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Author(s): K. N. Paige

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Bats and barometric pressure: conserving limited energy and tracking insects from the roost

K. N. PAIGE

Institute for Environmental Studies, Department of Ecology, Ethology and Evolution, University of Illinois, 1101 W. Peabody Drive, Urbana, IL 61801, USA

Summary

1. Studies were conducted to assess the response of a seasonal cave-dwelling bat and its insect prey to natural and experimental changes in barometric pressure.
2. The Eastern Pipistrelle, *Pipistrellus subflavus*, tracks barometric pressure metabolically.
3. Eastern Pipistrelles potentially use pressure as a cue for predicting the relative abundance of aerial insect prey outside the roost.
4. Barometric pressure tracking affords these bats an opportunity to conserve limited energy and make appropriate foraging decisions.
5. Barometric pressure tracking is viewed as an alternative evolutionary strategy to torpor and may be a widespread phenomenon among insect-feeding bats that roost deep within caves.

Key-words: Aerial insects, Eastern Pipistrelle, metabolic rate, *Pipistrellus subflavus*, Vitali organ

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Introduction

Numerous investigations on a variety of organisms have revealed significant correlations between barometric pressure and various biological activities (Brown, Webb & Macey 1957). For example, positive correlations between motor activity and barometric pressure have been found in domestic dogs, *Canis familiaris*, and rats, *Rattus norvegicus* (Hodge 1897; Stewart 1898). Significant relationships between metabolic rates and rates of barometric pressure change have been found in numerous organisms ranging from fiddler crabs, *Uca* sp., to salamanders, *Triturus* sp. (Brown *et al.* 1955). More recent studies have demonstrated that birds have an ability to detect changes in pressure (Lehner & Dennis 1971; Kreithen & Keeton 1974). Although, these studies suggest that barometric pressure may provide a useful environmental cue, its ecological or evolutionary significance remains largely unknown (but see Kreithen & Keeton 1974).

Insectivorous cave bats seem a likely addition to the list of animals sensitive to barometric pressure. The only physical environmental cue available to a bat roosting deep within a cave is barometric pressure; all other variables, such as light, temperature, relative humidity and wind currents are virtually constant. Thus, pressure represents the one environmental cue that bats could use to predict the abundance of aerial insects outside the roost without expending the energy of flight to assess directly insect activity and abundance.

By examining the response of a seasonal cave-dwelling bat, the Eastern Pipistrelle (*Pipistrellus subflavus*) Cuvier, and its insect prey to natural and experimental changes in barometric pressure, this paper addresses the following questions: (1) what is the relationship between insect activity, bat activity and barometric pressure, (2) are bats using barometric pressure as a cue to predict aerial insect prey outside the roost and (3) what is the relationship between barometric pressure and bat metabolism?

Methods and materials

BATS, INSECTS AND BAROMETRIC PRESSURE

Initially, field studies were conducted to assess the relationship between insect activity and barometric pressure. Relative measures of insect abundance were obtained using a Bug-Zapper, hooked into a chart recorder via a tape-recorder and microphone [using an integrated circuit (IN914B), a 0.1 µf monolithic capacitor and a 470K 1/4 W resistor between the tape-recorder and chart recorder (Tyrell 1989)]. Insects are attracted to the Bug-Zapper's blacklights and killed by electrocution. The sound of the insect being electrocuted by the Bug-Zapper was transduced and displayed as a spike on the chart recorder. These data were collected from 2000 to 2100 h on nine nights between 17 and 23 August and on 25 and 29 August 1989 in Urbana, IL. A second data set was collected using an omnidirectional blacklight against a

30×40 cm white cardboard background. The blacklight was turned on at 2045 h and at 2100 h the number of insects was counted and barometric pressure was recorded using a digital barometer/thermometer. Ambient temperature was also recorded. Readings were taken on 17 nights between 2 August and 13 September 1989. Samples included members of the following insect orders: Lepidoptera, Coleoptera, Homoptera, Diptera, Hemiptera and Hymenoptera (personal observation). Insects represented the kinds (primarily Homoptera and Lepidoptera) and size ranges (2–7 mm) taken by Eastern Pipistrelles (Paige 1981). Counts were generally lower for the omnidirectional blacklight than for the Bug-Zapper possibly because of the smaller light source and the shorter monitoring time. Nonetheless, both gave similar relative measures of abundance. Non-selective cylindrical traps covered with tangle-foot have been shown to give similar results to blacklight traps in terms of the kinds and numbers of insects (Paige 1981); thus blacklight traps are not significantly biased in terms of insect activity patterns.

