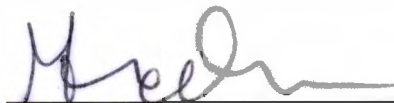


To the Graduate Council:

I am submitting herewith a dissertation written by Michael Glenn Scott entitled "The Detection of Atmospheric Pressure as a Sensory Modality". I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology and Evolutionary Biology.

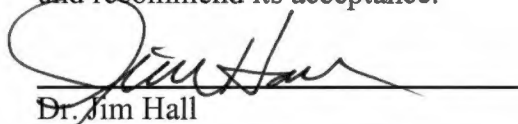
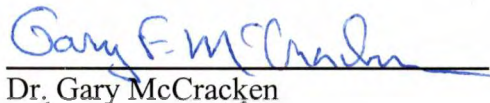
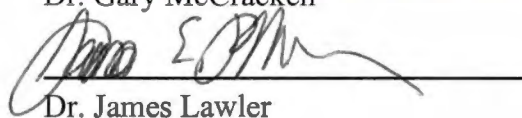


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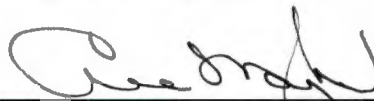


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THE DETECTION OF ATMOSPHERIC PRESSURE
AS A SENSORY MODALITY

A Dissertation
Presented for the
Doctor of Philosophy
Degree
The University of Tennessee, Knoxville

Michael Glenn Scott
August 2000

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ABSTRACT

My research objective was to investigate the detection of atmospheric pressure as a sensory modality in flying animals. For flying animals, atmospheric pressure is a potential source of information that might be used as the basis of a pressure altimeter and / or meteorological forecasting. The prominent properties of variation in atmospheric pressure are absolute pressure magnitude and the rate of pressure change. Absolute pressure magnitude is a reliable indicator of altitude while pressure changes can be separated into two types; rapid changes associated with altitude changes in flight and relatively slow changes associated with meteorological events. A prerequisite for an animal to have a functional response to variation in atmospheric pressure is that the animal be able to detect the variation.

I have demonstrated that insectivorous bats are able to detect and respond to the atmospheric pressure changes associated with flight altitude changes and meteorological events using behavioral assays. In laboratory tests, individuals of three species demonstrated spontaneous responses to induced atmospheric pressure changes that are equivalent to a 35m altitude change over 15 seconds. Monitoring of wild bat foraging activity demonstrated that wild bats might use atmospheric pressure changes associated with storm fronts to avoid poor flying conditions.

The paratympanic organ is a putative atmospheric pressure receptor. In the avian paratympanic organ, it has been suggested that air pressure changes induce conformational changes that stimulate mechanoreceptors in the sensory epithelium via fluid displacement. Using microscopy techniques, I discovered that the lumen of the paratympanic organ is not just a fluid-filled space. The lumen of the

paratympanic organ is filled with an extracellular collagenous matrix that is an apparent accessory structure. I propose that the function of the paratympanic organ matrix is to couple conformational changes in the paratympanic organ with the mechanoreceptors in the sensory epithelium, a function analogous to that of other accessory structures in the lateral line system. My anatomical survey of individuals from 11 bat species failed to confirm a previous report of a bat paratympanic organ.

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PART I
INTRODUCTION

The realization that atmospheric air exerts pressure as a consequence of the height and temperature of the air column and the development of the modern barometer (Middleton 1964) were soon followed by anecdotal reports that some animals apparently respond to changes in atmospheric pressure (Lombard 1892). Hodge (1897) was the first to publish data describing a relationship between atmospheric pressure and animal activity. In his study, mean daily distance moved by domestic dogs (*Canis*) fitted with pedometers was positively correlated with mean daily atmospheric pressure. In another study, Stewart (1898) reported that non-domestic gray rat (*Rattus*) movement in an actograph had a negative correlation with mean daily atmospheric pressure while domestic white rat (*Rattus*) movement had a positive correlation with mean daily atmospheric pressure.

Nearly 60 years later, exposed oyster (*Ostrea sp.*) and quahog (*Venus sp.*) shell opening was shown to coincide with falling atmospheric pressure and closing with rising atmospheric pressure (Brown et al. 1956). Martof (1960) reported that reproductive activity of the tree frog (*Hyla crucifera*) is induced by lowering atmospheric pressure. Endogenous body temperature rhythms in pocket mice (*Perognathus longimembris*) can be entrained by atmospheric pressure cycles in a pressure chamber (Hayden and Lindberg 1969). Albino mice (*Mus musculus*) spontaneous motor activity in a pressure chamber is inversely correlated with atmospheric pressure magnitude (Truchan and Boyer 1972). Twenty-one studies have correlated bird migration timing with the movement of atmospheric pressure fronts (Lehner and Dennis 1971) but these might have been better explained by the presence

of a following wind and no precipitation (Alerstam 1981). Newly hatched domestic chicks (*Gallus*) have an inverse relationship between activities and mean daily atmospheric pressure (Bateson 1974). Leopard frog (*Rana pipiens*) locomotor activity is positively correlated with mean daily atmospheric pressure (Robertson 1978). Insect abundance and dispersal are strongly influenced by meteorological conditions including atmospheric pressure (Johnson 1954, Haufe 1954 and 1967, Williams 1961a and 1961b).

An underlying assumption in studies correlating activity with atmospheric pressure is that the animal in question has the ability to detect characteristically encountered atmospheric pressures (Lehner and Dennis 1971). But, to date, the ability to detect atmospheric pressure has been tested in only two bird species. Lehner and Dennis (1971) trained mallard ducks (*Anas platyrhynchos*) to peck a key for a food reward after a positive atmospheric pressure cue and to peck a different key for a food reward after a negative atmospheric pressure cue. Trained ducks properly discriminated at least 86% of the smallest atmospheric pressure cues tested; 21 mmHg (about 240 m altitude change). Homing pigeons (*Columbia livia*) trained to respond to an atmospheric pressure cue by electrical stimulation and cardiac conditioning consistently discriminated positive and negative atmospheric pressure changes as small as 0.8 mmHg (about 10 m altitude change) (Kreithen and Keeton 1974).

Potential functions of atmospheric pressure detection in bird species include altitude control, pressure pattern navigation, meteorological forecasting and migration timing (Lehner and Dennis 1971, Kreithen and Keeton 1974). Presumably,

atmospheric pressure detection by other animals would allow similar functions. Potential features of an atmospheric pressure receptor might include a very low sensitivity threshold, ability to detect relative pressure change, discrimination of positive and negative changes and maintenance of an absolute magnitude reference (Kreithen and Keeton 1974).

To date, no atmospheric pressure receptor has been conclusively described (von Bartheld 1994). However, a small sense organ (paratympanic organ) that probably functions as an atmospheric pressure receptor (Vitali 1921, Jorgensen 1984, Giannessi and Pera 1986, von Bartheld 1994) has been described in the middle ear of several birds (Vitali 1911, 1912) and perhaps one bat species (Vitali 1924, Simonetta 1953). Lesion of the paratympanic organ (and surrounding tissue) in pigeons impaired flying and orientation (Vitali 1921). Paratympanic organ structure in bird species supports suggestions that it is an air pressure detector (Jorgensen 1984, Giannessi and Pera 1986). Air pressure applied to the ear canal results in differential expansion of parts of the lumen of the paratympanic organ due to tension in ligaments attached externally to the organ (von Bartheld 1994).

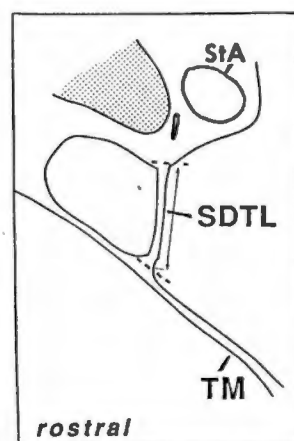
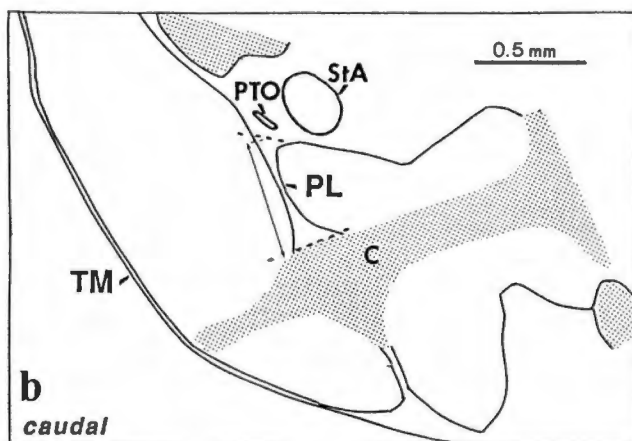
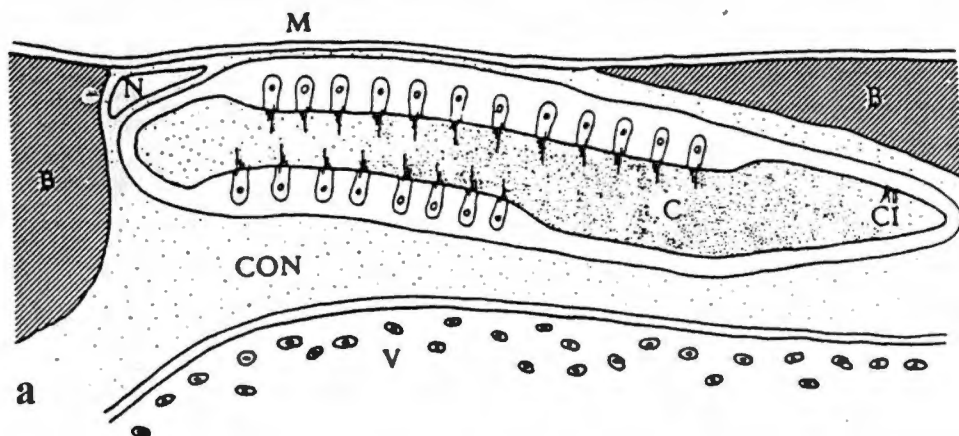
The paratympanic organ develops in association with the hyomandibular cleft in most or all vertebrates (reviewed in von Bartheld 1990), but persists throughout life in most birds (Vitali 1911, 1912), one bat (Vitali 1924), and many fishes (reviewed in von Bartheld 1990). The sensory epithelium of the paratympanic organ in chickens develops before the sensory epithelium of the inner ear, suggesting that the paratympanic organ is a phylogenetically old sensory structure (von Bartheld 1990).

Paratympanic organ structure in birds has been well described (Jorgensen 1984, Giannessi and Pera 1986, Giannessi 1989). Jorgensen (1984) best described the paratympanic organ as having the shape of a long tube found on the medial wall of the middle ear very close to the tympanic membrane and quadrum (Plate 1a). Parts of the organ are enclosed in bone while others are separated from the middle ear cavity by only a thin cornified membrane. The epithelium is separated from surrounding connective tissue by a basal lamina. Numerous nerve fibers and blood capillaries penetrate surrounding connective tissue. The lumen of the organ is filled with a gelatinous substance. The sensory epithelium is composed of sensory cells, supporting cells and nerve fibers. The extrasensorial parts have cuboidal cells. Sensory cells are like type-II hair cells with one apical kinocilium and a bundle of 50-102 stereocilia up to 9µm in length. Hair cell bodies contain numerous mitochondria. Supporting cells reach from the organ lumen to the basal lamina with microvilli projecting into the lumen. Tight junctions connect supporting cells and hair cells while gap junctions are common between neighboring supporting cells.

External attachment of two elastic ligaments to the paratympanic organ has been described (von Bartheld 1994). Platner's ligament originates on the extracolumella and inserts at the caudal end of the organ. The superior drum-tubal ligament originates on the tympanic membrane and inserts at the rostral end of the organ (Plate 1b).

