RESPIRATION, WING-BEAT AND ULTRASONIC PULSE EMISSION IN AN ECHO-LOCATING BAT

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During flight, echo-locating bats must adjust their pulmonary ventilation to satisfy a variety of requirements. The basic role of respiration, in gas exchange and in the maintenance of physiological homeostasis under exercise stress, must be achieved in a way that is compatible not only with the rhythmic contraction of powerful flight-muscles but also with the continual production of high-intensity vocalizations necessary for acoustic orientation. Moreover, the demand for accurate navigational information is often greatest during the stresses of rapid erratic flight. At such times bats continually emit brief, high-intensity orientation sounds at repetition rates varying from a few to many per second. Nothing is known regarding the relationship between respiration, sound production and wing movements during flight, or the extent to which changes in pulse-repetition rate affects respiration.

Schnitzler (1968) correlated flank movements with orientation pulses emitted by resting *Rhinolophus ferrumequinum*, *R. euryale* and *Myotis myotis*. *Rhinolophus* emitted single, long-duration (up to about 90 msec) pulses or a group of several short (about 10 msec) pulses during one expiration. Quietly resting bats had respiratory rates of 4–7/sec, increasing to about 10/sec when the animal became excited. Resting *M. myotis*, which emit shorter pulses at higher repetition rates, produced up to 30 pulses during one expiration as judged by flank movements. Orientation sounds of flying bats are also sometimes emitted in groups which, it has been suggested, may reflect an adjustment of sound production to the respiratory cycle (Grinnell & Griffin, 1958; Suthers, 1965; Pye & Roberts, 1970).

We have investigated the relationship between respiratory rate, sound production and the wing-beat cycle during flight of the neotropical bat *Phyllostomus hastatus* (Pallas) of the family Phyllostomidae. We have given particular attention to the timing of pulses in the respiratory cycle and the effect on respiration of marked changes in pulse-repetition rate. *P. hastatus* was selected for study primarily because it was large enough (80–110 g; maximum wing-span about 50 cm) to carry a small radio trans-mitter for telemetry of respiratory rate. The ultrasonic orientation pulses of this species are composed of frequency-modulated components between about 30 and 80 kHz (Fig. 1). The duration of a single pulse is typically a little more than 2 msec. Pye (1967) reported that orientation sounds are emitted through the nostrils. High-speed films which we have taken of *P. hastatus* show that the mouth is closed during flight, in

contrast to that of orally emitting species. The physiological responses of this bat to
flight are being reported separately (Thomas & Suthers, in preparation).

METHODS

The majority of our experiments were performed on *P. hastatus* flying in an outdoor
wire-mesh flight cage, 15×4 m, at the William Beebe Tropical Research Station of
the New York Zoological Society in Trinidad, West Indies, where the bats were
collected. Some bats were transported to Indiana, where a few additional experiments
were conducted in an indoor flight room, 11×6 m, at Indiana University.

(a)

1 msec.