Field studies were conducted to assess the relationship between bat activity at the roost, insect activity and barometric pressure. These studies were conducted during the late summer and early autumn (August/September) of 1989 and in the spring (April) of 1990 at the mouth of Slick Crawl Cave near Pittsfield, IL. On nine nights in September 1989 the number of emerging bats, barometric pressure and temperature were simultaneously monitored. Bats were monitored in two ways, using a broad-band ultrasonic detector and by counting bat silhouettes against the skyline, for 1 h beginning at dusk at the entrance to the cave. On six nights in April 1990 the number of emerging bats, insect activity (using a blacklight trap as described above) and barometric pressure were simultaneously monitored. Counts and measures were taken over a 2-h period beginning at dusk. Bats included primarily Eastern Pipistrelles, Little Brown Bats (*Myotis lucifugus*) and Keen's Myotis (*Myotis septentrionalis*). Eastern pipistrelles use caves extensively from August through May each year but roost most often in trees during the summer (Sealander 1979). Thus studies were restricted to the late summer, early autumn and spring. Insect counts were taken every 30 min over the 2-h period. The blacklight was turned on for 15 min every 30 min and at the end of the 15-min period the total number of insects was counted against the white background. Insects were totalled and pressures and temperatures were averaged over the 2-h period for analysis.

BAROMETRIC PRESSURE AND BAT METABOLISM

The effect of barometric pressure on bat metabolism was assessed. Measures of metabolic rate were made using a closed system respirometer where barometric pressure could be increased or decreased, then main-

tained at constant pressure, by the use of a syringe mounted through the wall of the sealed Plexiglas chamber (25×15×9 cm). Individual bats were placed in a small wire-mesh cage to roost during the course of the experiment. A digital barometer was placed inside the chamber so that barometric pressure could be monitored. The closed system relies on the ideal gas law ($PV=nRT$) which states that at a constant temperature, the amount of any gas (n in moles) is directly proportional to the product of pressure and volume (Stack & Rossi 1988). As O_2 was consumed the expired CO_2 was absorbed by Ascarite (sodium hydroxide on a non-fibrous silicate carrier). Moisture was absorbed with Drierite (calcium sulfate). To assess the amount of oxygen consumed, constant pressure was maintained by introducing additional air through the syringe. The volume injected (equivalent to that consumed) was read directly from the syringe and corrected to standard temperature and pressure (STP).

Experiments were conducted within a walk-in environmental chamber where temperature was maintained at a constant setting. Experiments were run at 22 °C and 15 °C at the same time each day, in mid-afternoon. Eastern Pipistrelles ($n=6$; three for each temperature run) were fed *ad libitum* prior to the run, weighed to the nearest tenth of a g and allowed to equilibrate in the (open) chamber for 1 h prior to initiating the experiment. Oxygen consumption was recorded following a 10-min period of adjustment at a given pressure. The chamber was then purged for approximately 30 s and the next pressure (at 5 mm intervals) was randomly selected and a reading was taken; pressures ranged from 726.4 mm of Hg to approximately 762 mm of Hg, a range common to central Illinois (224 m in elevation) where these experiments were conducted. Following the end of a run the chamber was opened and the bat was immediately removed and body temperature was measured with a quick-read digital thermometer held against the exterior of the rectum; exterior rectal temperatures reflect true body temperature (as measured by internal rectal temperature) but average a couple of °C lower. The experiment was terminated following six to eight readings.

