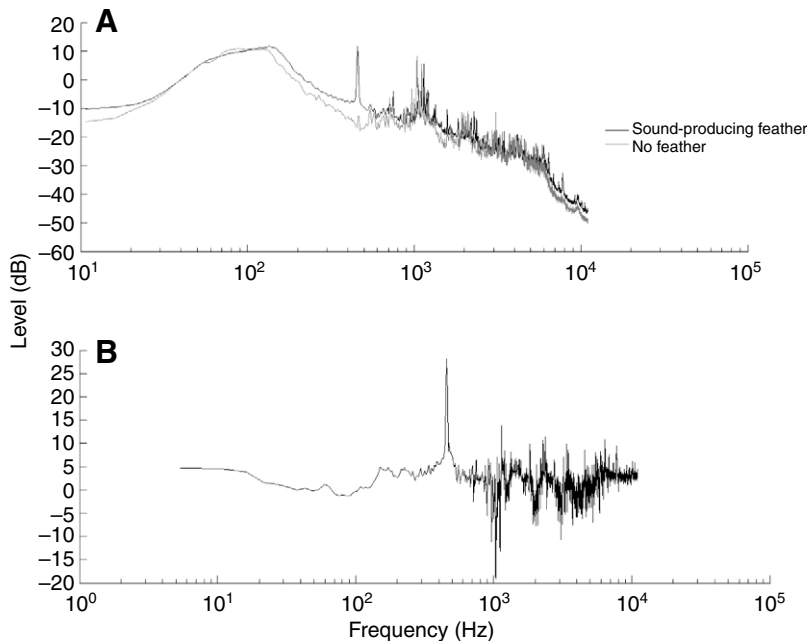$$f_V = \frac{St\mathbf{v}}{w} \,, \qquad (3)$$

Fig. 4. The results of wind tunnel tests, showing a fast Fourier transform (FFT) of the sounds produced with and without a snipe feather (A), and the difference between them (B). The main frequency can be clearly seen; there are few obvious higher harmonics.
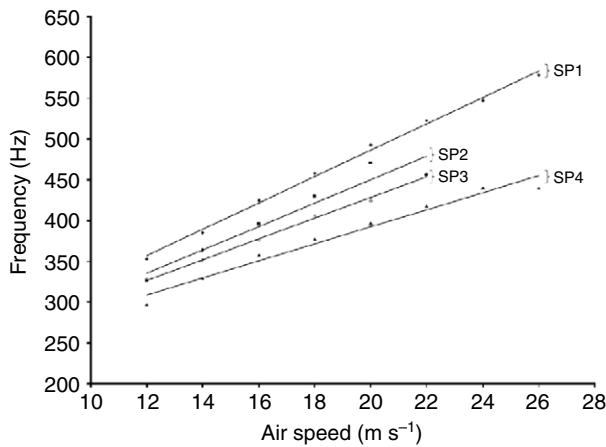
Fig. 5. The recorded frequencies for each feather tested in the wind tunnel at varying airspeeds. Frequency increases with airspeed for each feather tested.
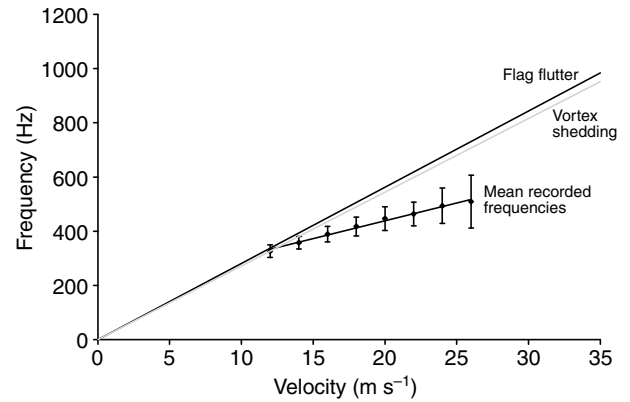

Fig. 6. The mean and standard deviation of actual frequencies of sound produced by the outer tail feathers (N=4) at different airspeeds (12–26 m s^{-1}) and comparison with the predicted frequencies if the sound was produced by each of the suggested models: flag flutter and vortex shedding with St=0.8.

where w is the width of the wake and the Strouhal number is 0.16 (Chen and Fang, 1996). Therefore the wake frequency should rise rather more slowly with velocity, as the wake width increases at higher speeds as the amplitude of flutter rises.

