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The energy cost of echolocation in pipistrelle bats (*Pipistrellus pipistrellus*)

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Summary. A positive relationship was established between energy expenditure and pulse rate of echolocation for 8 pipistrelle bats (*Pipistrellus pipistrellus*) when hanging at rest in a respirometry chamber at 28 °C. The least squares fit equation:

Energy expenditure ($J \cdot g^{-1} \cdot h^{-1}$) = 110.09 + 40.3 pulse rate (*n*/s) explained 14% of the minute by minute variation in energy expenditure. For a 6 g bat therefore each pulse costs approximately 0.067 Joules to produce. The net cost of echolocation at 10 pulses per second for a 6 g pipistrelle bat was predicted to be 9.5 × BMR with a range of 7.0–12.2 × BMR. We suggest that since a major portion of the cost of echolocation may result from contraction of the pectoralis and scapularis groups of muscles, the cost of echolocation is reduced for flying animals which contract these muscles anyway during flight. This may account for the high incidence of echolocation systems amongst flying vertebrates, when compared with terrestrial species.

Introduction

The sensory systems used by the majority of animals are passive. That is an animal detects energy or chemicals which are emitted directly from, or reflected by, the environment, but plays no part in the generation of that energy or matter. Dawkins (1986) suggested that since the intensity of energy in a signal declines as the inverse square of distance, most sensory systems are passive because active systems are precluded by the enormous cost of generating a sufficiently intense signal, that will not be too attenuated, after reflection, over any practically useful distance. The problem of signal reduction due to the inverse square law is compounded by imperfect transmission in the medium and imperfect reflection. In fact the intensity of an echo often varies as the cube or fourth power of target distance (Morse 1948). Moreover estimates of the energetic efficiency of sound production in animals (McNally and Young 1981; Prestwich and Breuer 1987; Ryan 1988) indicate it is very inefficient, and large amounts of energy must be expended to generate noises.

Nevertheless at least two active sensory systems have evolved. Electrolocation is found in several fish species (Machin and Lissmann 1960). A weak electric field is generated in the water surrounding the animal and objects entering the field are detected by the effect of their different conductance from the water on the field strength. Echolocation is used by several species of aquatic Cetacea (Norris et al. 1961), at least two genera of birds, oilbirds (*Steatornis*) (Griffin 1953) and cave swiftlets (*Collocalia*) (Novick 1959), but most notably the microchiropteran bats (Griffin 1958). Echolocation involves generation of a high intensity sound and detection of its faint echo. The favourable properties of water as a medium for conductance of sound signals (Griffin 1958) reduce the required intensity of the initial call signal, and hence probably the cost of its generation. Mammals which had already evolved the capacity to generate sounds, and then became secondarily aquatic were able to exploit their sound generating capacities, in the favourable medium, to evolve 'cheap' echolocation systems.

The advantage of water as a conductive medium, however, was not available to either the bats, or to cave dwelling birds. In consequence the signal calls of many of these species are of very high intensity, and in many bats may approach 120 dB (Griffin 1958; Simmons and Vernon 1971).

In recent years the overriding importance of echolocation as a universal system for detection of prey amongst the Microchiroptera has been challenged; other, passive systems have been suggested to be of importance, particularly passive listening (Fielder 1979; Bell 1982), olfaction (Kolb 1961) and vision (Bell 1982, 1985). One factor which may have been important in the evolutionary development of strategies for prey detection amongst the Microchiroptera is the energy cost of generating the very loud echolocation calls (Howell 1979; Dawkins 1986; Simmons and Vernon 1971). In this paper we present the first evaluations of the cost of echolocation for a microchiropteran bat.

Methods

Study species. Eight pipistrelle bats (*Pipistrellus pipistrellus*) were caught from a maternity roost in Scotland (57° N). They were trained to feed in captivity on mealworm larvae (*Tenebrio* sp.) and housed in a room (6 ×6×3 m) in which they could fly freely. A small wooden box was habitually used for roosting during the day. The bats had free access to food and water. A low intensity photoperiod was maintained, similar to light conditions in a natural roost, and the room was artificially heated and regulated at 22–27° C.

Protocol, apparatus and data analysis. Measurements of energy expenditure were made using an open flow, dual channel respirometry apparatus (Speakman and Racey 1987) with a modified respirometry chamber (Fig. 1) of 400 ml capacity. It was lined with foam which served a dual purpose; firstly, it provided a substrate on which the subject bat could hang, and secondly, it absorbed much of the energy in the echolocation calls generated by the subject so that it would not be inhibited from calling by loud and confusing echoes.