In addition to afferent and efferent terminal synapses (Jorgensen 1984), some hair cells have reciprocal synapses with efferent nerve fibers (Giannessi 1989).

Plate 1. The avian paratympanic organ. (a) a drawing of the avian paratympanic organ and its surrounding tissue (from Jorgensen 1984). (M = middle ear cavity, N = nerve, B = bone, C = cupula, CI = ciliated cell, CON = connective tissue, V = blood vessel) (b) drawings of ligament attachments in the middle ear at the caudal and rostral ends of the paratympanic organ (from von Bartheld 1994). (PL = Platner's ligament, C = columella, PTO = paratympanic organ, StA = stapedial artery, TM = tympanic membrane, SDTL = superior drum-tubal ligament)



Reciprocal synapses probably give rise to complex interactions between hair cells (Giannessi 1989). Afferent and efferent innervation of the paratympanic organ has been partially described in chicks and chicken embryos (von Bartheld 1994, von Bartheld 1990). In chick embryos, fluorescent tracer molecules injected into the paratympanic organ label afferent paratympanic nerve fibers, which join the posterior ramus of the facial nerve and enter the distal facial ganglion (about 45 cells labeled). Labeled cells are spread throughout the ganglion. At least 25 to 30 labeled paratympanic nerve fibers form a distinct fiber bundle in the dorsorostral portion of the facial nerve that enters the brainstem dorsal to the facial nerve proper and rostral to the vestibular nerve. In the brainstem, the paratympanic fiber bundle divides into a dorsal (15 - 20 fibers) and a ventral (20 - 25 fibers) component. The dorsal root projects along the cerebellar peduncle and caudally into ventral portions of the cerebellum. These fibers do not seem to terminate in one distinct nucleus. The ventral component projects throughout the rostrocaudal extent of the descending vestibular nucleus. Some (about five) labeled fibers from the ventral component terminate in the medial vestibular nucleus. No labeled fibers enter the brainstem auditory nuclei or contralateral brainstem. Labeled cell bodies were not observed in the brain. An additional observation was that paratympanic nerve fiber projections substantially overlap with lagenar (an inner ear equilibrium organ) nerve fiber projections (von Bartheld 1990). In chicks, efferent neurons are located ipsilaterally and adjacent to the superior olivary nucleus and facial motor nucleus (von Bartheld and Rubble 1989).

In the avian inner ear, bending hair cell stereocilia towards the kinocilium maximally excites the afferent nerve, while a bend in the opposite direction decreases the number of nerve impulses (Roberts et al. 1988). In the model proposed by Jorgensen (1984), paratympanic organ hair cells similar to inner ear hair cells are oriented parallel with the long axis of the tubular organ. With hair cells of opposite orientation on the medial and lateral sides, displacement of fluid in the organ lumen by tension in ligaments attached to either end of the organ will excite some hair cells while others are inhibited. Testing of this model has been limited to observations that air pressure applied to the external ear canal causes differential expansion of parts of the lumen of the paratympanic organ (von Bartheld 1994).

Vitali (1924) reported an observation of a paratympanic organ in the bat *Pipistrellus pipistrellus*. However, it was of variable occurrence and rudimentary in conformation compared with the paratympanic organ in birds. Only two of the six *P. pipistrellus* examined were reported to have a paratympanic organ. None of the specimens of *Rhinolophus ferrumequini*, *Rhinolophus hipposideros*, *Nyctalus noctula*, *Vespertilio murinus* and *Plecotus auritus* examined were reported to have a paratympanic organ.

If some bats have a paratympanic organ, they may use it to detect atmospheric pressure as sensitively as birds that have paratympanic organs. Atmospheric pressure reception by bats might include altimetric and meteorological forecasting functions, as with birds, as well as monitoring weather conditions from microhabitats isolated from climatic fluctuations (Nagel and Nagel 1994, Paige 1995). Environmental factors

strongly affect bat activity (Kunz 1974, Fenton et al. 1977, Swift 1980, Erkert 1982). In caves, atmospheric pressure may be the only indicator of prevailing environmental conditions. Arousal and flight are energetically expensive for bats (Hayward and Ball 1966, Thomas and Suthers 1972, Thomas 1975, Kunz and Nagy 1988, Thomas et. al. 1990). Therefore, atmospheric pressure detection may lead to energy conservation by economizing arousal and flight, which are necessary for direct assessment of external climate.

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PART II

INDUCED ATMOSPHERIC PRESSURE CHANGES ELICIT
SPONTANEOUS RESPONSES IN BATS

ABSTRACT

Individuals of three insectivorous species of bats (*Eptesicus fuscus*, *Myotis velifer* and *Tadarida brasiliensis*) were observed for spontaneous responses to induced atmospheric pressure changes. Visual observations of ventilation rate were compared between control periods and periods in which atmospheric pressure was increased or decreased 4.2 kPa over 3 min, a rate equivalent to flight altitude changes of 2.3 m per second. Bats of each species responded to the induced pressure changes. Therefore, the bats displayed a critical component of a functional pressure altimeter, the ability to detect pressure changes.

INTRODUCTION

Correlations of behavioral activities with atmospheric pressure have been reported for a variety of animals. For example, daily cycles in atmospheric pressure appear to synchronize behaviors in marine mollusks (Brown et al. 1956), house mice (*Mus musculus*; Truchan and Boyer 1972), and pocket mice (*Perognathus longimembris*; Hayden and Lindberg 1969). As an indicator of favorable weather conditions, atmospheric pressure may induce reproductive activity in the tree frog (*Hyla crucifera*; Martoff 1960) and bird migration events (Lehner and Dennis 1971; Alerstam 1981). Insect abundance is correlated with atmospheric pressure (Harker 1958) as is foraging activity of the leopard frog (*Rana pipiens*; Robertson 1978).

For flying animals (birds and bats) atmospheric pressure is a potential source of information that might be used as the basis of a pressure altimeter, navigation by

patterns of atmospheric pressure and meteorological forecasting (Lehner and Dennis 1971, Kreithen and Keeton 1974). Bats may use atmospheric pressure to monitor weather conditions from caves, which are isolated from weather fluctuations (Nagel and Nagel 1994), to predict local insect abundance (Paige et al. 1995) or to avoid inclement flying weather (see Part III).

The prominent properties of variation in atmospheric pressure are absolute magnitude and rate of pressure change. Absolute pressure magnitude is a reliable indicator of altitude while pressure change can be separated into two types: rapid changes associated with altitude changes in flight and relatively slow changes associated with meteorological events (Lutgens and Tarbuck 1989). Hypotheses linking animal activity with atmospheric pressure include the assumption that the animal in question can detect the type of atmospheric pressure conditions involved. The ability to detect atmospheric pressure has been experimentally demonstrated in only two species of birds (Lehner and Dennis 1971, Kreithen and Keeton 1974). It has been reported that some bats have a middle ear organ that may be an atmospheric pressure detector (Vitali 1924, von Bartheld 1990). Therefore, the purpose of this study was to investigate whether bats can detect and respond to atmospheric pressure changes typical of those they encounter during flight.

METHODS

Three species of insectivorous bats were used for this study. Fourteen *Eptesicus fuscus* were captured by hand in day roosts in eastern Tennessee, while 18 *Myotis velifer* and 18 *Tadarida brasiliensis* were captured by hand net as they exited

roosts in Mason Co., Texas. All bats were determined to be adult based on the degree of ossification of the metacarpal-phalangeal joint (Anthony 1988). After testing, bats were marked with dye (1% Eosin Y) and released near the capture site within 24 h. Recaptured bats were not retested.

A steel pressure chamber, 37 cm in length by 39 cm in diameter, was constructed to evaluate the response of bats to pressure changes. Ports provided for air inflow, air outflow, manometer attachment, and a pressure-release valve. The chamber, except for an observation port, was lined with eggshell foam to dampen sound. An air-vacuum pump isolated in an adjacent room drove air inflow and outflow. Modulating air outflow (0.6 or 1.2 l/min) while maintaining a set air inflow (0.9 l/min) produced pressure changes of ± 1.4 kPa/min. Pressure changes, initiated from ambient atmospheric pressure and measured using a water filled U-tube manometer, were repeatable ($\pm 2.6\%$) and linear with respect to time ($R^2 = 0.999$). Air flow in the chamber did not produce detectable sound between 0.1 and 165.0 kHz (Radio Shack[®] microphone 33-2001 and an Ultrasound Advice Mini 2 tunable bat detector). Temperature inside the chamber matched room temperature.

Movement of bats within the pressure chamber was restricted to a 15- by 13- by 7-cm Plexiglas and wire-mesh enclosure attached to the observation port at one end of the chamber. The rate of rhythmic movement of the posterior dorsal surface of bats, enhanced by reflective foil, was used as an index of a spontaneous response to induced pressure changes. This rhythmic movement is considered to be a measure of

ventilation rate (Constantine 1986) but is not significantly different from heart rate (pers. obser.). Behavior and responses of bats were recorded on videotape.

The apparatus was established in a quiet room with illumination from a diffused 15-watt, incandescent light. Between 1800 and 0400 h, a single bat with four reflective foil strips attached to its posterior dorsal surface was placed in the enclosure and sealed in the pressure chamber. Each bat was allowed to acclimate to the apparatus for 30 min before testing while being exposed to airflow with the pressure release valve open so the bat was at ambient pressure. Bats that did not settle to a resting position within 30 min were not tested. Each bat was observed during one pressure increase and one pressure decrease (± 1.4 kPa/min for 3 min; equivalent to 140-m change in altitude over 1 min). Each pressure increase and decrease was paired with a control period of the same duration and air flow, but no change in atmospheric pressure, in order to determine a resting rate for comparison with test sessions. Pressure increases and decreases were presented to each bat in random order with test and control sessions randomized within pairs. Accumulated pressure was released over 30-60 sec at the end of each test, and air outflow changed as necessary for the subsequent session. Sessions were separated by 5 min. The spontaneous response index was assessed during each 15-sec interval of the 3-min sessions from video records. Rates from test sessions were expressed as a percentage of the paired control session. The response index during both control sessions for each bat was compared within species to evaluate the effectiveness of the interspersed waiting periods. The response index during paired control and test sessions was compared to evaluate the

influence of induced pressure changes. Comparisons were made using paired difference t-tests with a significance criterion of 0.05.

RESULTS

The mean response index was not different between the two control sessions for *T. brasiliensis* ($\bar{n} = 18$, difference = 6.1, $\underline{SE} = 5.5$, $\underline{P} = 0.3$), *M. velifer* ($\bar{n} = 18$, difference = 0.3, $\underline{SE} = 7.8$, $\underline{P} = 0.97$) and *E. fuscus* ($\bar{n} = 14$, difference = 6.5, $\underline{SE} = 8.2$, $\underline{P} = 0.44$). The mean response index during control sessions was 154/min ($\underline{SE} = 9.7$) for *T. brasiliensis*, 223/min ($\underline{SE} = 6.7$) for *M. velifer*, and 130/min ($\underline{SE} = 7.5$) for *E. fuscus*. The mean response index during test sessions (expressed as percentage of control) was greater than the control for all pressure changes for all three species (Table 1). The spontaneous responses of *T. brasiliensis* to induced pressure changes in 15 second time intervals are shown in Figure 1 and Figure 2. The spontaneous responses of *M. velifer* to induced pressure changes in 15 second time intervals are shown in Figure 3 and Figure 4. The spontaneous responses of *E. fuscus* to induced pressure changes in 15 second time intervals are shown in Figure 5 and Figure 6. All species responded to increases and decreases in pressure within the first 15 second time interval (Table 2).

DISCUSSION

The observed increase in the response index during test sessions in this study was not an artifact of a shifting baseline because there were no differences when the response index was compared between the paired control sessions for each species. Furthermore, the observed responses to induced pressure changes were not passive

Table 1. Statistics from paired-difference *t*-tests used to test the mean response (expressed as percentage of control) during pressure decreases and increases for *T. brasiliensis*, *M. velifer*, and *E. fuscus*.