(b)   (c)
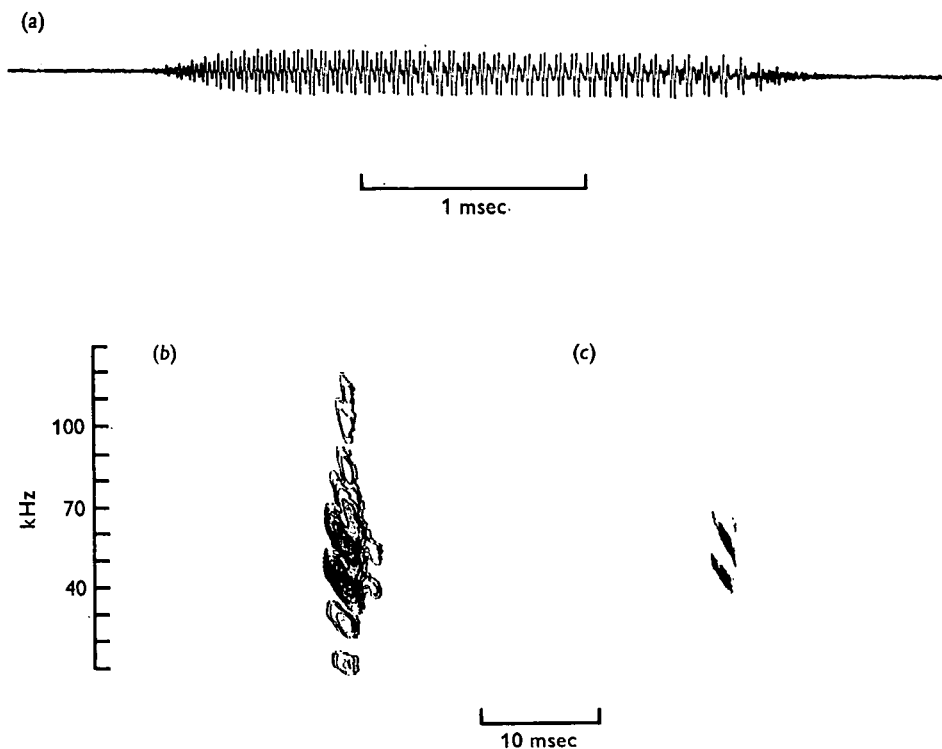
kHz

100

70

40

10 msec

Fig. 1. Ultrasonic orientation pulse of *Phyllostomus hastatus* flying in a large outdoor cage. (a)
Oscillographic display, (b) contour plot of frequency against time, (c) wide-band sonagram of
same pulse. Relative sound intensity is indicated in (b) by contours separated by 6 dB steps,
with the darkest shading representing the highest intensity. Figs. (b) and (c) were produced
on a Kay Electric Co. model 6061 B sound spectrograph.

Respiration

The respiratory cycle of resting and flying bats was monitored directly by a small
glass-bead thermistor (Fenwal GB 34J3) mounted about 2 mm in front of the animal's
nostrils so that it was alternately warmed and cooled by the exhaled and inhaled air,
respectively. This thermistor was connected by fine leads to the input of a modified
miniature FM transmitter (E & M Instrument Co., model FM-1100-E3) mounted
behind the bat's head (Fig. 2). The telemetered signal was detected with an FM
receiver (E & M Instrument Co., model FM-1100-7). The output of the receiver was

displayed on an oscilloscope for photography and recorded in an FM mode on one channel of a Precision Instrument PI-6100 tape recorder.

The approximate frequency response and phase lag of the telemetered thermistor signal were tested by mounting the thermistor in front of the tip of a small syringe whose plunger was driven by a variable-speed electric motor. The telemetered signal faithfully followed slightly warmed puffs of air approximately equal to the bat's tidal volume when these were delivered at rates up to 12/sec, the maximum frequency of which the motor-driven syringe was capable. This frequency was slightly above the respiratory rate of the flying bat. The actual upper limit of the thermistor's frequency response in this system is probably considerably higher since the amplitude of the telemetered sinusoidal signal was not visibly attenuated or distorted at 12 c/sec.

The phase lag of the thermistor was measured by arranging an electrical contact on the end of the syringe's plunger so that a circuit was momentarily closed when the plunger reached its outward-most position (corresponding to the end of inspiration). This circuit was connected to one beam of a dual-beam oscilloscope and the telemetered thermistor output was displayed on the other beam. The extent to which the telemetered signal lagged behind the motion of the plunger could thus be accurately determined from the oscillographic display. At the typical respiratory frequency of 10/sec there was a phase lag of almost 26°, or 8 msec, which equals 8% of a respiratory cycle (Fig. 3). No attempt has been made to correct the data presented below for this phase lag for the following reasons. First, a significant – but unknown – portion of the thermistor's lag is offset by the time required for the bat's pulse to reach the microphone. Sound in air travels about 34·4 cm/msec. The propagation time of the pulse to the microphone is of course continuously changing when the bat is flying but must average close to 4 msec and may sometimes approach 8 msec. The pulse-propagation time from a resting bat probably averages closer to 2 msec. Secondly, the amount of error introduced by the phase lag is dependent upon the frequency of the signal. The above estimate applies only to the basic respiratory rhythm of 10 breaths/sec. The telemetered signal, however, is not a simple sinusoid of this frequency, but has a more complex wave-form including considerably higher-frequency components, such as the apparent 'mini-breaths' described below. Since these high-frequency components have a much shorter period their horizontal displacement along the abscissa, due to phase lag, is much less than that of the lower-frequency components. The phase lag therefore cannot be corrected by simply sliding the whole complex respiratory wave-form along the abscissa. Finally, the phase lag is probably less in the case of the flying bat, since continuous air flow over the thermistor would increase its rate of heat dissipation and decrease its time constant.