The broadband microphone of a QMC S200 bat detector (QMC Instruments Ltd) was glued into the top of the chamber to detect calls from the animal. Inlet and outlet tubes to the chamber terminated at opposite ends of the chamber to promote mixing of the gases. Bats placed in respirometry chambers were initially reluctant to echolocate spontaneously. We discovered, however, that by placing a few small live dipteran flies in the chamber, such as are the natural prey of this species (Racey and Swift 1985; Swift et al. 1985) the incidence of spontaneous echolocation dramatically increased. The total mass of these insects was approximately 0.01 g, less than 0.2% of the mass of the subject bats. The presence of insects exerted no detectable effect on the difference in O_2 concentration between inlet and outlet gas streams and the CO_2 content of the exhaust stream. Bats were weighed to the nearest 0.01 g, and their body temperature measured to the nearest 0.1 °C by insertion of a 0.5 mm diameter probe into the rectum prior to being placed in the chamber.

The flow rate of air through the system was maintained at 8–10 ml/s. Analog outputs from the sample and reference channels of a Taylor Servomex OA-184 oxygen analyser (Servomex Ltd) monitoring input and output gases to the chamber, an infrared CO_2 analyser (Mine Safety Appliances Limited) monitoring the output gas stream and a precision flowmeter (DM3A Alexander Wrights Limited) were all fed to the A–D converter (μPD 7002) of a BBC microcomputer (Acorn Limited). The computer logged inputs from each channel at 40 ms intervals and these readings were then integrated over periods of 30 s. The mean difference in oxygen concentration between air entering the chamber and leaving (ΔO_2), mean carbon dioxide in the exhaust air (CO_2), and mean flow rate, were used to calculate the oxygen consumption, CO_2 production and RQ. These data, corrected to STDP, were used to calculate the mean expenditure of the bat using the equation of Lusk (1926) over each 30 s the subject spent in the chamber.

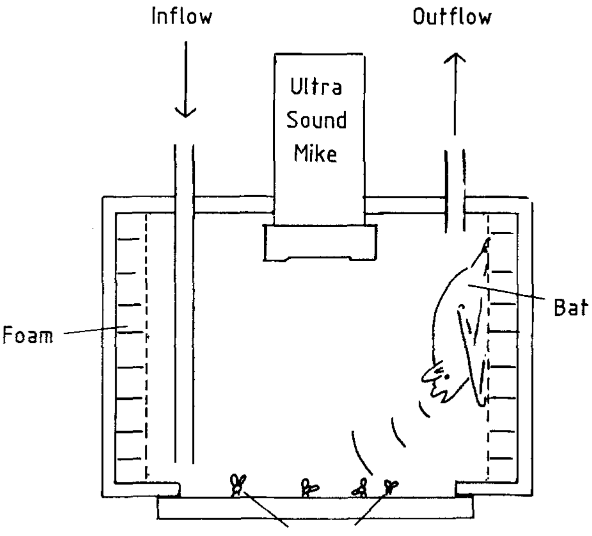

Fig. 1. Respirometry chamber for the study of echolocation in pipistrelle bats. The chamber was foam lined and had an integral ultrasound microphone (USM) to pick up echolocation calls. The whole chamber was made of transparent perspex which allowed observations to be made of gross activity, without disturbing the animal

Simultaneous to the measurement of energy expenditure, the echolocation calls of the subject bat were detected by the microphone (Fig. 1) linked to a S200 bat detector (QMC Limited) tuned to 45 kHz, which represents the frequency at which peak intensity of calls of this species are recorded in the wild (Ahlen 1987). The audible output of the bat detector was then recorded onto one channel of a stereo cassette tape recorder (Stellavox). The call record was synchronized with the oxygen consumption and energy expenditure record using a tone emitted by the BBC microcomputer at the start of each 30 s period, recorded in the second channel of the cassette recorder, together with a verbal note of the record number.

A consequence of placing dipteran flies in the chamber with the bats was that the bats moved around more, possibly attempting to catch the flies. Furthermore these movements were synchronized with periods of high echolocation activity. A continuous observation of the bat's position in the chamber was therefore maintained via the opaque top of the chamber. Opacity allowed an observer to record gross movements of the bat without disturbing it. 'Activity' involving whole body movements was recorded as present or absent in each 30 s interval, but did not include changes in head orientation which commonly accompany echolocation. Only continuous records in excess of 20 min during which no activity was recorded were included in the analysis.