Species	Pressure		Mean				
	change	<u>n</u>	diff.	<u>SE</u>	<u>d.f.</u>	<u>t</u> -value	<u>P</u> -value
<i>T. brasiliensis</i>	Decrease	18	26.3	5.1	17	3.9	0.001
	Increase	18	26.8	4.7	17	4.1	0.001
<i>M. velifer</i>	Decrease	18	25.2	4.6	17	4.4	0.001
	Increase	18	19.5	4.6	17	4.2	0.001
<i>E. fuscus</i>	Decrease	14	28.2	4.8	13	4.2	0.001
	Increase	14	29.8	5.7	13	3.7	0.001

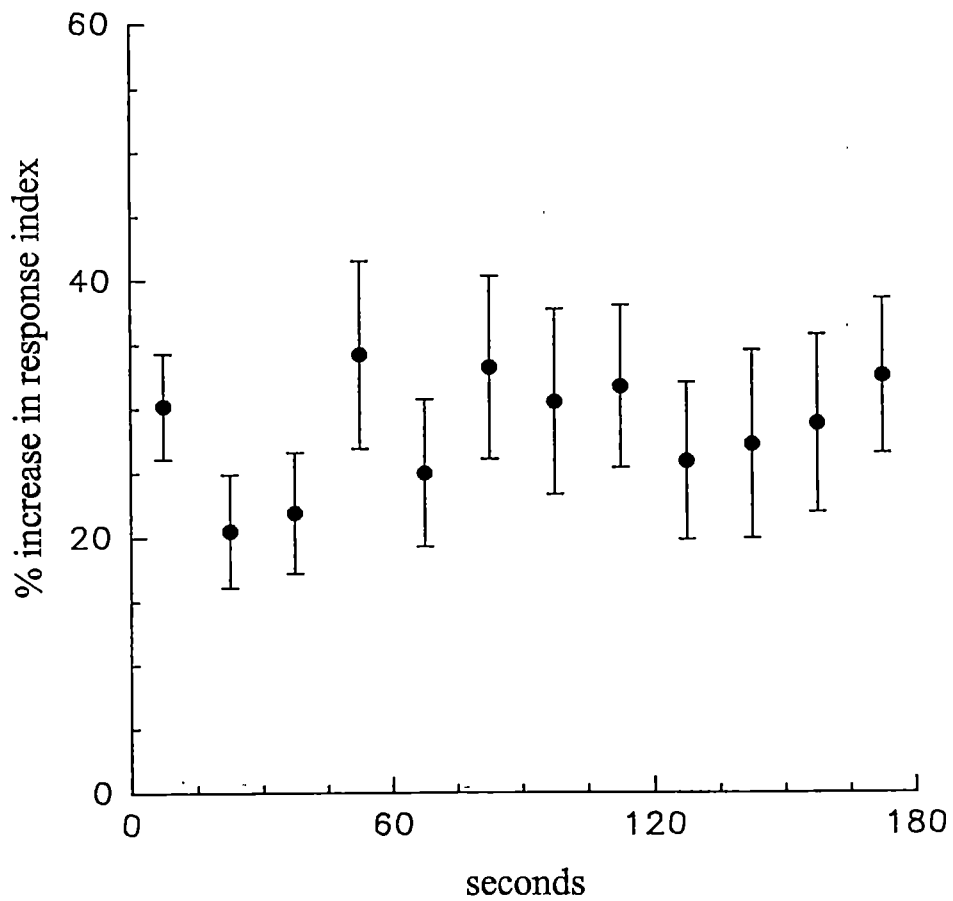


Figure 1. Spontaneous responses to induced pressure decreases for *T. brasiliensis*. Points represent the mean percent increase during test sessions compared to controls for each 15 second interval of three minute pressure changes (with SE).

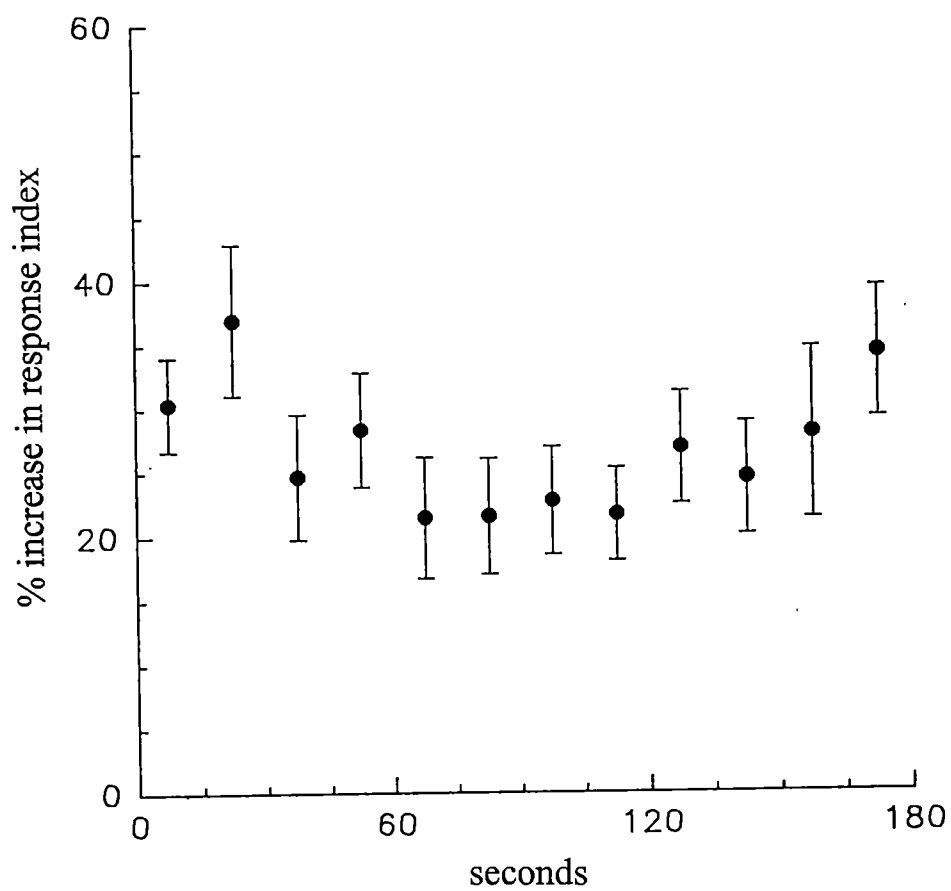


Figure 2. Spontaneous responses to induced pressure increases for *T. brasiliensis*. Points represent the mean percent increase during test sessions compared to controls for each 15 second interval of three minute pressure changes (with SE).

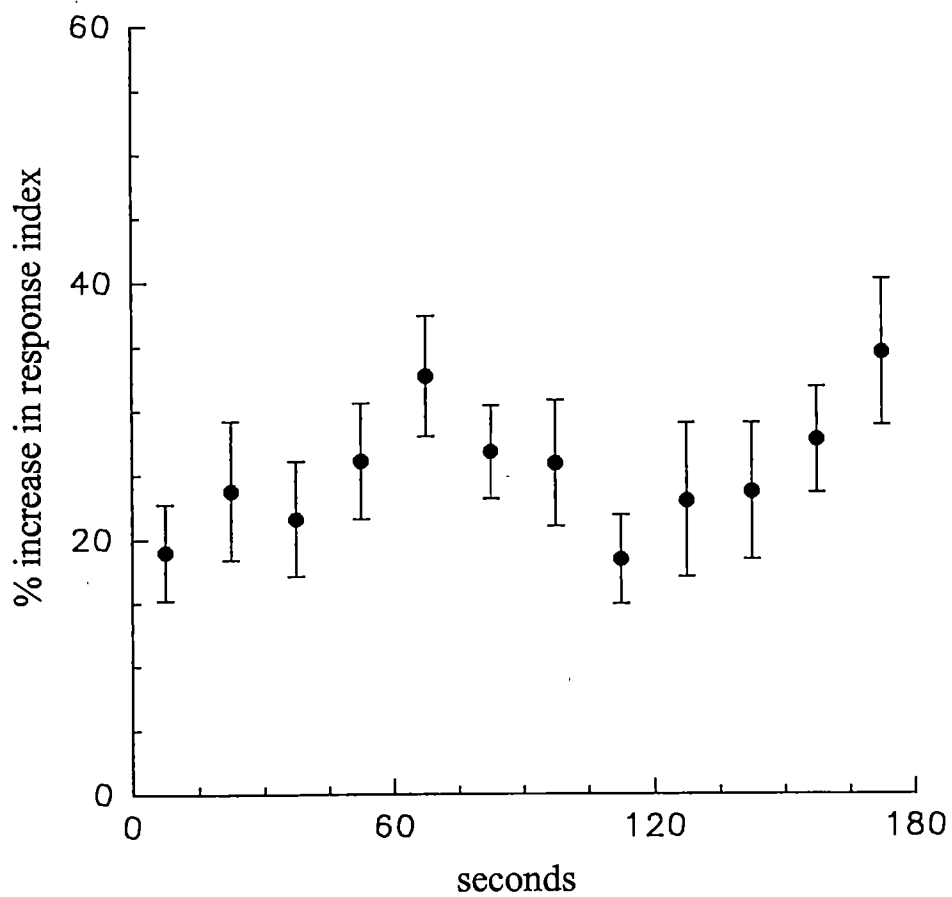


Figure 3. Spontaneous responses to induced pressure decreases for *M. velifer*. Points represent the mean percent increase during test sessions compared to controls for each 15 second interval of three minute pressure changes (with SE).

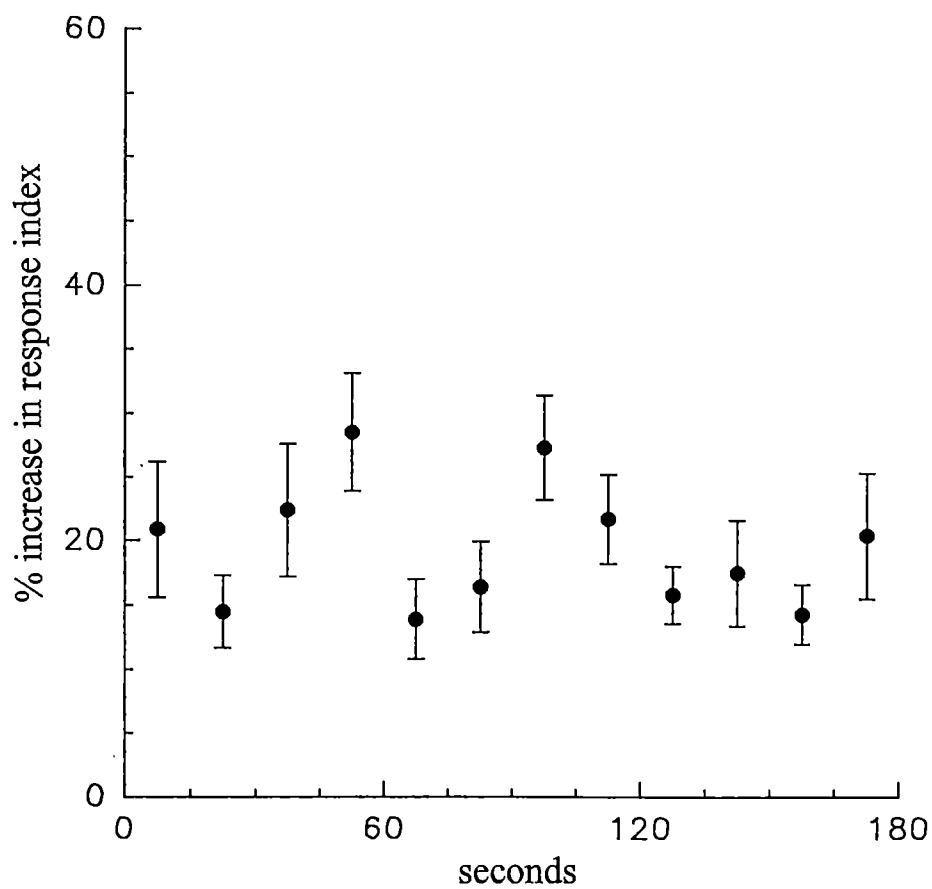


Figure 4. Spontaneous responses to induced pressure increases for *M. velifer*. Points represent the mean percent increase during test sessions compared to controls for each 15 second interval of three minute pressure changes (with SE).