Precautions were taken to eliminate other kinds of artifacts from the telemetered respiratory signal. For example, movement of the thermistor leads relative to the transmitter during flight resulted in extraneous electrical signals. Such movement was eliminated by attaching the thermistor leads and transmitter to a rigid aluminium frame. This lightweight frame, which was fastened by collodion to the animal's fur, consisted of a metal open-fronted mask around the bat's snout from which a small metal strip extended posteriorly over the head, where it was supported by a flange attached to the fur at the base of the skull (Fig. 2). The transmitter was attached to this extension just behind the head with double adhesive tape, and the leads were run

anteriorly along the frame, to which they were cemented. The thermistor projected
through a small hole in the band around the nose just anterior to the nostrils. The
aluminium frame did not interfere with the animal's vision or with movement of the
neck, ears or mouth. The transmitter, with its batteries, aluminium frame and therm-
istor weighed about 10 g and did not seriously impair the bat's ability to fly.

We also performed tests to verify that what we took to be the respiratory signal
was not caused by rhythmic acceleration of the body associated with the wing-beats
or possible capacitive effects of the moving wings on the transmitter. When a short
length of PE tubing, sealed at its outer end, was carefully slipped over a thermistor
without moving it, the transmitted signal lacked the sinusoidal wave-form, which
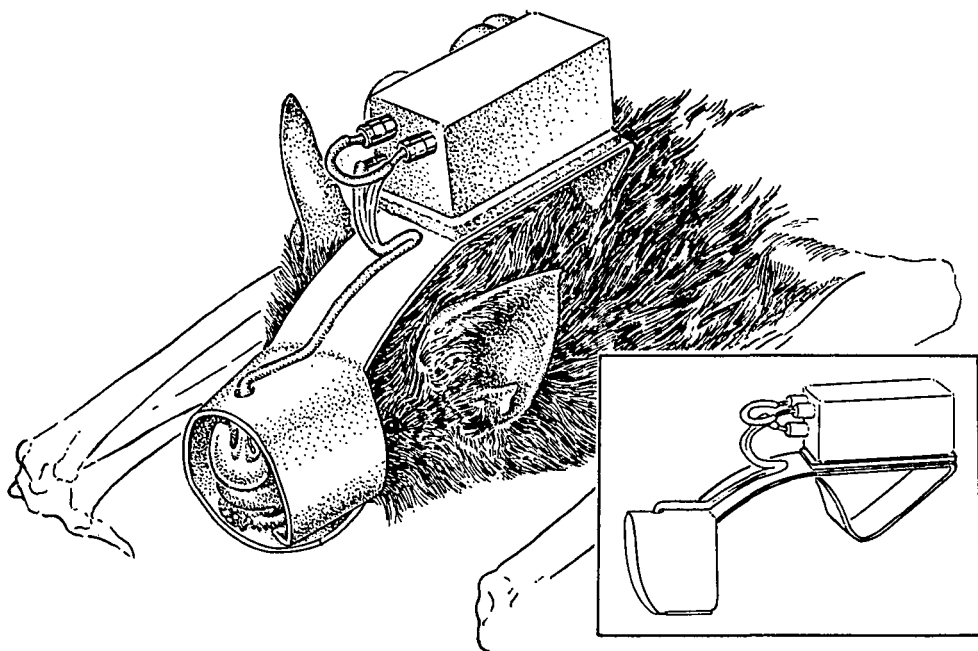thus reflected only the pulmonary ventilation (Fig. 3).

Fig. 2. *Phyllostomus hastatus* wearing the open-fronted aluminium mask containing the
thermistor and supporting the transmitter used to telemeter respiratory rate.

Vocalizations

Ultrasonic orientation pulses were recorded with a condenser microphone mounted
on a stand a short distance in front of the bat and connected to an ultrasonic amplifier
of either the type described by McCue & Bertolini (1964) or that manufactured by
Holgates of Totten Ltd. The sounds were recorded simultaneously with the respiratory
signal on a separate channel of the tape recorder. Respiration and orientation pulses
were also displayed simultaneously on separate traces of an oscilloscope.