Although in theory the gases in the respirometry chamber could be replaced completely in 40–60 s at the flow rates employed, the assumption of perfect mixing in the chamber did not hold. A test change in input calibration gas from 0% CO_2 to 1% CO_2 at the input to the chamber suggested there was a lag of 1 min to 90 s between gases entering the respirometry chamber and entering the gas analysers due to dead space in the tubing and drying system, and that gases in the chamber mixed over approximately 80 to 100 s. The measurement of energy expenditure over a given 30 s period could not therefore be justifiably compared with behavioural events observed simultaneously in the respirometry chamber. To account for imperfect mixing in the chamber an average call rate (echolocation pulses/s) was calculated over the 90 s prior to each oxygen consumption reading. To account for the lag between gases leaving the respirometry chamber and being measured at the gas analysers, sequential data of energy expenditure estimates were correlated with 'simultaneous' evaluations of call rate over the 90 s prior to each measurement. The call rates were then stepped forwards one position (effectively simulating a time lag of 30 s in the energy expenditure measurement) and the correlation recalculated. This stepping procedure was iterated 4 times simulating lags of up to 2 min. The position of peak correlation was used in all subsequent analyses.

Subject bats were removed from the chamber after periods of 40 to 60 min and weight and body temperature (T_b) were remeasured. Short experimental periods were used because over longer periods (hours) the bats became torpid. During torpor the energy demand decreased due to lowered T_b and the bats ceased to echolocate. T_b was consequently an important covariable which we were able to eliminate by taking short duration measurements during which T_b varied only slightly (<2 °C). Ambient temperature during all measurements was 27–29 °C.

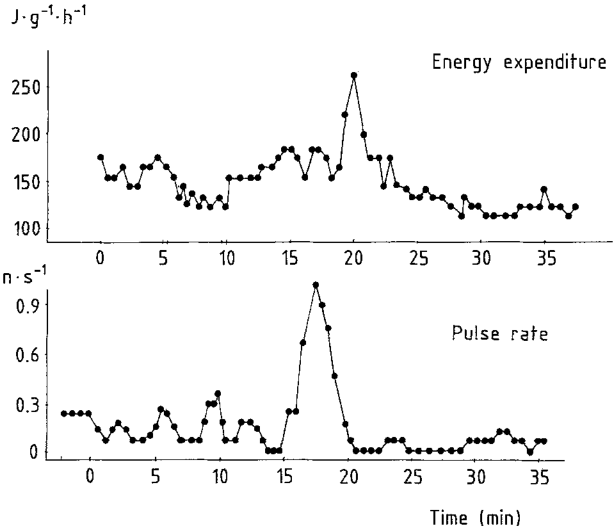

Fig. 2. Simultaneous records of energy expenditure ($J \cdot g^{-1} \cdot h^{-1}$) at 30 s intervals and echolocation calls (*n*/s over 90 s prior to energy expenditure measurement period) for an individual pipstrelle bat over 35 min

Results

The pattern of energy expenditure of an individual *P. pipistrellus* and the simultaneous echolocation record is shown in Fig. 2. There was a broad positive correlation between the two records which was typical. The evident lag between the two was a consequence of the lag in response of the energy expenditure measures due to dead space between the respirometry chamber and the gas analysers. Table 1 shows correlations between the mean energy expenditure ($J \cdot g^{-1} \cdot h^{-1}$ over 30 s) and echolocation pulse rate (pulses/s in previous 90 s) for iterative steps of the pulse rate up to 4 steps forward on energy expenditure for all 8 individuals. In all cases shifts of 2 or 3 positions of the call rate forward on energy expenditure resulted in a peak in correlation between the 2 variables. This simulates a lag of 60–90 s between the chamber and the gas analysers which was anticipated by empirically observed lags of the same duration for step changes in the concentration of CO_2 entering the respirometry chamber.

In all 8 individuals there was a significant positive relationship between energy expenditure ($J \cdot g^{-1} \cdot h^{-1}$) and pulse rate (*n*/s) (Fig. 3). In all cases log transformation of variables resulted in a slight reduction in the correlation coefficient ($\bar{x}$ reduction = 0.05) and linear combination of variables always produced the greatest correlation. In some cases this was probably because the variables were not normally distributed. However, in most individuals the relationship was evidently linear. We retained the use of the linear variables in the calculation of regression coefficients and constants for all individuals.