Another way of modelling the process is to assume that the feather is acting as a hinged plate, with the rear of the vane being free to flap up and down. Above the resonant frequency of such a hinged plate, it will oscillate up and down, driven by the lift produced by the rear vane. We developed a mathematical model to predict the frequency of oscillation produced by this motion based on the work of Argentina and Mahadevan (Argentina and Mahadevan, 2005) (see Appendix). The model calculates the frequency of oscillation of a hemi-elliptical uniform plate with the dimensions and mass of the rear of the trailing edge vane. We also modelled the resonant frequency of the rear of the trailing edge vane using these assumptions and by carrying out mechanical tests on the stiffness of the hinge region. The results of this resonance model were experimentally verified by mechanically oscillating the feather at different frequencies and examining the movements of the rear of the vane.

The results of the modelling (see Appendix) show that for speeds above 2 m s^{-1}, the rear vane should flutter at frequencies given by the expression f_F=(28.1±1.6)v. For the speed of 12 m s^{-1} this gives a figure for the frequency of 337 Hz, once again very similar to that observed. However, because the model predicts that frequency should be proportional to velocity it gives an unrealistically high predicted frequency of 730 Hz for speeds of 26 m s^{-1}. There may be several reasons for this. As the amplitude of the oscillations increased with air-speed, the rate of increase of lift coefficient with angle would have fallen below the predicted value of 2π, so the frequency rise would be lower than predicted. The width of vane affected might also increase at higher airspeeds, because the hinge on the hind vane is not precisely localised; this would have reduced the predicted frequencies. Considering the crudity of the aerodynamic model, and the fact that the vane did not hinge precisely along a single line, it is not surprising that the predictions of the model are not exact.

The vortex shedding model and the flag fluttering model are probably, in fact, just two different ways of thinking about the same process; a fluttering flag will inevitably give off vortices, whereas vortex shedding from a flexible plate will inevitably cause it to flutter, and it is encouraging that the models give very similar estimates of frequency for the limiting case of 12 m s^{-1}, when flutter is just starting. For both models, there are also good explanations of why frequency is not directly proportional to velocity at higher speeds and fluttering amplitudes. It seems likely, in fact, that the high flexibility of the rear vane, and its consequent fluttering improves sound production in two ways. First, as we have seen, it prevents the frequency of sound from rising too much at high flight speeds. Second, it no doubt greatly magnifies the loudness of sound produced, since a greater volume of air is disturbed and large vortices shed.

Both vortex shedding and flag fluttering models also correctly predict the fact that species of snipe with narrower outer tail feathers, such as Wilson's snipe, *Gallinago delicata*, produce a much higher pitched noise than the common snipe (Bahr, 1907).

However, in one way, neither model agrees with our observations. Flutter was not detected until an air-speed of 6 m s^{-1} was reached and sound could not be detected until 12 m s^{-1}. By contrast, the flag model predicts that flutter should start when the flutter frequency equals the resonant frequency of the plate, which was calculated and found by experiment to be around 50 Hz. One would therefore expect flutter to start at airspeeds around 2 m s^{-1}. The vortex shedding model predicts that vortices should start to be shed at the even lower speed of 0.7 m s^{-1}. Maybe at low speeds the flutter amplitude is simply too low to detect, or maybe the feather shaft acts to shelter the rear vane at low speeds and so delays flutter.

Although tail feathers of the hummingbirds examined by Clark and Feo (Clark and Feo, 2008) also seemed to show aerodynamically induced flutter, they showed quite different behaviour. The main difference, however, was in the movements of the vanes. In our snipe the entire length of the rear part of the trailing vane swung upwards and downwards more or less together, suggesting it acted as a single unit. By contrast, in the hummingbirds travelling waves moved up and down the vane, suggesting that different parts of the vane can move more independently. These differences may be related to the morphology of the vanes. In snipe the low angle of the barbs means that the base and tip of the broad hind vanes are closely connected. However, in the much narrower feathers of the hummingbirds each barb extends a much shorter

distance along the vane, although Clark and Feo (Clark and Feo, 2008) give no measurements of the barb angle. This would mean the tip and base can be mechanically uncoupled. It is possible that the hummingbirds do have some mechanism to locally reduce the flexural rigidity of their vanes, though as several of the tail feathers of hummingbird make sounds in airflow, it may not be so clear cut as in snipe. Clearly there is room for much further study of both the morphological and aerodynamic adaptations of other bird species to sound production.