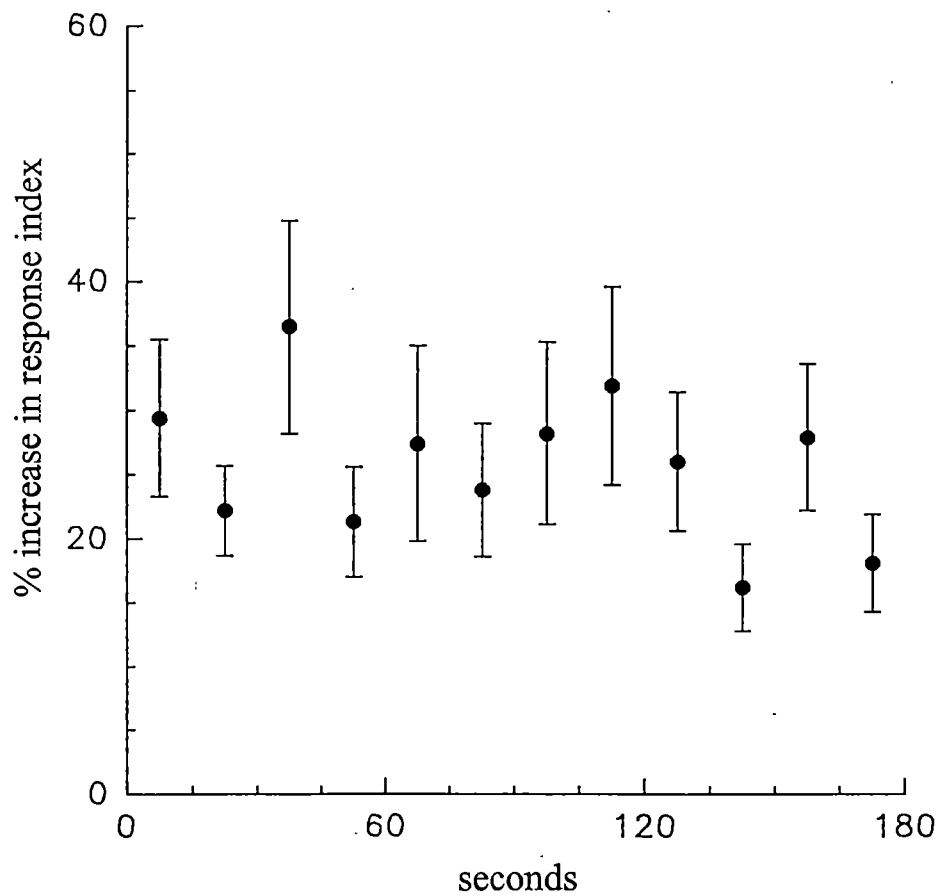


Figure 5. Spontaneous responses to induced pressure decreases for *E. fuscus*. Points represent the mean percent increase during test sessions compared to controls for each 15 second interval of three minute pressure changes (with SE).

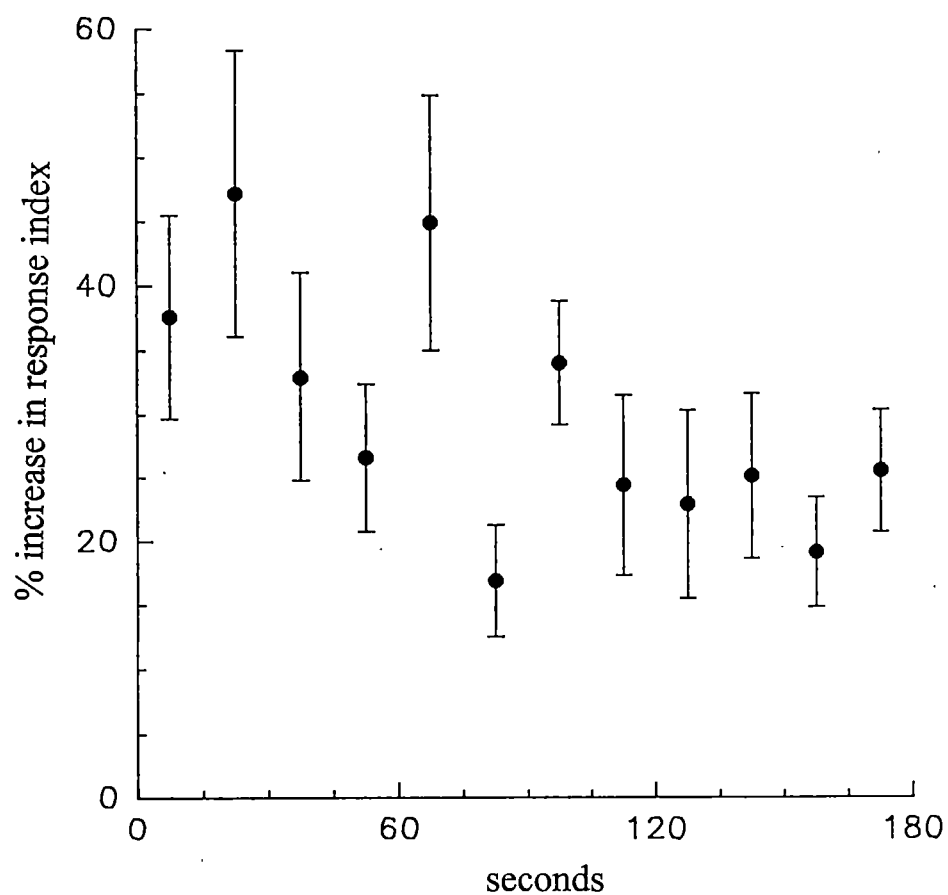


Figure 6. Spontaneous responses to induced pressure increases for *E. fuscus*. Points represent the mean percent increase during test sessions compared to controls for each 15 second interval of three minute pressure changes (with SE).

Table 2. Statistics from paired-difference t -tests used to find the first time interval in which a significant increase in the response index (expressed as a percentage of control) occurred for *T. brasiliensis*, *M. velifer*, and *E. fuscus*.

Species	Pressure		Mean					
	change	Interval	<u>n</u>	diff.	<u>SE</u>	<u>d.f.</u>	<u>t</u> -value	<u>P</u> -value
<i>T. brasiliensis</i>	Decrease	1	18	30.2	4.1	17	2.3	0.01
	Increase	1	18	30.4	3.7	17	2.4	0.01
<i>M. velifer</i>	Decrease	1	18	19.0	3.8	17	2.3	0.02
	Increase	1	18	20.9	5.3	17	2.1	0.03
<i>E. fuscus</i>	Decrease	1	14	29.4	6.1	13	2.1	0.03
	Increase	1	14	29.9	11.3	13	2.7	0.02

respiratory responses to changes in air pressure as the type of response (an increase in the response index) was uniform across increasing and decreasing air pressure changes.

All three species of bats responded to the induced increases and decreases in atmospheric pressure with an increase in the spontaneous response index compared with controls. These spontaneous responses are presumed to be respiratory responses as part of a general "startle" response to an unexpected stimulus. For a response to occur, the bat must be able to detect the stimulus. Therefore, *T. brasiliensis*, *M. velifer*, and *E. fuscus* must be able to detect atmospheric pressure changes of 4.2 kPa over 3 min, a rate equivalent to flight altitude changes of 2.3 m per second.

The sensitivity of the ability of bats to detect atmospheric pressure change was demonstrated by the latency of the spontaneous response following the onset of the pressure change. The latency period of the response fell within the first 15 second time interval after the pressure change was initiated for all three species for pressure increases and decreases. The pressure change over this 15 second time period was plus or minus 0.35 kPa; equivalent to a 35 m change in altitude. Detection of the pressure change and the spontaneous response must have been early in the 15 second time interval as the mean response during the first time interval following the onset of the pressure change was significantly greater than the control. The ability of bats to detect pressure changes of this rate and magnitude demonstrate their potential to detect pressure changes normally encountered in flight.

The response to small atmospheric pressure changes in this study indicates that some bats have the ability to sense atmospheric pressure changes of the magnitude normally encountered during altitude changes in flight. Therefore, these bats possess a critical component of a functional pressure altimeter, a pressure detector. It is not known if flying bats actually use altimetric information for flight control. This study also did not test the ability of bats to detect pressure changes representative of the small, slow pressure changes associated with weather fronts that might be used for meteorological forecasting. Foraging bat activity is correlated with atmospheric pressure conditions, although it is unknown whether bats can detect such small pressure changes (see Part III).

Few animals have been tested for the ability to detect changes in atmospheric pressure. The only mammalian species that has been tested, besides the three bat species in this study, is humans (Rockley and Hawke 1992). In this study human volunteers were trained to detect small, induced pressure changes. The threshold for detection was about 0.5kPa over 5 seconds; equivalent to a 50 m altitude change. The functional basis for pressure detection by humans is not known. Of two bird species tested, homing pigeons are the most sensitive (Kreithen and Keeton 1974). Homing pigeons (*Columbia livia*) that were trained to respond to an atmospheric pressure cue by electrical stimulation and cardiac conditioning consistently discriminated positive and negative atmospheric pressure changes as small as 0.1 kPa; equivalent to a 10 m altitude change. Considering the limitations of the methods in the current study with

bats, it is possible that some bats will be as sensitive to atmospheric pressure changes as birds when more detailed studies are conducted.

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PART III

THE INFLUENCE OF ATMOSPHERIC PRESSURE ON
INSECTIVOROUS BAT FORAGING ACTIVITY

ABSTRACT

It has been suggested that insectivorous bats may use atmospheric pressure to predict the relative abundance of aerial insects and / or favorable flying weather. In this study I examined both of these potential explanations for observed correlations of bat activity with atmospheric pressure. In the first year, observations of bat foraging activity, aerial insect abundance and meteorological conditions were collected on 115 nights at two study sites in Tennessee. Precipitation, atmospheric pressure, temperature, aerial insect abundance and date were significantly correlated with the number of feeding bats. However, atmospheric pressure conditions that corresponded with the highest aerial insect abundance, typically preceding thunderstorms, appeared to depress bat feeding activity. In the second year, observations of bat roost exit time, roost exit intensity, aerial insect abundance and meteorological conditions were collected on 79 evenings at 2 maternity colonies in Tennessee. Roost exit time was correlated with light intensity. Roost exit intensity was correlated with atmospheric pressure change, temperature and date. Insect abundance was not correlated with atmospheric pressure conditions. Bats and insects apparently respond differently to variations in atmospheric pressure conditions. Therefore, the influence of atmospheric pressure on insectivorous bat foraging activity may be related to avoidance of poor flying conditions rather than prediction of insect abundance.

INTRODUCTION

Variation in the activity patterns of bats may be caused by a variety of factors with effects that may be area and / or species specific (Hayes 1997). Factors that are

known to influence bat activity include insect abundance (Anthony et al. 1981, Avery 1985, Taylor and O'Neill 1988, Barclay 1991, de Jong and Ahlen 1991), moonlight (Crespo et al. 1972, Fenton et al. 1977, Morrison 1978, Usman et al. 1980, Reith 1982, Adam et al. 1994), air temperature (Kunz 1973, Anthony et al. 1981, Lacki 1984, Avery 1985, Audet 1990, Rydell 1991, Maier 1992, Whitaker and Rissler 1992), heavy rainfall (Fenton 1970, Kunz 1973, Fenton et al. 1977, Bell 1980, Reudi 1993), wind (O'Farrell et al. 1967, O'Farrell and Bradley 1970, Avery 1985, Rydell 1991, Adam et al. 1994), relative humidity (Lacki 1984, Adam et al. 1994) and atmospheric pressure (Nagel and Nagel 1994, Paige 1995). The abundance of aerial insects, the prey of insectivorous bats, is known to be influenced by environmental factors including atmospheric pressure, air temperature, precipitation, relative humidity and wind with the effects being area and / or species specific (Johnson 1954, Haufe 1954, Harker 1958, Williams 1961a and 1961b, Haufe 1967, Atkins 1978, Pedgley 1982).