Wing-beat cycle

Wing position was correlated with respiration and pulse emission by photographing
simultaneously the bat, carrying the transmitter, as it flew towards the microphone
and an oscilloscope screen displaying the pulses and respiration. Photography of the

bat was accomplished through a wide-angle lens attached to a Hycam model K 2001 R 16 mm high-speed motion-picture camera (Red Lake Laboratories, Inc.) operated at 100 or 150 frames/sec. Wing position was determined directly from the film. The wings were considered to be horizontal when they were level with the tip of the animal's nose. This camera uses a rotating prism, instead of a shutter, to form successive framed images on the film. This design allows the film to move at a constant speed, rather than in the jerky motion of conventional cine cameras. Furthermore, a supplementary lens on the back of the camera focused a dual-beam oscillographic display of the bat's vocalizations and telemetered respiratory signals directly on to the emulsion through the back of the film without interruption by the rotating prism. The sweep
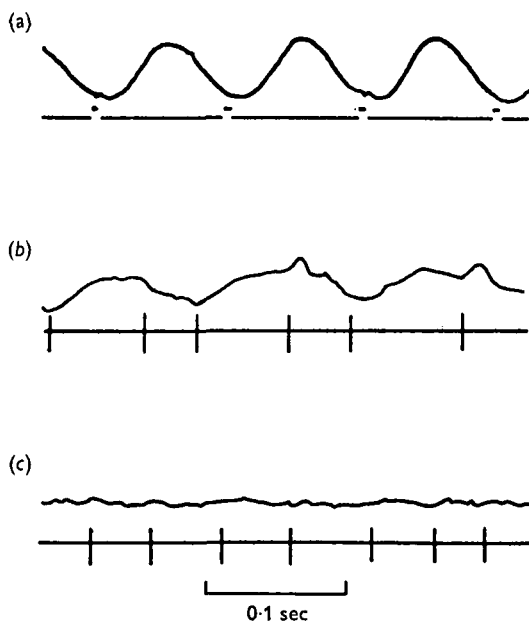
(a)

(b)

(c)

0·1 sec

Fig. 3. (*a*) Phase lag of the thermistor response. Telemetered signal from the thermistor (upper trace) mounted 2 mm in front of a small, slightly warmed syringe, the plunger of which was being driven at about 10 c/sec by an electric motor. Upward deflexion of the thermistor signal indicates warming. The momentary vertical displacement of the lower trace indicates the instant at which the plunger reached its outward-most position (analogous to the end of inspiration). This displacement precedes the inflexion of the telemetered signal, which can thus be shown to have a phase lag of about 26° (see text). (*b*) Telemetered signal from thermistor (upper trace) and orientation pulses (indicated by vertical lines across lower horizontal line) of a flying bat. Thermistor mounted about 2 mm in front of nostrils. (*c*) Thermistor in same position but covered by a small segment of PE tubing shielding it from the respiratory air flow. Absence of major deflexions in telemetered signal in (*c*) confirmed that these deflexions in (*b*) did indeed reflect the respiratory cycle. Expiration is associated with an upward deflexion of the respiratory signal.

of the oscilloscope was stopped during photography so that the vocalizations and respiratory wave-form were superimposed as continuous traces across the framed images of the bat flying in front of the camera. In this way both the orientation sounds and respiratory rhythm were recorded on the same film with the image of the flying bat – greatly facilitating analysis of their temporal relationships. A timing light provided an accurate time base and the microphone was visible at one side of the

camera's forward field of view so that its distance from an approaching bat could be¹ measured. The usual procedure consisted of releasing a hand-held bat at one end of the flight cage and photographing it as it flew through the camera's field of view, past the microphone, and towards the opposite end of the cage.