The data were combined across all 8 individuals (Fig. 4: total $n = 605$). The least squares fit linear regression:

Table 1. Correlation coefficients (r) between energy expenditure ($J \cdot g^{-1} \cdot h^{-1}$) averaged over 30 s periods and echolocation pulse rate (*n*/s) averaged over 90 s periods, with the 2 measurement periods ending simultaneously (no displacement), and with the echolocation pulse rates displaced forwards by units of 30 s, for 8 *P. pipistrellus*. Peak correlations, indicated in bold, occurred with either 2 or 3 displacements indicating a lag of 60 to 90 s

Individual displacement	1	2	3	4	5	6	7	8
None	0.57	0.26	0.44	0.33	0.57	0.07	0.69	0.09
30 s	0.67	0.01	0.41	0.42	0.73	0.26	0.76	0.18
60 s	**0.74**	0.21	**0.46**	**0.54**	**0.74**	0.49	**0.86**	**0.31**
90 s	0.68	**0.38**	0.44	0.36	0.68	**0.64**	0.82	0.30
120 s	0.60	0.20	0.34	0.35	0.50	0.63	0.71	0.29

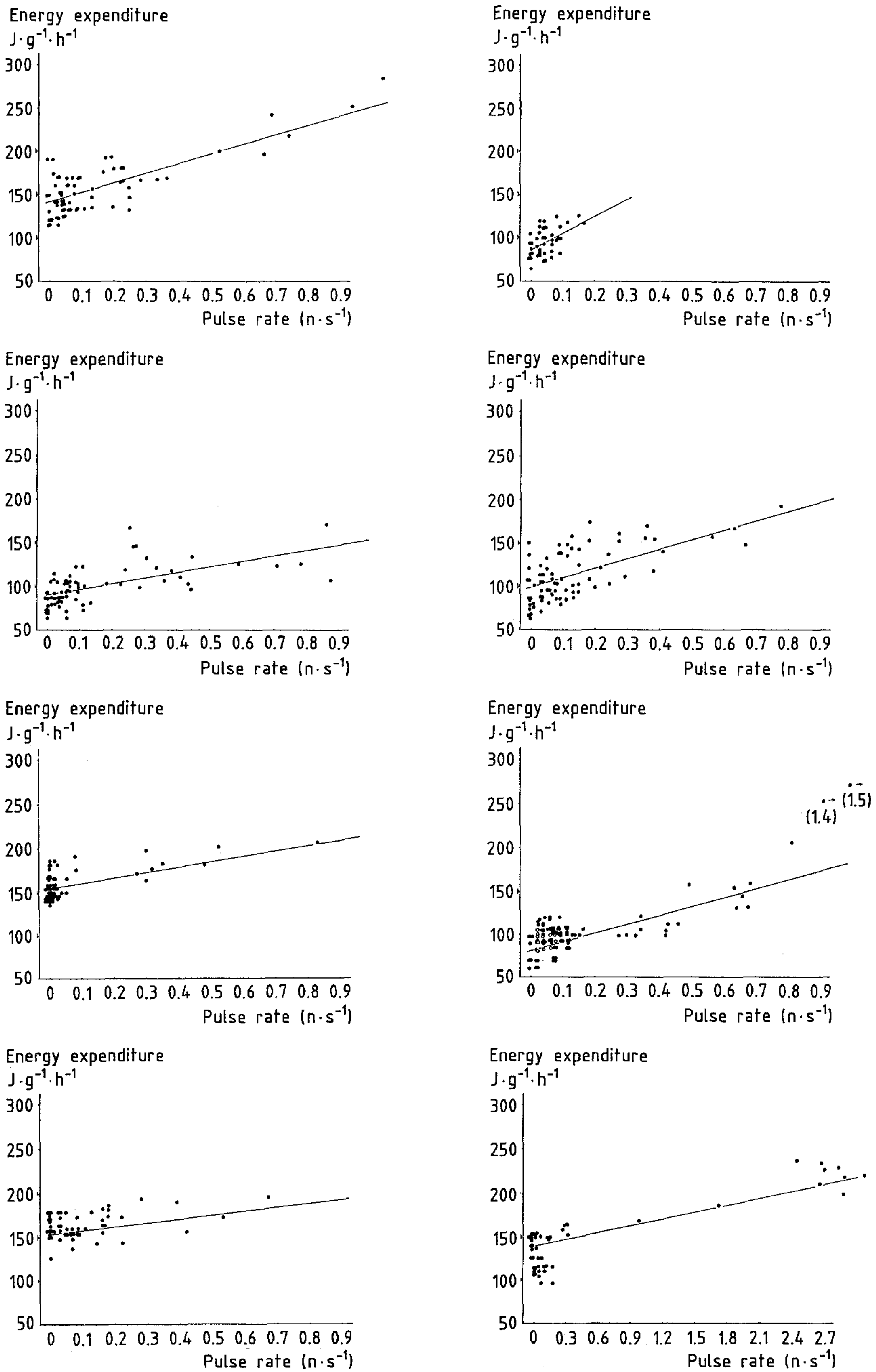

Fig. 3. Energy expenditure ($J \cdot g^{-1} \cdot h^{-1}$) averaged over 30 s periods plotted against the echolocation pulse rate (*n* pulses/s) averaged over 90 s and displaced forwards by 60–90 s (dependent on individual – see text) relative to the metabolism estimate (to account for the imperfect mixing in the respirometry chamber and time lag between gas leaving the chamber and entering the gas analysers) for 8 individual *P. pipistrellus*. In all 8 individuals there was a significant positive linear relation shown by the fitted regression curves in each figure

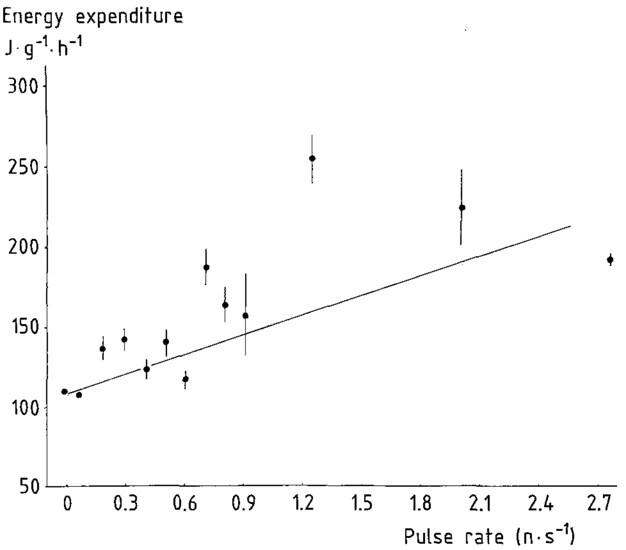

Fig. 4. Energy expenditure ($J \cdot g^{-1} \cdot h^{-1}$) plotted against echolocation pulse rate summed across all 8 individuals. Means and standard errors are shown with the least squares fit linear regression $y = 110.9 + 40.3\,x$ which explained 14% of the minute by minute variation in energy expenditure