Recent studies have suggested that bats may be able to detect and respond to small variations in atmospheric pressure (Nagel and Nagel 1994, Paige 1995, see Part II). The variations in atmospheric pressure to which bats are exposed include the absolute magnitude and the rate of pressure change. Absolute pressure magnitude is a reliable indicator of altitude while pressure change can be separated into two types; rapid changes associated with altitude changes in flight and relatively slow changes associated with meteorological events. The only study that has specifically addressed the ability of bats to detect changes in atmospheric pressure is limited to pressure changes that are typical of altitude changes in flight (see Part II). The ability of bats to

detect the relatively small, slow pressure changes associated with meteorological events has not been specifically tested. However, two studies have reported correlations of bat activity with variations in atmospheric pressure due to meteorological events (Nagel and Nagel 1994, Paige 1995). Nagel and Nagel (1994) reported that bat flight activity in a winter hibernacula in southern Germany increased during periods of low atmospheric pressure that generally corresponds with warmer air temperatures in that geographic area. They suggested that bats might use atmospheric pressure to determine favorable flying conditions outside the hibernacula. Paige (1995) reported that the number of bats emerging from a cave roost in Indiana (USA) was positively correlated with atmospheric pressure, which was also positively correlated with insect abundance at that location. He suggested that the bats were using atmospheric pressure to predict insect availability outside the cave. Unfortunately, neither of these studies accounted for the variety of other factors that are widely known to influence bat activity patterns.

This study was conducted to assess the relative importance of atmospheric pressure as a factor influencing bat activity patterns compared with the other environmental variables that are also known to influence these patterns. I also examined two previously suggested explanations for the correlations of bat activity and atmospheric pressure. If insectivorous bats use atmospheric pressure to predict the relative abundance of aerial insects, bat foraging activity should be positively correlated with the atmospheric pressure conditions that indicate high insect abundance. If bats are using atmospheric pressure to predict flying conditions, bat

foraging activity should be positively correlated with atmospheric pressure conditions that indicate favorable flying weather regardless of insect abundance.

METHODS

I monitored bat foraging activity, insect abundance and meteorological conditions between June and September during two years in east Tennessee, USA. During the first summer, one study site was established near River Mile Marker 625.5 on the north shore of Fort Loudon Lake. Fort Loudon Lake is an impoundment of the Tennessee River. The study site was located on the shoreline under an overhanging tree canopy. Most of the bats foraging in this area were *Myotis lucifugus*. Bat foraging activity was concentrated along the edge of the canopy over the open water. The second study site was located about 10 km away at the edge of a small forest opening on the Maryville College campus in Maryville, Tennessee. Most of the bats foraging in this area were *Eptesicus fuscus*. Bat foraging activity was dispersed across the open area. During the second year, bats were observed exiting from two different maternity roosts of *E. fuscus* on the Maryville College campus. One maternity roost was located in the attic of Anderson Hall and the other was in the attic of Faerywether Hall.

During the first year of the study I monitored bat foraging activity, insect abundance and meteorological conditions from 30 min before sunset to 5 hr after sunset for 60 evenings at Fort Loudon Lake and 55 evenings at Maryville College. An index of bat foraging activity was measured using bat detectors to detect feeding buzzes (Griffin 1958). Feeding buzzes, rather than all bat passes, were selected as the

index for foraging activity as they are more specifically related to feeding activities. An Ultra Sound Advice S-25 bat detector was used at the Fort Loudon Lake site. Two Ultra Sound Advice Mini-2 bat detectors were used at the Maryville College site. One was tuned to 30 kHz and the other was tuned to 60 kHz. Insect abundance was measured as the number of insects caught using custom made non-attractant suction traps (Southwood 1978). The insect traps used electric fans to move air across a funnel-shaped screen that captured the flying insects. Date and moon phase were recorded. Light intensity was measured using ambient light meters (Sper Scientific). Atmospheric pressure and atmospheric pressure change were measured using aneroid barometers. Temperature and relative humidity were measured using sling psychrometers. Wind speed was measured using anemometers (Dwyer). Precipitation was collected in standard rain gauges.

During the second summer I visually observed bat roost exits, insect abundance and meteorological conditions from 30 min before sunset to 1hr after sunset for 59 evenings at Anderson Hall and 21 evenings at Faerywether Hall. The time at which the first bat left the roost, scaled to official sunset time, was recorded as the exit time. The number of bats that exited the roost within 15 minutes of the first bat to leave the roost was recorded as a measure of exit intensity. Insect abundance, date, moon phase, light intensity, atmospheric pressure and atmospheric pressure change, temperature, relative humidity, wind speed and precipitation were measured as in the previous year.

Data were analyzed using stepwise multiple regression to create descriptive models that included the environmental variables that were most correlated with bat foraging activity, roost exit time, roost exit intensity and insect abundance. Levels for entry and retention in the models were set at $P < 0.05$. The wind speed and precipitation variables were not included in the statistical analysis as the presence of either during these observations apparently precluded any level of bat activity.

RESULTS

At the Fort Loudon Lake site, the mean number of bat feeding buzzes per evening was 106 (range 4 - 296) which was 13% of the total observed bat passes. The mean number of insects captured per evening was 408 (range 120 - 996). Based on the frequency range of echolocation sounds and visual observations, most of the foraging bats were identified as *M. lucifugus*. Multiple regression models describing the factors that influenced bat foraging activity and insect abundance at Fort Loudon Lake are in Table 1.

Bat foraging activity, insect abundance and meteorological conditions were observed over 55 evenings at the Maryville College site. The mean number of bat feeding buzzes per evening was 47 (range 0 - 325), which was 26% of the total observed bat passes. The mean number of insects captured per evening was 518 (range 77 - 1273). Based on the frequency range of echolocation sounds and visual observations, most of the foraging bats were identified as *E. fuscus*. Multiple regression models describing the factors that influenced bat foraging activity and insect abundance at Maryville College are in Table 1.

Table 1. Multiple regression models describing the factors that influenced bat foraging activity and insect abundance at Fort Loudon Lake and Maryville College. Specific values for the model intercept (I) and coefficients are not given as these are only intended to be descriptive models.

Multiple Regression Models	R ²	P
Fort Loudon Lake		
Buzzes = I - Temperature + Insects - Pressure Change	0.48	0.0001
Insects = I - Date + Pressure Change	0.35	0.0001
Maryville College		
Buzzes = I - Atmospheric Pressure	0.21	0.0028
Insects = I - Relative Humidity + Temperature	0.27	0.0023

Over 21 nights of observations at Faerywether Hall, the mean exit time was 11 min after sunset (range 0 - 28) and mean exit intensity was 18 bats (range 1 - 68). The mean number of insects captured per evening was 38 (range 0 - 80). The bats were exiting from a previously identified *E. fuscus* maternity roost. Multiple regression models describing the factors that influenced bat roost exit time, exit intensity and insect abundance at Faerywether Hall are in Table 2.

Over 59 nights of observations at Anderson Hall, the mean exit time was 13 min after sunset (range 10 min before sunset - 25 min after sunset) and mean exit intensity was 40 bats (range 1 - 149). The mean number of insects captured per evening was 27 (range 0 - 61). The bats were exiting a previously identified *E. fuscus* maternity roost. Multiple regression models describing the factors that influenced bat roost exit time, exit intensity and insect abundance at Anderson Hall are in Table 2.

DISCUSSION

The primary goals of this study were to investigate whether wild, insectivorous bat activity patterns are correlated with ambient atmospheric pressure conditions and to see if those correlations are consistent with predicting insect availability and / or assessing local flight conditions.

Bats clearly alter their foraging activity in response to wind and precipitation events. In this study, all of the observed wind and precipitation occurred during localized thunderstorms. In every case, bat flight activity completely ceased at the study site until the thunderstorm passed. Therefore it seems likely that these frequent summer events represent significant interruptions to foraging bats. Since these events

Table 2. Multiple regression models describing the factors that influenced bat roost exit time, exit intensity and insect abundance at two locations at Maryville College. Specific values for the model intercept (I) and coefficients are not given as these are only intended to be descriptive models.

Multiple Regression Models	R ²	P
Faerywether Hall		
Exit Time = I - Light Intensity	0.67	0.0001
Exit Intensity = I - Date	0.61	0.0001
Insects = no significant model was described		
Anderson Hall		
Exit Time = I - Light Intensity	0.65	0.0001
Exit Intensity = I - Date - Temperature + Pressure Change	0.36	0.03
Insects = I - Date + Temperature	0.39	0.008

are almost always preceded by a rapid change in atmospheric pressure, bats may be able to assess foraging and flight conditions in advance if they can detect the variation in pressure.

In considering the multiple regression models that describe bat foraging activity and insect abundance in relation to the environmental variables in this study, it is important to notice the relatively low R^2 values. The models are all statistically significant. The low model R^2 values may indicate either that there are large variations in the data or that variables not included in the models are important (Sokal and Rohlf 1981). Even so, the models may help to describe how bats are influenced by atmospheric pressure.

At the Fort Loudon Lake site during the first year of the study, bat foraging activity decreased when temperatures were high, increased on evenings with large numbers of insects and decreased when there were large changes in atmospheric pressure. Insect abundance decreased later in the summer and increased on evenings that had large changes in atmospheric pressure. It is interesting to note that even though bat foraging activity increased at this site when insect numbers were high, the atmospheric pressure conditions that had a positive correlation with large numbers of insects had a negative correlation with bat foraging activity. In other words, if foraging activity is suppressed during atmospheric pressure conditions that increase insect abundance, bats are giving up feeding opportunities that have a potentially greater harvest rate. This result would be consistent with the prediction that bats are assessing local flight conditions rather than relative abundance of insects.

At the Maryville College site during the first year of the study, bat foraging activity appeared to be lower during high atmospheric pressure conditions. Insect abundance decreased when relative humidity was high and increased with warmer temperatures. It appears that at this study site bat foraging activity was influenced by atmospheric pressure conditions even when insect abundance was not. This result would also be consistent with the prediction that bats are assessing local flight conditions rather than using atmospheric pressure conditions to predict insect abundance.

At Faerywether Hall during the second summer of the study, bat roost exit time was primarily influenced by light intensity. Roost exit time was earlier when light intensity was lower. Roost exit intensity at this site decreased over the course of the summer as the bats abandoned this roost by the middle of July. Insect abundance at this location was not correlated with any of the variables measured.

At Anderson Hall during the second summer of the study, bat roost exit time was also primarily influenced by light intensity with exit time being earlier when light intensity was lower. Roost exit intensity was higher earlier in the summer, decreased on hot days and increased when there were large changes in atmospheric pressure preceding a thunderstorm. Insect abundance at this location decreased later in the summer and was greater on hot days. This result is consistent with the prediction that bats are responding to local flight conditions rather than using atmospheric pressure conditions to predict insect abundance.

This study demonstrates that there are significant correlations of bat foraging activity and insect abundance with atmospheric pressure conditions even when a variety of other meteorological variables are included in the analysis. However, the results are variable and site and / or species specific. Nonetheless, the overall results of this study support the suggestion by Nagel and Nagel (1994) that bats may use atmospheric pressure conditions to assess local flight conditions more strongly than they support the suggestion by Paige (1995) that bats use atmospheric pressure conditions to predict insect abundance.