Since wing position was determined from photographs of the flying bat, its recording involved no propagation-time delay. Careful inspection of Fig. 5 shows that the recorded respiratory signal did sometimes lag slightly behind the wing position. This slight lag may well be an artifact introduced by the thermistor's time constant discussed as above. If so, the beginning of expiration may be even more precisely synchronized with the start of the upstroke than is indicated by Fig. 5.
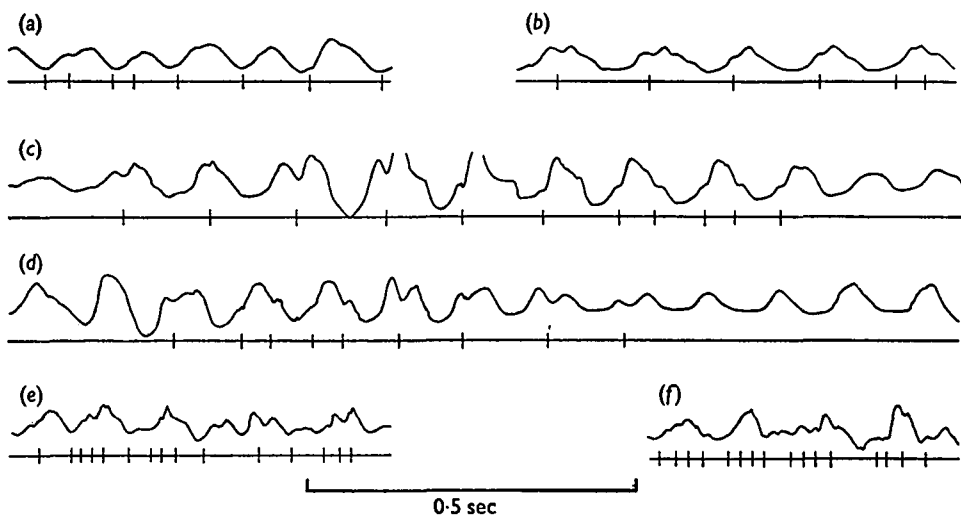

Fig. 4. Relationship between respiration (upper line) and orientation pulses (vertical bars across lower line) in resting *P. hastatus* emitting pulses at various repetition rates. The duration of each orientation pulse is fairly accurately indicated by the width of the vertical bars. Expiration is associated with an upward deflexion of the respiratory signal.

RESULTS

Respiration and ultrasonic pulse emission in the resting bat

P. hastatus, scanning their environment while resting or crawling about, emitted orientation pulses at almost any point in their respiratory cycle – even at low pulse-repetition rates. Although pulses frequently occurred at the beginning of expiration (Fig. 4a), they also were emitted in the middle of expiration or near the reversal point between expiration and inspiration (Fig. 4b, c). When two pulses were emitted during a single respiratory cycle, one often occurred during the expiratory phase – the other during the inspiratory phase (Fig. 4c, d). At higher pulse-repetition rates of 3 or 4 pulses per cycle the sounds tended to be evenly spaced over part or all of the respiratory cycle (Fig. 4e, f). Fig. 4 (f) is an example of ultrasonic pulses arranged in groups of four with one group emitted during each respiratory cycle. In such cases the first pulse of each group tends to occur just after the start of expiration. It is noteworthy that in both resting and flying bats the majority of pulses in each group occur during expiration and the silent period between groups is usually associated with the final portion of the inspiratory phase.

Echo-locative sounds in Fig. 4 are often associated with an inflexion in the trace of the basic respiratory cycle. The thermistor position is critical for the recording of these inflexions so their absence during many pulses is not necessarily significant. The momentary excursions of the respiratory trace associated with pulse emission could be caused by a marked change in the velocity of air flow, a cessation of air flow – perhaps associated with a glottal stop, or a brief reversal in the direction of air flow. We believe the largest of these inflexions, which almost bisect the respiratory cycle (Fig. 4*c, d*), probably represent temporary reversals of air flow preparatory to sound emission. They are associated with the end of expiration, suggesting that the bat was replenishing part of its tidal volume to obtain sufficient air in its lungs for a final expiratory pulse.
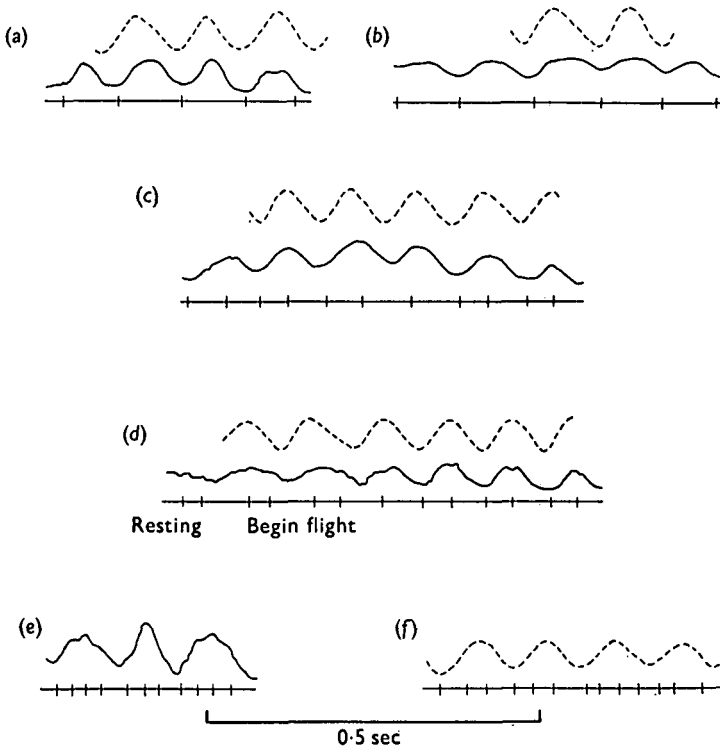