Energy expenditure ($J \cdot g^{-1} \cdot h^{-1}$) = 110.9 + 40.3 Pulse rate (*n*/s), explained 14% of the minute by minute variation in energy expenditure.

For a typical 6 g pipistrelle bat the predicted energy cost of rest without echolocation at 28 °C by substitution into the fitted regression equation is 0.185 J/s. When echolocating at 1 pulse every s the predicted energy cost increases to 0.252 J/s. Since the relationship between energy expenditure and pulse rate was linear the energy cost of generating a single pulse is 0.067 Joules.

During normal searching flight, bats routinely produce pulses at faster rates than the maximum we observed in the respirometry chamber, up to 10 pulses each s. Although we are conscious of the dangers of extrapolation beyond the observed data the predicted cost of echolocation for a 6 g bat at these rates from the fitted equation was 3.085 kJ/h (95% predictive interval (PI) = 2.43–3.74 kJ/h). Subtracting the resting costs without echolocation (0.66 kJ/h) yields 2.42 kJ/h (95% PI = 1.76–3.07) for the net cost of echolocating at 10 pulses each s. Since the predicted BMR (Kleiber 1961) for a 6 g mammal is 0.253 kJ/h, the net cost of echolocation is equivalent to 9.5 × BMR (6.97–12.2 × BMR). During the latter stages of prey capture an insectivorous bat may produce up to 200 pulses/s, the so-called 'feeding buzz'. These pulse rates are produced for only very short periods of time, less than 0.5 s, are of much lower intensity and probably involve a different mechanism of sound production (Suthers and Fattu 1973). We are not concerned here with the feeding buzzes, and would hesitate to extrapolate our data to this level of pulse repetition rate.