Bats were also subjected to runs of constant low pressure (736.6 mm) and temperature (15 °C) to see if lowered rates of metabolism were maintained independent of entering torpor (i.e. with a significant drop in body temperature). Bats were fed *ad libitum* prior to the run and allowed to equilibrate in the (open) chamber for 1 h prior to initiating the experiment. At the end of the hour, body temperature was taken immediately to assess whether the bats were substantially lowering temperature.

Results

BATS, INSECTS AND BAROMETRIC PRESSURE

Results showed that insect activity was negatively

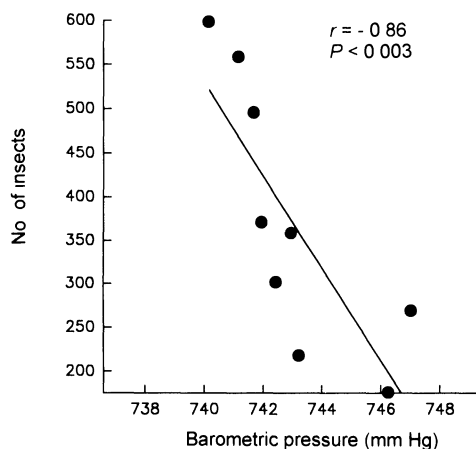


Fig. 1. The relationship between insect relative abundance and barometric pressure in Illinois. As barometric pressure increases, aerial insect abundance declines. Insect data were obtained using a Bug-Zapper hooked into a chart recorder via a tape-recorder and microphone.

correlated with barometric pressure ($r = -0.86$, $n = 9$, $P < 0.003$, Bug-Zapper, Fig. 1; $r = -0.50$, $n = 17$, $P < 0.05$, blacklight). Although activity is correlated with barometric pressure, insects may be cueing on environmental variables other than pressure. For example, ambient temperature is known to influence insect flight activity (Kunz 1988) and measures of insect activity in this study were also positively correlated with ambient temperature ($r = 0.65$, $n = 17$, $P < 0.006$; $r = 0.91$, $N = 9$, $P < 0.001$). Furthermore, pressure and temperature were negatively correlated ($r = -0.62$, $n = 17$, $P < 0.01$; $r = -0.88$, $n = 9$, $P < 0.002$). Such correlations are not merely fortuitous. For example, 4 years (1986–1989) of temperature and pressure data taken during the month of August (weather bureau records, Urbana, IL) also demonstrated a significant negative relationship ($r = -0.59$, $n = 123$, $P < 0.0001$). Therefore, pressure could be used as a predictor of insect activity (or the relative abundance of aerial insects) by cave-roosting bats even if insects respond to temperature because pressure may be the only variable environmental cue available.

Bat activity at the roost was negatively correlated with barometric pressure ($r = -0.93$, $n = 9$, $P < 0.0003$, September 1989 cave data, Fig. 2; $r = -0.75$, $n = 6$, $P < 0.08$, April 1990 cave data, although only marginally significant the pattern is in the same direction) and positively correlated with insect activity ($r = 0.85$, $n = 6$, $P < 0.03$). As in the aforementioned studies, temperature and pressure were negatively correlated at the bat cave in September 1989 ($r = -0.89$, $n = 9$, $P < 0.001$). A Stepwise regression using a forward selection procedure ($F = 4.00$ to enter and remove) showed that pressure alone explained 87% of the variation in bat activity. Temperature was not entered into the model and, when forced into the model, explained only an additional 1% of the varia-

tion. Interestingly, identical analyses showed that temperature alone explained 38% and 78% of the variation in insect activity (data from blacklight and Bug Zapper samples from Urbana in August and September 1989, respectively). Barometric pressure did not enter into the model in either case. Thus, temperature is likely to be more important than pressure in determining insect activity.