A further consideration is that many bats spend only a short time foraging each night compared to the length of the night (Fenton 1990). Many species spend less than two hours foraging each night (Barclay 1985, Brigham and Fenton 1986, Fenton and Rautenbach 1986, Fenton et al. 1987, Audet et al. 1988, Fenton et al. 1990, Kunz et al. 1998). *E. fuscus*, one of the predominant species in this study, spends two hours or less foraging each night (Brigham and Fenton 1986). *M. lucifugus*, the other predominant species in this study, may spend up to 3 hours or more foraging each night (Anthony and Kunz 1977). If a relatively short foraging period is sufficient to sustain an animals total energy budget, that animal may be able to modify foraging activities in response to variable conditions (Townsend and Calow 1981). This study may provide an example of this as the bats appear to be able to defer foraging activities to avoid the risk of flying in inclement weather and still catch sufficient insect prey.

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PART IV

THE CHIROPTERAN PARATYMPANIC ORGAN

ABSTRACT

Atmospheric pressure is a potential source of information that might be used as the basis of a pressure altimeter and / or meteorological forecasting by flying animals if the animals can detect the variations in pressure. A putative atmospheric pressure receptor in the avian middle ear, the paratympanic organ, has also been reported to occur in the middle ear of some bats. In that study, four species of Vespertilionidae and two species of Rhinolophidae were examined. The paratympanic organ was reported to be of variable occurrence in *Pipistrellus pipistrellus* but was not observed in any of the other five species. The results of my study indicate that the paratympanic organ is not found in microchiropteran bats. I could not confirm the previous report of the paratympanic organ in *Pipistrellus pipistrellus* and I did not observe the paratympanic organ in representatives of ten other bat species from Vespertilionidae, Molossidae, Rhinolophidae, Mormoopidae, Natalidae and Phyllostomidae.

INTRODUCTION

A small sensory structure that develops in association with the hyomandibular cleft in vertebrate embryos (von Bartheld 1990) is retained beyond ontogenetic development in many vertebrates (Simonetta 1953). This embryonic sensory structure persists throughout adult life as the spiracular organ in nonteleost fish (Wright 1885) and the paratympanic organ in a few reptiles (Simonetta 1953), most birds (Vitali 1911) and perhaps one bat species (Vitali 1924). The anatomy of the spiracular organ in nonteleost fish has been described (Wright 1885, Barry and Boord 1984, Barry et al. 1988a) and appears to have a proprioceptive function that responds to movements

of the hyomandibular-cranial joint (Barry et. al. 1988b). The reptilian paratympanic organ has received little study (Simonetta 1953). The avian paratympanic organ has been described in great detail (Vitali 1911, Vitali 1912, Simonetta 1953, Petrash et. al. 1983, Jorgensen 1984, Giannessi and Pera 1986, Giannessi 1989, von Bartheld 1994, Giannessi and Ruffoli 1996) and functions in a manner that is consistent with the detection of atmospheric pressure (von Bartheld 1994). Vitali (1924) reported an observation of a paratympanic organ in the bat *Pipistrellus pipistrellus* that was of variable occurrence and rudimentary in conformation compared with the paratympanic organ in birds. Only two of the six *P. pipistrellus* examined were reported to have a paratympanic organ. None of the specimens of *Rhinolophus ferrumequini*, *Rhinolophus hipposideros*, *Nyctalus noctula*, *Vespertilio murinus* and *Plecotus auritus* examined were reported to have a paratympanic organ.

The occurrence of the paratympanic organ in bats is of interest because it has been suggested that several species of temperate, insectivorous bats can detect changes in atmospheric pressure (Paige 1995, see Part II). In these studies, the detection of atmospheric pressure was discussed in relation to the presumed function of the paratympanic organ as an atmospheric pressure detector. However, the report by Vitali (1924) does not support the presence of the paratympanic organ in most bats. In fact, an alternate mechanism for pressure detection by mammals has been suggested by the presence of stretch receptors in the human tympanic membrane (Rockley and Hawke 1992). The objectives of this study were to reexamine *P. pipistrellus* and to increase the number of bat species surveyed for the paratympanic organ.

METHODS

Adult specimens from 11 microchiropteran bat species were obtained and examined. Two specimens of *P. pipistrellus* (Vespertilionidae) that had been fixed by immersion in ethanol were obtained from collections at the American Museum of Natural History. A third *P. pipistrellus* specimen fixed by immersion in 4% paraformaldehyde after piercing the tympanic membrane was provided by D. H. Pauza, Kaunas Medical Academy. Four specimens each of *Pipistrellus subflavus* (Vespertilionidae), *Eptesicus fuscus* (Vespertilionidae), *Myotis velifer* (Vespertilionidae) and *Tadarida brasiliensis* (Molossidae) were immersion fixed in 3% glutaraldehyde in phosphate buffered saline (PBS) after piercing the tympanic membrane. The entire middle ear region of all specimens was removed by dissection, rinsed in PBS, decalcified for seven days in 10% EDTA (pH 7), stained in 2% osmium tetroxide in PBS for 1 hour, dehydrated in alcohol and propylene oxide and embedded in Epon. Serial sections 10 μ m thick were taken throughout the middle ear. Alternate sections were collected on gelatin coated slides, stained with 1% Toluidine Blue O in 1% Borax. Six other bat species examined included *Rhinolophus rouxi* (Rhinolophidae, n = 1), *Pteronotus parnellii* (Mormoopidae, n = 2), *Pteronotus quadridens* (Mormoopidae, n = 1), *Natalus stramineus* (Natalidae, n = 1), *Eumops perotis* (Molossidae, n = 1) and *Leptonycteris sp* (Phyllostomidae, n = 1). These specimens were provided as slides containing serial sections throughout the middle ear of bat specimens that had been prepared for previous research (Henson 1961). All slides were examined using light microscopy.

RESULTS

Table 1 lists the species of bats examined in this study as well as the bat species examined by Vitali (1924). In my study, none of the *P. pipistrellus* specimens examined had a paratympanic organ. I also did not observe a paratympanic organ in the specimens of *P. subflavus*, *M. velifer*, *E. fuscus*, *T. brasiliensis*, *R. rouxi*, *P. parnellii*, *P. quadridens*, *N. stramineus*, *E. perotis* and *Leptonycteris* sp.

DISCUSSION

The results of my study indicate that the paratympanic organ is not found in the middle ear of microchiropteran bats. Of a total of 16 bat species examined from six different families, the only reported occurrence of the paratympanic organ in a bat is in *P. pipistrellus* (Vitali 1924). In that report, the occurrence of the paratympanic organ was variable with it only being observed in 2 of 6 specimens. The current examination was unable to confirm the earlier report as the paratympanic organ was not observed in the three *P. pipistrellus* specimens examined. Assuming that Vitali (1924) was correct in reporting his observations, there are two possible explanations for the discrepancy in the observations. If the occurrence of the paratympanic organ in *P. pipistrellus* is variable, it may have simply not been in some of the specimens examined. Alternatively, the discrepancy might be due to species confusion as *P. pipistrellus* has been discovered to exist as two separate cryptic species (Barratt et al. 1997). If only one of the two species has the paratympanic organ, it is possible that the specimens examined by Vitali (1924) contained individuals of each species and

Table 1. Bat species examined for the occurrence of the paratympanic organ.

Species	# examined	paratympanic organ
from Vitali (1924)		
<i>P. pipistrellus</i>	6	yes, in 2 of 6
<i>R. ferrumequini</i>	1	no
<i>R. hipposideros</i>	1	no
<i>N. noctula</i>	2	no
<i>V. murinus</i>	1	no
<i>P. auritus</i>	1	no
This study		
<i>P. pipistrellus</i>	3	no
<i>P. subflavus</i>	4	no
<i>E. fuscus</i>	4	no
<i>M. velifer</i>	4	no
<i>T. brasiliensis</i>	4	no
<i>R. rouxi</i>	1	no
<i>P. parnellii</i>	2	no
<i>P. quadridens</i>	1	no
<i>N. stramineus</i>	1	no
<i>E. perotis</i>	1	no
<i>Leptonycteris. sp</i>	1	no

that all three of my specimens were of the species without a paratympanic organ. Further examination of known *P. pipistrellus* would be necessary to resolve this issue.

Since some bats are able to detect variation in atmospheric pressure (Paige 1995, see Part II), there must be an alternative pressure detection mechanism besides the paratympanic organ. One possible alternative is an atmospheric pressure detection mechanism that has, to date, only been partially described in humans (Rockley and Hawk 1992). This atmospheric pressure detection mechanism presumably operates via stretch receptors (specialized nerve endings) in the tympanic membrane that are stimulated as air pressure changes in the external ear displace the tympanic membrane. Further details of this mechanism have not been reported. If bats have stretch receptors in their tympanic membranes, it is possible that they detect variation in atmospheric pressure using this mechanism. An anatomical survey of bats and other mammals for tympanic membrane stretch receptors would determine whether this is a general anatomical characteristic of mammals or limited to humans.

The ability to detect atmospheric pressure change is a widespread phenomenon that is found across a diversity of animals from different taxonomic groups and with very different modes of locomotion. Humans are sensitive to small atmospheric pressure changes with a rate equivalent to 10m altitude change per second (Rockley and Hawk 1992) even though they do not naturally experience altitude changes at that rate. Even three bat species (*E. fuscus*, *M. velifer* and *T. brasiliensis*) that do not have the paratympanic organ but are known to be able to detect variation in atmospheric pressure (see Part II) exhibit very different flight patterns. *E. fuscus* and *M. velifer*

generally fly at altitudes less than 50m (Fitch 1981, Kurta and Baker 1990), while *T. brasiliensis* frequently fly at altitudes exceeding 3000m (Wilkins 1989).

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PART V

THE AVIAN PARATYMPANIC ORGAN

ABSTRACT

The paratympanic organ, a probable atmospheric pressure detector, is located on the medial wall of the middle ear of most birds. The central portion of the elongated, vesicular organ contains a sensory epithelium from which hair cell bundles project. The long axis of the organ is in a rostrocaudal orientation adjacent to the stapedia artery. Two elastic middle ear ligaments attach to the paratympanic organ. The columellar-squamosal ligament inserts at the suprastapedial process of the extracolumella and attaches adjacent to the caudal end of the paratympanic organ. The rostral end of the paratympanic organ is connected to the superior part of the tympanic membrane by the superior drum-tubal ligament. Air pressure changes in the external ear can change the tension of the superior drum-tubal ligament and influence conformation of the paratympanic organ. It has been suggested that conformational changes in the paratympanic organ stimulate hair cells in the sensory epithelium via fluid displacement. In this paper I describe the paratympanic organ matrix, an apparent accessory structure that is closely associated with hair cells in the paratympanic organ. Previous descriptions of the lumen of the paratympanic organ as a simple, fluid-filled space appear to be incorrect. The lumen of the avian paratympanic organ is filled with an extracellular, fiber-form collagenous matrix in which the ciliary bundles of hair cells are embedded. I propose that the function of the paratympanic organ matrix is to directly couple conformational changes in the paratympanic organ with the ciliary bundles of hair cells.

INTRODUCTION

In most vertebrate embryos, the paratympanic organ develops in association with the hyomandibular cleft (von Bartheld 1990). However, it is retained beyond the embryo only in birds and a limited number of other vertebrates (Simonetta 1953). The anatomy of the paratympanic organ and its retention primarily in flying animals led to speculation that the organ might function as an atmospheric pressure detector (Vitali 1921, Jorgensen 1984, Giannessi and Pera 1986, von Bartheld 1994). Results from early experiments were inconclusive, although surgical destruction of the tissues surrounding the paratympanic organ in the pigeon middle ear caused a loss of flight equilibrium and vertical orientation (Vitali 1921). In more recent experiments (von Bartheld 1994), three dimensional reconstruction of paratympanic organs perfusion-fixed while under pressure revealed a volume shift in the rostral end of the organ that was dependent on the sign of the pressure change. The length of the superior drum-tubal ligament, attached to the rostral end of the organ, increased with negative pressure and decreased with positive pressure. However, Platner's ligament did not exhibit length changes with pressure changes. Repetition of the paratympanic organ ablation experiment (Vitali 1921) demonstrated no impairment of flight or navigation in free-flying homing pigeons (Giannessi et al. 1996).