APPENDIX
The flag flutter model of wing fluttering
Resonant frequency

Consider the flag-like fluttering of the hind vane, vibrating up and down along the hinge that we identified at the rear of the black region (Fig. 1). The flutter of such a structure is due to the changing aerodynamic forces as it flexes up and down; the further down it flexes the greater the upward restoring aerodynamic forces caused by lift and drag; the further up it flexes the greater the downward restoring lift and drag. The flutter frequency, f_F, of a freely hinged plate will depend on the aerodynamic restoring moment per angular displacement of the rear of the vane and its moment of inertia (Argentina and Mahadevan, 2005) according to the equation:

$$ f_F = \frac{(j/I)^{0.5}}{2\pi} \, , \qquad (A1) $$

where j is the change in aerodynamic moment per unit angle (in Nm per radian) and I is the moment of inertia.

The factor j cannot be readily measured but it can be approximated from aerodynamic theory. Assuming that lift forces are much greater than drag, the aerodynamic force on the rear vane is given by the equation for lift:

$$ \text{Lift} = \tfrac{1}{2}\rho C_L A \mathbf{v}^2 \, , \qquad (A2) $$

where ρ is the air density ($1.2\,\text{kg m}^{-3}$), C_L is the lift coefficient, A the area of the rear part of the hind vane, and $\mathbf{v}$ is the air velocity. Therefore the change in lift force per unit angular displacement is:

$$ \frac{d\mathbf{F}}{d\theta} = \tfrac{1}{2}\rho A \mathbf{v}^2 \frac{dC_L}{d\theta} \, . \qquad (A3) $$

This force will act at around the quarter chord position so that the change in restoring moment $\mathbf{M}$ per angular displacement:

$$ \frac{d\mathbf{M}}{d\theta} = j = \tfrac{1}{8}\rho L A \mathbf{v}^2 \frac{dC_L}{d\theta} \, , \qquad (A4) $$

and L is the maximum perpendicular distance from the hinge line to the trailing edge. Since the area of the hemielliptical rear part of the vane, A, is given by the expression:

$$ A = \frac{\pi S L}{4} \, , \qquad (A5) $$

where S is the span then:

$$ j = \tfrac{1}{32}\pi\rho S L^2 \mathbf{v}^2 \frac{dC_L}{d\theta} \, . \qquad (A6) $$

Aerodynamic theory states that for an aerofoil at low angles of attack:

$$ \frac{dC_L}{d\theta} = 2\pi \, , \qquad (A7) $$

so:

$$ j = \tfrac{1}{16}\pi^2\rho S L^2 \mathbf{v}^2 \, . \qquad (A8) $$

The rear part of the hind vane is approximately hemielliptical and so its moment of inertia, I, is approximated by the expression:

$$ I = \frac{mL^2}{4} \, , \qquad (A9) $$

where m is the mass of the rear part of the hind vane, and L is the maximum perpendicular distance from the hinge line to the trailing edge.

Combining equations A1, A8 and A9 gives:

$$ f_F = \frac{(\pi^2\rho S \mathbf{v}^2/4m)^{0.5}}{2\pi} $$
$$ f_F = \frac{\mathbf{v}(\rho S/m)^{0.5}}{4} \, . \qquad (A10) $$

Therefore the predicted frequency is proportional to the air velocity, and should rise with the span of the rear vane region and fall with its mass.

For the four feathers on which morphological measurements of the rear part of the trailing vane were made, the mean span was $5.1\pm0.7\,\text{cm}$ and mass was $4.95\pm0.31\,\text{mg}$. The predicted flag flutter frequency was therefore $(28.1\pm1.6)\mathbf{v}$.