Fig. 5. Relationship between the wing-beat cycle (upper dashed line), respiratory cycle (middle solid line) and orientation pulses (represented by vertical bars across lower horizontal line) of *P. hastatus* during flight at various pulse-repetition rates. Expiration is associated with an upward deflexion of the respiratory signal.

Relationship between pulse emission, respiratory and wing-beat cycles during flight

During normal flight the respiratory cycle is correlated on a 1:1 basis with wing movement. Inspiration occurs during each downward power stroke of the wings and expiration is associated with their upward recovery stroke (Fig. 5). The respiratory and wing-beat frequency during flight is about 10 c/sec (the observed range was 9·7–10·2).

We have recorded pulse-repetition rates up to about 40/sec from flying *P. hastatus*. Respiratory and wing-beat frequency appear to be unaffected by marked changes in

the rate of ultrasonic pulse production. The lowest pulse-repetition rates during flight were observed in bats that had become familiar with our experimental procedure. Under these conditions one orientation sound was usually produced during one wing-beat or respiratory cycle (Fig. 5a, b). Each pulse was typically emitted near the point of reversal in the direction of respiratory air flow associated with the end of inspiration and the beginning of expiration. This was also the instant at which the wings were at their downward-most position. At repetition rates of less than about 10 pulses/sec the animal must remain silent during some respiratory cycles. This situation may be more common in nature than the data from our captive bats, flying in a relatively confined space, would suggest.

Higher pulse-repetition rates are accomplished by producing two or more pulses per respiratory cycle. When two orientation sounds are emitted per respiratory cycle, one is normally placed at the beginning and the other near the end of expiration or during early inspiration (Fig. 5c). Our data suggest that P. hastatus times its pulses to coincide with the beginning and end of expiration more consistently in flight than it does at rest for similar pulse-repetition rates (compare Fig. 4c, d, with Fig. 5c). This more consistent synchronization of pulse emission with respiratory phase develops during the first few wing-beats of flight (Fig. 5d). The last three respiratory cycles of this sequence (Fig. 5d) show a small inflexion at the end of expiration similar to those noted above in the case of non-flying bats.

At higher pulse-repetition rates sound production is not confined to the beginning and end of expiration. One P. hastatus emitted three and four orientation pulses per respiratory cycle while manoeuvring to avoid the microphone (Fig. 5e). Wing-position data are absent in this case since the bat passed out of view of the camera. The respiratory signal shows, however, that pulses can be emitted during almost any part of the basic respiratory cycle – even the middle of the inspiratory phase. We doubt that such pulses are examples of inspiratory voice, however, even though there is often no indication in the respiratory signal of an air-flow reversal (see Discussion). Thermistor position and sensitivity may be even more critically important in detecting momentary expirations in the middle of the inspiratory phase because the tiny volume of air reaching the thermistor may not have entered the bat's airway far enough or long enough to be heated sufficiently to warm the thermistor. Temporal grouping of pulses reflecting respiration is more pronounced at high pulse-repetition rates as has been noted above in the case of resting bats. A further example of the relationship of sound emission to wing-beat at high pulse-repetition rates is shown in Fig. 5 (f). Although the respiratory signal is absent it may be assumed to be synchronized with the wing-beat cycle.