Discussion

Using the doubly labelled water technique we have previously estimated the energy cost of free flight in a small microchiropteran bat (*Plecotus auritus*) at 25 °C (Racey and Speakman 1987) as 21 × BMR. This evaluation is very high when compared with steady state evaluations of flight cost using wind tunnels and larger bats (Thomas 1987; Carpenter 1986) which average 14.6 × BMR. Nevertheless, despite the disparate evaluations of the total energy cost of flight, and the large range of error upon our estimate of echolocation costs at 10 pulses/s, it is apparent that the cost of echolocation is a major contributor to the energy cost of flight, amounting to at least 50% of the flight cost (and possibly as much as 70%).

During sound production in bats the cricothyroid muscles tension membranes overlying a cavity on one side of the larynx (Griffin 1946, 1958). A high air flow is required to achieve the necessary amplitude modulations of the membranes to produce high intensity sounds (Fattu and Suthers 1981). Tidal volume increases significantly during echolocation (Suthers and Fattu 1973) and it is expiratory airflow that results in modulation of the vocal folds (Schnitzler 1968). The wingbeat of bats is highly correlated with the respiratory cycle; a 1:1 relationship existing in all bats studied to date (Thomas 1987). In fact, each echolocation pulse is correlated with one wingbeat and one respiratory cycle (Suthers et al. 1972; Schnitzler 1968). For the two species where the phase relationship was studied, inspiration always accompanied the downstroke of the wings (reviewed in Thomas 1987). The data on phase relationships suggest that it is activity of the pectoralis and scapularis muscles during inspiration and expiration which enable the high airflows to be achieved. Hence a major proportion of the cost of echolocation probably represents the cost of contracting the pectoralis and scapularis groups of muscles rather than the relatively small cricothyroid muscles. A flying bat contracts the pectoral and scapular muscles to provide power for flight. It is not surprising therefore that our evaluations of the energy cost of echolocation at 10 pulses/s, the rate routinely employed by flying bats, is a significant proportion of estimates of the total energy cost of flight. However, this attribution of the costs to echolocation is spurious since the costs of contracting the pectoralis and scapularis muscle groups are the major costs of flight itself. By not echolocating, the costs of contracting the flight muscles are not saved. For actively flying vertebrates therefore the net costs of echolocation are probably much lower than we have inferred. The actual saving for flying animals still remains to be quantified.

In small terrestrial animals where no large muscle system like the pectoralis and scapularis groups ventilate the respiratory system at the same high rates and depths as those observed in flying mammals and birds, echolocating might be a much more costly option. Indeed, if our evaluation of 7.0–12.2 × BMR for the net cost of echolocation, at 10 pulses/s, is realistic for small terrestrial mammals this cost may take up almost the entire available metabolic scope (Hemmingsen 1960; Peters 1981) of such animals. It is significant therefore that whilst many small terrestrial mammals can produce low intensity ultrasound, are receptive to it, and often communicate with it (Sales and Pye 1974), none has developed a system of echolocation involving high intensity ultrasound calls. In contrast, amongst flying vertebrates ultrasound-based echolocation systems have apparently evolved independently on at least 4 separate occasions – amongst the Microchiroptera, amongst the genus *Rousettus* of the Megachiroptera, and amongst oilbirds (Griffin 1953) and cave swiftlets (Novick 1959). We suggest that this high incidence of echolocation amongst flying vertebrates is a consequence of the relatively low cost of producing high intensity echolocation calls during flight. On the other hand, the low incidence of echolocation amongst terrestrial mammals is a result of the high cost of producing such calls in these animals.

The widespread absence of echolocation amongst the Megachiroptera probably reflects a phylogenetic constraint. It is currently thought that the Megachiroptera have evolved from a primate group, and their origins are divergent from the Microchiroptera (Pettigrew 1986). Although the origins of the Microchiroptera are obscure it is widely believed that they originated from nocturnal insectivores (Jepsen 1970). Similar animals today use ultrasound for communication, and developing bats could have capitalised on already having the essential hardware for production and processing of such signals, when flight made the production of high intensity echolocating calls energetically feasible.

In contrast, vision is the predominant sensory mode which has developed in primates and highly specialized visual systems are a defining characteristic of the order. Megachiroptera probably had highly developed visual systems when they began to fly and were therefore unable to take advantage of the cheap potential to echolocate by an evolutionary reversal from the cul-de-sac of visual specialization.

In conclusion our evaluations of the energy costs of echolocation in the pipistrelle bat highlight why echolocation systems have repeatedly evolved amongst flying vertebrates, but not amongst their terrestrial counterparts. Although a study of energetics has improved our understanding however, a complete picture of the distribution of echolocation systems is not possible without consideration of other factors, for example phylogenetic constraints on evolution.

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