The start of resonance

Aerodynamic theory (Argentina and Mahadevan, 2005) states that flag flutter will not occur until the flutter frequency exceeds the resonant frequency of the flag. We both calculated what the resonant frequency should be, and measured it directly.

For the tail feather, the resonant frequency f_R will depend on the angular stiffness of the hinge at the rear of the black region (Fig. 1) and the moment of inertia of the rear region of the hind vane according to the equation:

$$ f_R = \frac{(k/I)^{0.5}}{2\pi} \, , \qquad (A11) $$

where k is the spring constant (in Nm per radian) and I is the moment of inertia.

To calculate the spring constant of each feather we used a similar mechanical testing apparatus to that used by Combes and Daniel (Combes and Daniel, 2003) in their investigation of the stiffness of insect wings. The feather was clamped at the calamus with the vane horizontal. The equipment used to flex the vane (Fig. A1) was composed of a 1:1 pivoting arm made from a drinking straw. To
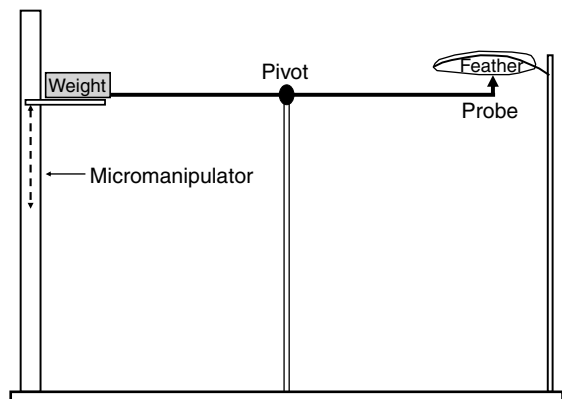

Fig. A1. Diagram of the equipment used to measure the compliance of the rear part of the feather vanes of the snipe. Weights applied in the container on the left push the rear of the vane upwards. Deflection of the trailing vane was measured using a micromanipulator.

one arm was attached a 1 cm long probe that contacted the rear feather vane from below and 4–5 mm behind the hinge. At the end of the other arm was a container into which paper weights of 0.0082 g (8.04×10^{-5} N) could be placed. As more weights were added the probe pushed the feather vane upwards, and the deformation of the vane was measured by a micromanipulator. The forces involved were so small that the rachis of the feather was not significantly bent. This allowed a plot of force against displacement to be drawn. From this, the spring constant, k, of the rear vane was calculated using the equation:

$$k = \frac{d\mathbf{M}}{d\theta}$$

$$k = x^2 \frac{d\mathbf{F}}{dy} \ , \tag{A12}$$

where x is the distance of the probe behind the hinge, and $d\mathbf{F}/dy$ is the initial slope of the force–displacement curve.

Therefore combining Eqns A9, A11 and A12 gives the expression for frequency:

$$f_{\mathrm{R}} = \frac{x}{\pi L} \frac{(d\mathbf{F}/dy)^{0.5}}{m} \ . \tag{A13}$$

To calculate the flag flutter and resonance frequencies, the span and the maximum perpendicular distance from the hinge line to the trailing edge were measured. Finally, the feathers were cut up and the mass of the rear part of the trailing vane was measured using a five-figure balance. These measures were then incorporated into Eqns A10 and A13. For the four feathers on which mechanical tests were performed, the average spring constant of the rear vane was $4.17 \pm 2.32 \times 10^{-6}$ Nm radian^{-1}. Since the mean distance from the hinge to the trailing edge was 6.0 ± 0.5 mm, this would give a mean resonant frequency of 50.5 ± 14.1 Hz.

Resonant frequency was also measured directly on three feathers. Feathers were mounted by their calamus with the vane extending over the front of a Matsui MHF 808R loudspeaker. Sounds rising from 10 to 2000 Hz were then emitted from the speaker, powered by a SigJenny audio signal generator Signal generator (Natch

Engineering, Framlingham, Suffolk, UK) while the movements of the feather were filmed using a Sony Handycam HDR-XR520VE in smooth slow motion at 100 fps. Fluttering movements of the hind vane were seen at frequencies between 20 and 80 Hz (see supplementary material Movie 2), indicative of a heavily damped oscillator with a resonant frequency of around 50–60 Hz.

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