DISCUSSION

Correlation of respiration with wing-beat

Each respiratory cycle of P. hastatus is accompanied by one complete wing-beat cycle during normal flight. Inspiration is associated with the downward stroke of the wings. Respiratory rate during flight is thus almost constant – the adjustment of ventilation to changing metabolic demands presumably being made by varying the tidal volume. The rigid synchronization of ventilation with wing motion may reflect thoracic volume changes brought about by the action of the flight muscles. The

association of inspiration with the power stroke of the wings is surprising in this respect, since one might anticipate that contraction of the flight muscles would tend to compress the thorax. We have not monitored thoracic movements during flight. In the resting bat, however, there was no noticeable movement of the thorax associated with respiration, even after strenuous flight. Pulmonary ventilation in resting *Phyllostomus* seemingly depends on action of the diaphragm which is accompanied by a rapid motion of the dorsal body wall posterior to the rib cage and lateral to the spine.

Birds, while sharing with bats the ability to fly, differ profoundly in their thoracic and pulmonary anatomy. Both must meet the energetic and aerodynamic demands of flapping flight, however, and it is interesting to note the various relationships between wing-beat and respiration in birds. Tomlinson & McKinnon (1957) found pigeons (*Columba livia*) had a 1:1 relationship between respiratory and wing-beat cycles, with inspiration associated with the upstroke. Hart & Roy (1966) confirmed the 1:1 co-ordination but found the peak rates of expiration and inspiration coincided with the bottom of the downstroke and top of the upstroke, respectively. Lord, Bellrose & Cochran (1962) concluded, on the basis of telemetered changes in thoracic shape, that mallard ducks (*Anas platyrhynchos*) took one or two breaths per wing-beat. Tucker (1968) found that although the wing-beat frequency of budgerigars (*Melopsittacus undulatus*) was a constant 840 beats/min at all flight speeds, respiratory rate varied continuously with changes in flight speed. Fraenkel (1934) likewise obtained tentative evidence of respiratory independence from the wing-beat cycle in the chaffinch (*Fringilla coelebs*). Berger, Roy & Hart (1970) studied the co-ordination of respiration with wing-beat in nine species of birds of weights ranging between about 7 and 1700 g. They report that, whereas respiration was usually correlated with wing movement, in the sense that the reversal of respiratory air flow tended to be associated with certain phases of the wing cycle, this co-ordination was often such that several wing-beats occurred during one respiratory cycle. An individual bird could exhibit several kinds of co-ordination during a single flight. In general, inspiration began at the end of the upstroke and expiration started at the end of the downstroke. Although this phase relationship is similar to that which we have found in *Phyllostomus*, only pigeons and crows are known to have respiration/wing-beat ratios of 1.

Echo-location and the respiratory cycle

P. hastatus crawling about a cage produces echo-locative sounds at almost any point in its basic respiratory cycle – even at low pulse-repetition rates of only one or two per cycle. At higher pulse-repetition rates the vocalizations are more or less evenly spaced during the complete respiratory cycle with the possible exception of a tendency to be silent during the final portion of inspiration. When in flight, ultrasonic pulses are preferentially emitted at the beginning and/or end of the expiratory phase unless higher repetition rates are required, in which case they tend to be spaced over both expiration and all but the final portions of inspiration. It may be that sound emission is less disruptive to pulmonary ventilation when it occurs near the instant at which the direction of tidal air flow reverses.

The maximum pulse-repetition rate of *P. hastatus* seems to be appreciably lower than that of many insectivorous bats. Whereas repetition rates of the latter approach 200 pulses/sec when capturing food, *P. hastatus* rarely exceeds 40–50 pulses/sec and

we have not recorded more than four pulses during one respiratory cycle. These maximum pulse-repetition rates are consistent with those found in previous experiments (Chase & Suthers, 1969) with this species. Schnitzler (1968) reported that resting *Myotis myotis* could emit up to 30 pulses during one expiration (representing a pulse-repetition rate of over 100/sec), in contrast to resting *Rhinolophus* which produced only one to several pulses of much longer duration during a single breath. High pulse-repetition rates may not be needed by *Phyllostomus*, which is primarily frugivorous and lacks the agility of smaller insectivorous species which feed on rapidly and erratically moving prey. Whatever insects *Phyllostomus* does catch are probably relatively large and slow flying. Vision is also relatively better developed in this bat (see Suthers, 1970), although it is probably of little help in detecting nocturnal insects.