The internal sensory epithelium of the paratympanic organ is composed of sensory cells, supporting cells and nerve fibers. It is separated from surrounding connective tissue by a basal lamina. Sensory cells are like type-2 hair cells with one apical kinocilium and a bundle of 50-102 stereocilia up to 9 μ m in length that project

into the lumen of the organ (Jorgensen 1984, Giannessi and Pera 1986, Giannessi 1989, Giannessi and Ruffoli 1996). The lumen of the paratympanic organ has been reported to contain a viscous fluid (Jacksoll and Maderson 1978).

The model of paratympanic organ function as an atmospheric pressure detector is dependent on ligaments in the middle ear. Two elastic middle ear ligaments attach to the paratympanic organ. The columellar-squamosal ligament inserts at the suprastapedial process of the extracolumella and attaches adjacent to the caudal end of the paratympanic organ. The rostral end of the paratympanic organ is connected to the superior part of the tympanic membrane by the superior drum-tubal ligament. Variations in air pressure in the external ear change the tension of the superior drum-tubal ligament and, therefore, the conformation of the paratympanic organ. The conformational change in the paratympanic organ may stimulate the sensory hair cells in the sensory epithelium via fluid displacement (von Bartheld 1994). My own observations of the paratympanic organ demonstrate that the lumen of the organ is not a simple fluid-filled space. In this paper I describe an extracellular, fiber-form collagenous matrix that fills the lumen of the paratympanic organ and in which the ciliary bundles of sensory hair cells are embedded. I propose that the function of this matrix is to directly couple conformational changes in the paratympanic organ with the ciliary bundles of hair cells rather than relying on stimulation via fluid displacement.

This project was originally initiated to provide a comparative analysis for examination of the paratympanic organ in bats (Vitali 1924). However, the

comparative study was discontinued as no paratympanic organ was observed in the 11 species of bats examined (see Part IV).

METHODS

All paratympanic organs were obtained from adult chickens, *Gallus gallus*. Chickens were selected as the model species as they are readily available and have been the model species in most of the anatomical studies of the paratympanic organ. For scanning electron microscopy, paratympanic organs were immersion-fixed in 2.5% glutaraldehyde in phosphate buffered saline (PBS) and stained with 2% osmium tetroxide in PBS. Then the lateral wall was dissected away using forceps. The remaining portions of paratympanic organs were dehydrated in acetone, critical point dried in liquid CO₂ and coated with palladium / gold before viewing with an ETEC Autoscan scanning electron microscope.

For transmission electron microscopy, paratympanic organs were immersion-fixed in 2.5% glutaraldehyde in PBS, stained with 2% osmium tetroxide in PBS and 2% tannic acid (pH 7), dehydrated in alcohol and embedded in Epon. Ultrathin sections were stained with uranyl acetate and lead citrate before viewing with a Hitachi H-600 transmission electron microscope. The 2% tannic acid staining step was introduced to enhance visualization of the hair cell stereocilia. Tannic acid also had the unexpected effect of strongly staining the fibers of the paratympanic organ matrix. The paratympanic organ matrix is much less apparent when tannic acid is not included in the protocol.

For immunogold staining, paratympanic organs were immersion-fixed in 4% paraformaldehyde and 0.1% glutaraldehyde in PBS, rinsed in glycine, dehydrated in alcohol and embedded in LR White. Ultrathin sections were incubated in primary and then 10nm gold-labeled secondary antibodies. Labeled sections were stained with uranyl acetate and lead citrate before viewing with a Hitachi H-600 transmission electron microscope. Antibody labeling controls included elimination of the primary antibody, replacement of the primary antibody with preimmune serum and negative labeling tissues. All of the primary antibodies were obtained from the Developmental Studies Hybridoma Bank maintained by The University of Iowa, Department of Biological Sciences, Iowa City, IA 52242 under contract NO1-HD-7-3263 from the National Institute of Child Health and Development.

RESULTS

The lumen of the paratympanic organ is filled with a matrix of fibers that are generally oriented parallel with the long axis of the organ (Plate 1a). At least two types of fibers are present; 20nm diameter unbranched electron dense fibers and 10nm diameter branched electron transparent fibers (Plate 1b). Stereociliary bundles of sensory hair cells are completely embedded in the fibrous matrix (Plate 1c). The fibers in the matrix are interspersed among and very closely associated with individual stereocilia of the sensory cells (Plate 1d). It is not apparent whether fibers are attached to the stereocilia or the surface of the epithelial cells.

Some fibers in the lumen of the organ are labeled with antibodies to type II collagen. Gold labeling is diffuse, but greater than in controls (Plate 2a). Other

Plate 1. Electron micrographs of the avian paratympanic organ. (a) A scanning electron micrograph of the interior of the paratympanic organ after removing its lateral wall. Bar = 5 μ m. (b) A transmission electron micrograph of a longitudinal section through the lumen of the paratympanic organ. Bar = 0.1 μ m. (c) A transmission electron micrograph of a stereociliary bundle projecting into the paratympanic organ matrix. Bar = 1 μ m. (d) A transmission electron micrograph of a cross section through a stereociliary bundle. Bar = 0.2 μ m.

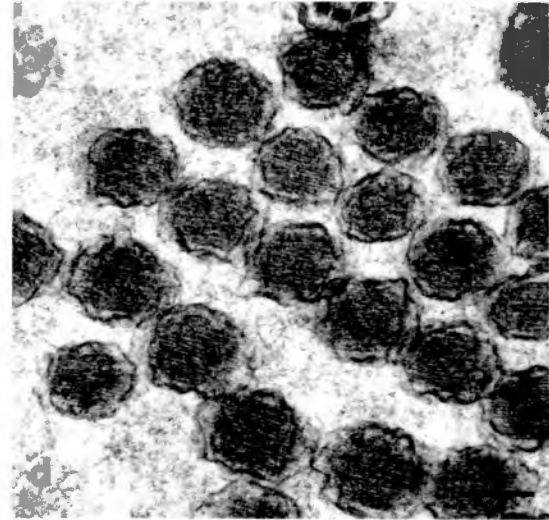
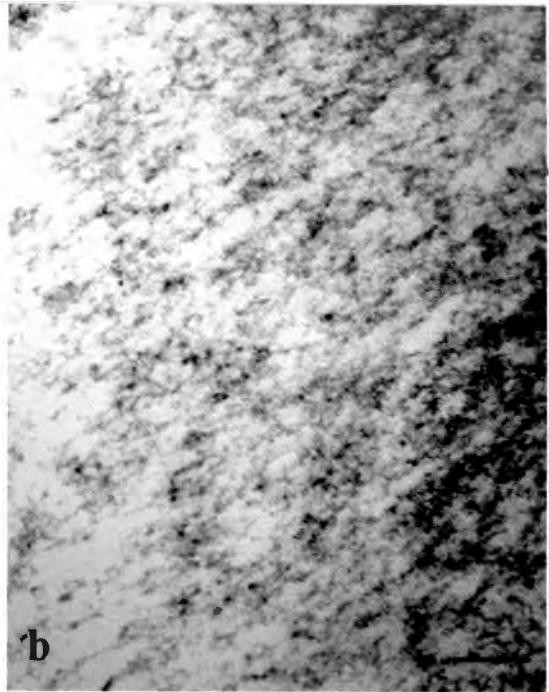
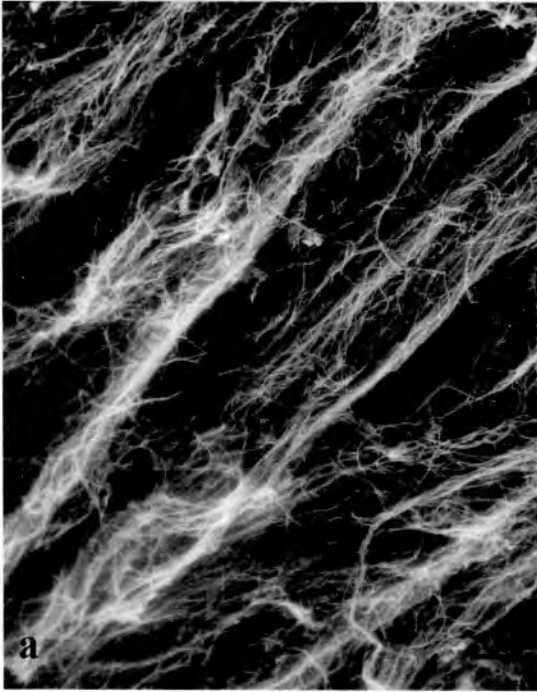
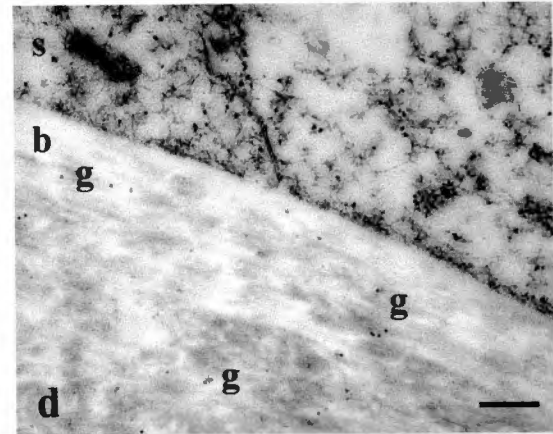
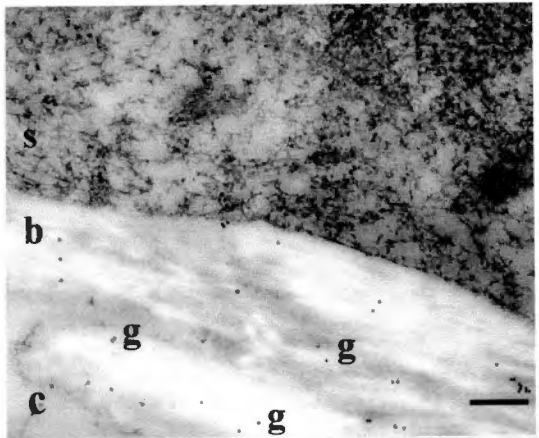
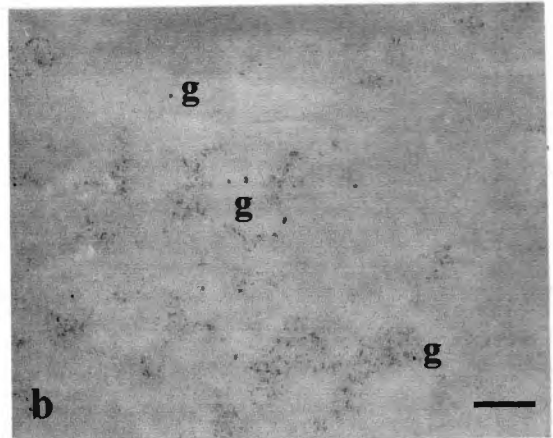
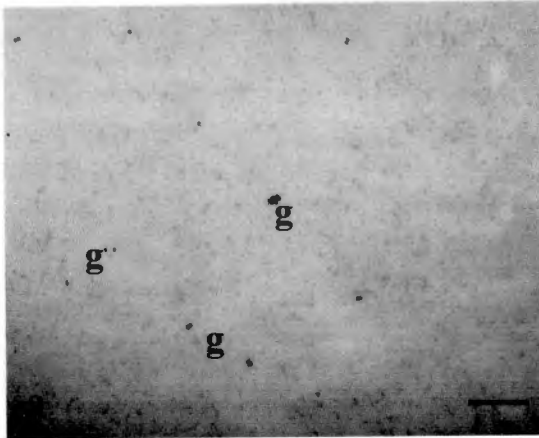


Plate 2. Immunochemical labeling in the avian paratympanic organ. (a) A transmission electron micrograph of a cross section through the lumen of the paratympanic organ labeled with monoclonal mouse anti-collagen II and goat anti-mouse IgG conjugated with 10nm colloidal gold particles. Bar = 0.2 μ m. (b) A transmission electron micrograph of a cross section through the lumen of the paratympanic organ labeled with monoclonal mouse anti-collagen IX and goat anti-mouse IgG conjugated with 10nm colloidal gold particles. Bar = 0.2 μ m. (c) A transmission electron micrograph of a longitudinal section through the basal lamina of the paratympanic organ and a few sensory cells labeled with monoclonal mouse anti-collagen III and goat anti-mouse IgG conjugated with 10nm colloidal gold particles. Bar = 0.2 μ m. (d) A transmission electron micrograph of a longitudinal section through the basal lamina of the paratympanic organ and a few sensory cells labeled with monoclonal mouse anti-collagen VI and goat anti-mouse IgG conjugated with 10nm colloidal gold particles. Bar = 0.2 μ m.



fibers in the lumen of the paratympanic organ are labeled with antibodies to type IX collagen. Gold labeling is diffuse, but greater than in controls (Plate 2b). Some fibers in the basal lamina of the paratympanic organ are labeled with antibodies to type III collagen (Plate 2c). Other fibers in the basal lamina of the paratympanic organ are labeled with antibodies to type VI collagen (Plate 2d).