BAROMETRIC PRESSURE AND BAT METABOLISM

Metabolic studies confirmed that bats can respond to barometric pressure. With an increase in barometric pressure oxygen consumption also increased ($r = 0.61$, $df = 1, 22$, $P < 0.0017$ at 22 °C, and $r = 0.77$, $df = 1, 16$, $P < 0.0002$ at 15 °C, Fig. 3a and b, respectively). Changes in metabolism were also found to be independent of any substantial changes in body temperature in my experiments, indicative of entering torpor. Exterior rectal temperature was maintained at approximately 35 °C (range 33–35 °C) in all experiments; this coincides with a body temperature of approximately 37 °C (range 35–37 °C; unpublished data).

Discussion

TRACKING INSECTS FROM THE ROOST

The only physical environmental characteristic that changes for a bat roosting deep in a cave is barometric pressure, while all other variables remain constant. Thus pressure represents the one environmental cue that bats could use to predict the abundance of aerial insects outside the roost without expending the energy of flight to assess insect activity directly. Of course, use of barometric pressure as a cue is contingent upon the relationship between the activity (relative abundance) of aerial insects and barometric pressure. Results here show that insect activity is sig-

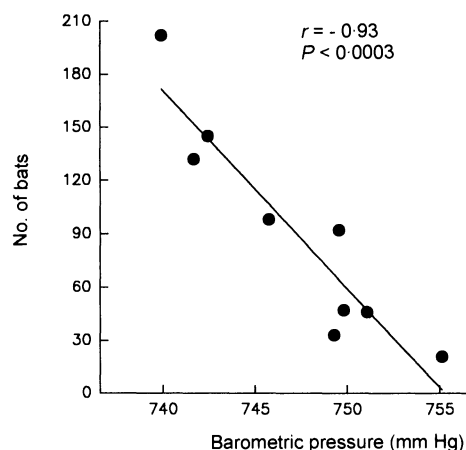


Fig. 2. The relationship between the number of bats exiting a cave on a given night in September 1989 and barometric pressure in Illinois. As barometric pressure increases, the number of bats leaving the roost declines.

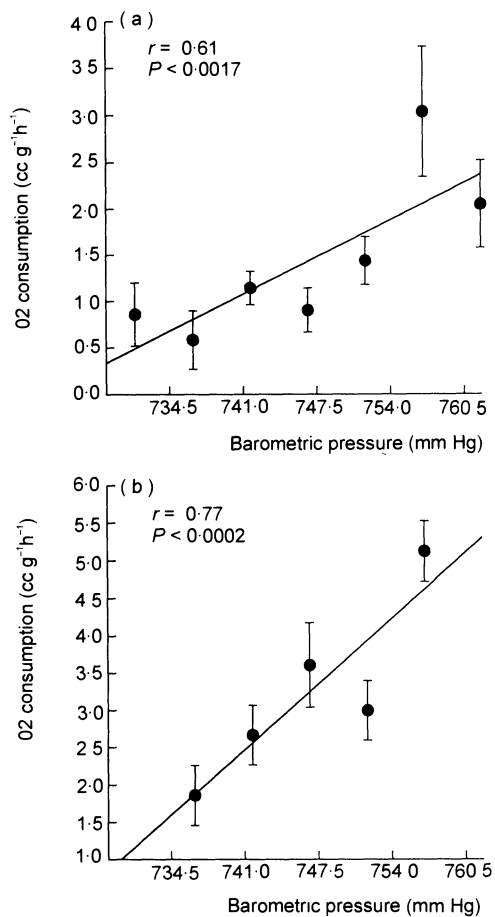


Fig. 3. The relationship between oxygen consumption by Eastern Pipistrelles and barometric pressure. As barometric pressure increases, bat metabolism also increases. Oxygen consumption is shown for two temperatures (a) 22 °C and (b) 15 °C. Means \pm SE are shown.

nificantly negatively correlated with barometric pressure. Thus, pressure could serve as a predictor of insect activity (or the relative abundance of insects) by cave-roosting bats.

If bats are using pressure as a cue to predict aerial insects, then bat activity in the field should be negatively correlated with barometric pressure. Results of my field studies confirmed that prediction. Furthermore, stepwise regression showed that barometric pressure alone explained 87% of the variation in bat activity.