Since the need for acoustic information is independent of the respiratory requirements, it is clearly advantageous to be able to produce sound at any point in the respiratory cycle. In order to do this the bat must either be able to produce echo-locative pulses regardless of the direction in which air is flowing through the larynx or, if sound production is possible only during laryngeal air flow in one direction (e.g. caudo-cephalad as during expiration), then sounds emitted during the opposite respiratory phase must be accompanied by a brief reversal of the direction of flow which momentarily interrupts the basic respiratory rhythm. In considering which of these techniques *P. hastatus* has utilized it is important to resist anthropocentric assumptions. Human vocalization requires expiratory air flow but this condition is exceptional among vertebrates. The elimination of inspiratory voice during vertebrate evolution is in fact sufficiently unique that man's nearly total dependence on expiratory voice has been referred to as 'a pathological phenomenon' (Kelemen, 1963).

It is difficult to measure the flow of minute volumes of air during a 1–2 msec orientation pulse. We estimate the entire tidal volume of a flying *P. hastatus* to be less than 2 ml (Thomas & Suthers, in preparation). As indicated above, the occasional small inflexions of the respiratory signal coinciding with pulse emission could represent a change in the direction or velocity of respiratory air flow or a cessation of flow. Momentary air-flow stoppage may be associated with a glottal stop needed to allow an increased pulmonary pressure during sound emission. The intensity of human vocalization increases with increasing subglottic pressure. Pye (1967) has suggested that the various wave-forms of most varieties of orientation pulses could be produced by a pulsed glottal wave-form which, together with its harmonic components, undergoes phase and amplitude modulation due to passive resonance properties of the air-filled vocal cavities. Further modulation would be possible in bats emitting sounds orally by using muscles to vary the shape of the oral cavities.

The largest interruptions of the basic respiratory cycle were recorded from resting bats (Fig. 4c, d) at the end of normal expiration. The timing and size of these particular inflexions lead us to believe that they probably represent momentary inhalations needed to provide enough pulmonary air for an additional expiratory vocalization prior to normal inspiration. A respiratory interruption of this kind at the end of expiration would seem unnecessary if the bat were capable of inspiratory voice, since normal inspiration was about to begin.

Similar interruptions of respiration for the purpose of vocalization have been noted by Calder (1970), who used an impedance pneumograph to monitor respiration during

song in resting canaries. These vocalizations differ, of course, in many respects from the orientation pulses of bats. A single song is composed of a sequence of complex phrases which last many seconds – the equivalent of several respiratory cycles in the non-singing bird. Each sound pulse uttered by the canary – whether in a fast trill or slower phrase – was accompanied by a small exhalation followed by a rapid inspiration before the next sound pulse. Calder refers to these as 'mini-breaths' and believes them to ventilate primarily the pulmonary dead space and thus be of little respiratory value. Though of longer duration, they are qualitatively similar to the momentary interruptions of the respiratory cycle which we have found associated with some orientation pulses of *P. hastatus*.

The timing of these 'mini-breaths', together with the fact that at both low and high repetition rates pulses are most frequently associated with the expiratory phase of respiration, suggests that laryngeal air flow during ultrasonic pulses is in the caudocephalad direction. Whereas we favour this hypothesis of expiratory voice in regard to the ultrasonic orientation pulses of *P. hastatus*, we do not wish to imply that inspiratory voice might not play a role in other non-echo-locative sonic and ultrasonic vocalizations of this bat or possibly even in the orientation cries of other species, some of which are more variable.

SUMMARY

1. The relationship between respiration (by telemetry), wing-beat (by cinematography) and ultrasonic pulse emission (by telephony) was studied in the echo-locating bat, *Phyllostomus hastatus*, at rest and when flying in a large enclosure.

2. In resting bats echo-locative pulses were produced at almost any point in the respiratory cycle, in flying bats more frequently near the beginning and/or end of expiration.

3. During flight the respiratory cycle showed a one-to-one relationship with the wing-beat cycle, both having a frequency of about 10 c/sec. Expiration was associated with the upward recovery stroke of the wings.

4. Both resting and flying bats emitted up to four pulses per respiratory cycle. Grouping of pulses was prominent during flight, the first pulse in each group being normally emitted at the start of expiration, with the last pulse and the silent period between groups being associated with inspiration.

5. Momentary inflexions in the respiratory signal associated with pulse production may represent momentary reversals in the direction of air flow, or 'mini-breaths', to permit vocalization. This and other evidence suggests that the production of pulses during the inspiratory phase is probably accompanied by a very brief expiration.

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