DISCUSSION

Even though the function of the avian paratympanic organ as an atmospheric pressure detector has not been categorically demonstrated (Giannessi et al. 1996), its structure and probable mechanism of function has been previously described (Jorgensen 1984, Giannessi and Pera 1986, Giannessi 1989, von Bartheld 1994, Giannessi and Ruffoli 1996). The results of this study demonstrate a novel anatomical component in the paratympanic organ and suggest an addition to the previously proposed model of function (von Bartheld 1994).

In contrast to an earlier report that the lumen of the paratympanic organ is filled with a viscous fluid (Jacksohl and Maderson 1978), observations in this study indicate that the lumen of the paratympanic organ is completely filled with a fibrous matrix that has been named the paratympanic organ matrix. The paratympanic organ matrix is made up of at least two distinct types of fibers that are oriented parallel with the long axis of the organ. One fiber type is about 20nm diameter, electron dense and unbranched. A second fiber type is about 10nm diameter, electron transparent and highly branched. The long, unbranched fibers that run parallel with the long axis of the organ may provide longitudinal stability to the paratympanic organ matrix. They

may also provide a mechanism for force transfer along the long axis of the paratympanic organ. The highly branched fibers may provide three-dimensional stability to the paratympanic organ matrix, as their branches are likely to overlap extensively with other branched fibers and long, unbranched fibers. It is not known whether the overlapping fibers are attached to one another or only in close proximity. The fibers of the paratympanic organ matrix fill the lumen of the paratympanic organ and completely surround all of the stereociliary bundles that project from the epithelial surface of the paratympanic organ sensory hair cells. Furthermore, paratympanic organ matrix fibers are interspersed among the stereocilia within each hair cell bundle. It is not apparent whether paratympanic organ matrix fibers are attached to the stereocilia and the surface of the epithelial cells or only in close proximity.

Some of the fibers in the paratympanic organ matrix label with antibodies to Type II and Type IX collagen. The 20nm diameter, electron dense unbranched fibers label with Type II collagen antibodies. Type II collagen is an important structural component of a number of extracellular matrices (Linselmayer and Hendrix 1980) including the tectorial membrane in the inner ear (Slepecky et al. 1992a, Slepecky et al. 1992b). In the tectorial membrane, large diameter, unbranched fibers that play a large role in structural stabilization and contribute the principal tensile elements (Zwislocki 1988, Zwislocki et al. 1988) also label with antibodies to Type II collagen (Slepecky et al. 1992a). The 10nm diameter, electron transparent branched fibers in the paratympanic organ matrix label with Type IX collagen antibodies. Type IX collagen is fibril associated collagen (Vaughan et al. 1988). It is often found on the

surface of heterotypic fibers in association with a number of different fibrillar collagens (Vaughan et al. 1988, Fitch et al. 1988, Brewton et al. 1991, Swiderski and Solursh 1992). Type IX collagen is described as being suitable for simultaneous interactions with collagen fibrils and other matrix components (Hay 1991) that are likely to be found in the paratympanic organ matrix. Type III and Type VI collagens were not immunolocalized in the paratympanic organ matrix but rather in the basal lamina of the paratympanic organ. Given the three-dimensional network of branched and unbranched fibers that make up the paratympanic organ matrix and their fibrillar collagen components, the paratympanic organ matrix is likely to be a relatively rigid structure with high tensile strength.

Considering the close association of the fibers that make up the paratympanic organ matrix with the sensory hair cells in the paratympanic organ and a strong structural composition, it seems reasonable to suggest that the paratympanic organ matrix has a mechanical role in the model of sensory transduction in the paratympanic organ. I propose that the function of the paratympanic organ matrix is to mechanically couple conformational changes in the external shape of the paratympanic organ with the ciliary bundles of hair cells that are located in the organ lumen. This proposed function is analogous to the function of other accessory structures in the lateral line system that are considered to be homologous to the paratympanic organ (von Bartheld 1990). It is also possible that the paratympanic organ matrix acts as a filtering system to eliminate the potential effects of fluid movement in the lumen of the paratympanic organ that might occur with head orientation changes during behavioral activities.

Random fluid movement in the lumen of the paratympanic organ might stimulate the sensory hair cells if they were not surrounded and supported by the paratympanic organ matrix.

The avian paratympanic organ is generally considered to be an atmospheric pressure detector (Jorgensen 1984, Giannessi and Pera 1986, Giannessi 1989, von Bartheld 1994, Giannessi and Ruffoli 1996). Variations in atmospheric air pressure in the external ear displace the tympanic membrane and result in tension changes in the superior drum-tubal ligament. The superior drum-tubal ligament connects the superior part of the tympanic membrane with the rostral end of the paratympanic organ. A change in the tension of this ligament causes conformational changes in the shape of the paratympanic organ. Previously, it was thought that conformational changes in the shape of the paratympanic organ stimulate sensory hair cells via fluid displacement (von Bartheld 1994). My observations in this study suggest that, rather than stimulating sensory cells via fluid displacement, sensory cells are stimulated via mechanical coupling through the fibers that make up the paratympanic organ matrix. In fact, the paratympanic organ matrix may act as a filter to reduce spurious stimulation of sensory hair cells by fluid movements.

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PART VI

CONCLUSIONS AND RECOMMENDATIONS

The primary objective of my dissertation research was to investigate the detection of atmospheric pressure as a sensory modality in flying animals by examining atmospheric pressure detection and a putative atmospheric pressure detector in bats and birds. For flying animals atmospheric pressure is a potential source of information that might be used as the basis of a pressure altimeter and / or meteorological forecasting (Lehner and Dennis 1971, Kreithen and Keeton 1974). The prominent properties of variation in atmospheric pressure are absolute magnitude and the rate of pressure change. Absolute pressure magnitude is a reliable indicator of altitude while pressure change can be separated into two types; rapid changes associated with altitude changes in flight and relatively slow changes associated with meteorological events (Lutgens and Tarbuck 1989). A prerequisite for an animal to have a functional response to variation in atmospheric pressure is that the animal be able to detect the pressure variation.

Little was known about atmospheric pressure detection by bats previous to this study (Vitali 1924, Nagel and Nagel 1994, Paige 1995). In contrast, atmospheric pressure detection and a putative pressure detector in birds have been well described (Vitali 1911, Vitali 1912, Vitali 1921, Lehner and Dennis 1971, Kreithen and Keeton 1974, Jacksoll and Maderson 1978, Jorgensen 1984, Gianessi and Pera 1986, Gianessi 1989, von Bartheld 1990, von Bartheld 1994, Giannessi and Ruffoli 1996, Gianessi et. al. 1996). Therefore, most of my research was directed towards studies of atmospheric pressure detection by bats. I investigated the minimum pressure changes detectable by bats, the functional significance of atmospheric pressure detection by wild bats and a putative atmospheric pressure receptor. I also further examined the anatomy of a

putative atmospheric pressure receptor in birds for possible comparison with a putative atmospheric pressure receptor in bats.

The major conclusions of my study and recommendations for continuing studies are summarized in the following statements:

1. A critical component of an atmospheric pressure detection system, the ability to detect pressure changes, was observed in three different species of insectivorous bats. Individuals of *Eptesicus fuscus*, *Myotis velifer* and *Tadarida brasiliensis* consistently responded to induced atmospheric pressure changes with spontaneous increases in ventilation rate. Spontaneous responses were compared between control periods and periods in which atmospheric pressure was increased or decreased 4.2 kPa over 3 min, a rate equivalent to flight altitude changes of 2.3 m per second. As this study tested only one rate of pressure change, it is recommended that more detailed studies be conducted to more thoroughly characterize the ability of bats to detect small atmospheric pressure changes. It might also be possible to investigate whether bats can discriminate between the pressure increases and decreases they encounter during flight altitude changes. However, further study on this topic should use behavioral training procedures rather than observing spontaneous responses to induced pressure changes. Behavioral training procedures could be modeled after those used for birds (Kreithen and Keeton 1974) with modifications designed to accommodate the physical and behavioral characteristics of bats. It is expected that some bats will prove to be as sensitive to atmospheric pressure changes as birds.

2. Insectivorous bat foraging activity and flying insect abundance are correlated with ambient changes in atmospheric pressure. However, atmospheric pressure conditions that are correlated with an increase in flying insect abundance are correlated with a decrease in bat foraging activity. Bats and insects apparently respond differently to variations in atmospheric pressure conditions. Therefore, the influence of atmospheric pressure on insectivorous bat foraging activity is more likely related to avoidance of poor flying conditions rather than prediction of insect abundance. It is unlikely that further studies like this will be able to determine the specific atmospheric pressure variations responsible for influencing bat foraging activity given the number of different environmental influences, the magnitude of variability in meteorological events and the flexibility of bat behavioral responses. Further studies would be best conducted under more controlled conditions in captive colonies that are isolated from many environmental variables. Working with captive bats would also make it possible to use more intensive instrumentation approaches such as long-term recording of activity patterns for individual animals and / or physiological responses such as variations in metabolic rate and energy use.

3. The paratympanic organ, a putative atmospheric pressure receptor in birds, is not found in bats. This study failed to confirm a previous report of the paratympanic organ in *Pipistrellus pipistrellus* (Vitali 1924) and the paratympanic organ was not observed in representatives of ten other bat species. Further research on atmospheric pressure detectors in bats should be focused on something other than the paratympanic organ. One possibility is that an atmospheric pressure detection

mechanism described in humans (Rockley and Hawk 1992) that operates using stretch receptors in the tympanic membrane is a general mammalian characteristic. This possibility could be easily examined by conducting an anatomical survey of bat tympanic membranes for similar stretch receptors. If stretch receptors are located in the bat tympanic membrane, the methodological approach described by Rockley and Hawk (1992) could be combined with behavioral conditioning procedures to determine if this is the mechanism bats use to detect variations in atmospheric pressure.

4. The avian paratympanic organ, a putative atmospheric pressure detector, contains a novel anatomical structure. The paratympanic organ matrix is an extracellular, fiber-form collagenous matrix in which the ciliary bundles of hair cells are embedded in the lumen of the avian paratympanic organ. The proposed role of the paratympanic organ matrix in the function of the paratympanic organ is to couple conformational changes of the paratympanic organ with the internal sensory hair cells. Further immunochemical labeling is needed to more completely describe the chemical composition and structural properties of the paratympanic organ matrix. It should also be possible to test the functional role it may play in the detection of atmospheric pressure by birds.

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