To respond to barometric pressure bats must be able to sense it and they are reported as the only mammal having a paratympic organ (Vitali organ) in the middle ear (Vitali 1914; Ranzi 1926; Von Bartheld 1990). Although the function of the paratympic organ has yet to be demonstrated conclusively, measurement of air pressure seems the most likely function (Griffin 1969; Jorgensen 1984; Von Bartheld & Rubel 1989).

Although my studies are only correlational and do not necessarily imply cause and effect, the patterns do lend credence to the idea that cave bats use pressure as a cue to predict insect activity outside the roost. For

a deep cave-dwelling bat, such as the eastern pipistrelle, pressure represents the only available environmental cue for predicting the abundance of insects outside the roost. This in combination with insect and bat activity patterns and a unique middle-ear receptor for detecting pressure makes it difficult to argue alternatives.

TRACKING PRESSURE METABOLICALLY

Experimental studies on the effects of barometric pressure on bat metabolism demonstrate that eastern pipistrelles track barometric pressure metabolically. With an increase in barometric pressure oxygen consumption increased (Fig. 3a and b). The 2.5–4.4-fold differences in metabolism at the extremes of pressure (Fig. 3a and b), with relatively small changes in body temperature, have been reported in other studies where temperature and oxygen consumption have been measured. For example, for *Myotis lucifugus*, Kurta, Johnson & Kunz (1987) showed as high as a 3.2-fold difference in metabolism while maintaining body temperatures within the range reported here. Thus, with little change in body temperature, changes in metabolism were independent of torpor, which can be characterized as a concomitant drop in temperature and metabolism. In fact, bats entered torpor only in ‘emergency’ situations (e.g. when energy reserves were clearly depleted; unpublished data); the literature is replete with similar observations (e.g. Stones & Wiebers 1967; Kurta *et al.* 1987).

Metabolic pressure tracking represents an alternative energy conservation strategy to torpor for these small flying mammals. For example, a 6.7 g pipistrelle roosting at a pressure of 756.9 mm and a temperature of 15 °C will expend approximately 14 979 J over a 24-hour period, whereas, the same animal roosting at a pressure of 10.2 mm lower (746.7 mm) will expend only 10 376 J over the same period of time, all else being equal. Energy consumption was calculated by multiplying cm³ O₂ consumed/g/h at a given pressure (from Fig. 3) by 19.87 J/cm³ O₂ used (Hainsworth 1981) by 24 h. This reduction in metabolism represents an approximate 31% saving in energy. At the extremes, for example, with a 25.4 mm difference (736.6–762 mm) in pressure, which can occur naturally, there can be as much as a 64% savings in energy. Thus, barometric pressure tracking can delay or even eliminate the necessity for entering torpor.

Metabolic pressure tracking may also function as ‘a bet-hedging’ strategy. When pressure is low, insects are most abundant (Fig. 1), except during substantial rainfall (Rydell 1990; personal observation). Comparisons of barometric pressure during rain and during periods of no rain ($n=64$ days), taken from weather bureau records in Urbana showed that pressure was significantly lower on days when it rained [742.2 \pm 4.8 mm (\pm SD) vs 750.6 \pm 2.8 mm, rain vs no rain, respectively; $t=10.65$, $df=94$, $P<0.001$]. Because

it is unlikely that bats can detect whether it is raining or not from deep within a cave roost and low pressure is indicative of greater aerial insect abundance, bats will possibly fly out of the roost to check. With low insect abundance, as a result of rain, bats may return to the roost. No matter what their decision, these bats will benefit from the substantial energy savings incurred at low pressure (see Fig. 3) both prior to their exodus and following their return to the roost (whether immediate or not).

The results of these studies demonstrate that barometric pressure tracking allows these bats to conserve energy, remain cognizant (of predators) and extend a previously taken meal. Thus, barometric-pressure tracking is viewed as an alternative evolutionary strategy to torpor. In general, barometric-pressure tracking may be a widespread phenomenon among insect-feeding bats that roost deep within caves.

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