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VARIATION IN THE CAVE ENVIRONMENT AND ITS BIOLOGICAL IMPLICATIONS

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INTRODUCTION

Constancy of the cave environment has too often been assumed and emphasized. The most common generalization is that cave temperature varies only near entrances (the variable temperature zone) while the remainder of a cave is constant (the constant temperature zone), with temperature closely approximating the local mean annual surface temperature. Humidity also is often considered to be near saturation and relatively invariant. These generalizations are true in some cases. Certainly, the cave environment is buffered in relation to the outside environment. Overall temporal and spatial variation of temperature and humidity among and within caves, however, is far greater than is generally suspected, and even a small amount of such variation can have great impact on cave faunas (Jegla and Poulson 1969; Juberthie and Delay 1973; Delay 1974; Juberthie 1975; Poulson 1975; Tuttle 1975, 1976; Wilson 1975; Peck 1976).

Although literature demonstrating considerable variation exists, it is scattered, often in foreign or little-known publications, and sometimes is authored by laymen who publish only once on the subject. Consequently, few individuals, even among biospeleologists, are adequately aware of much of the available literature and its biological implications. Another source of confusion has been the fact that many authors, while presenting a thorough discussion of one or more variation- producing factors, still have opened or concluded with general statements about the constancy of the cave environment.

Despite the confusion, in the existing literature a variety of factors-such as number, size, and position of entrances, passage size, contour and slope, overall cave volume, distance of greatest volume from entrances, amount and seasonal timing of entry of surface water, air flow, and the annual range of outside temperature- have been noted to strongly influence cave temperature and humidity (see Halliday 1954; Moore and Nicholas 1964; Plummer 1964; Cropley 1965; Geiger 1965; Peters 1965; Vandel 1965; Conn 1966; Barr 1968; Daan and Wichers 1968).

This paper integrates current knowledge of the cave environment with particular emphasis on air flow and temperature; it presents some of our data on the subject, and discusses the importance of such information to biological research and cave management. We believe that familiarity with factors influencing cave environments can be highly useful in biospeleology and cave management, both for the generation of hypotheses and predictions in ecological and distributional studies and for predicting the biological uniqueness and potential of any given cave under investigation.

METHODS

From 1960 to 1975 the senior author visited several hundred caves, primarily in Alabama, Florida, Tennessee, and Virginia, and recorded temperatures at hundreds of winter and summer roosts of the gray bat (*Myotis grisescens*). Temperature and humidity readings were recorded using a Bendix Psychron motor-driven psychrometer. Since gray bats prefer caves that provide the greatest possible deviations from mean annual surface temperatures, the caves visited during these bat studies provided examples of strikingly different structures and temperature regimes. Many other caves, not used by gray bats, provided additional comparisons.

From the winter of 1975-76 through the winter of 1976-77 a more detailed study of cave temperature was conducted. Thousands of temperature measurements were made in 25 caves and mines from Wisconsin to Florida, in an effort to test the predictions generated incidental to the previous bat studies. A quick, accurate temperature measuring device was essential, and a Bailey Thermalert, Model TH-2 digital readout thermometer with a 1-mm diameter thermister probe was used initially. Testing in controlled water baths at temperatures of 0-30°C demonstrated precision of ±0.1°C. However, accuracy under field conditions varied with the temperature of the instrument itself, forcing one to carry it beneath one's coveralls and to repeatedly recalibrate against a laboratory-tested Wesco mercury thermometer. Though readings could be made in only a few seconds, accuracy with the Thermalert in the field was only ±0.3°C.

Accuracy was greatly improved with the purchase of an IMC Digital Thermometer, Model 2100 (produced by IMC Instruments, Inc., Glendale, Wis.), with a range of -40° to +250°F. This thermometer proved far more suitable for use in caves. It weighed only about 500 grams (including batteries), was extremely sturdy, provided accuracy and precision of ±0.1°F, and continued such reliability over an instrument temperature range of 0 to 110°F. Using a sensor probe 2.2 mm in diameter, this instrument had a response time of 3 seconds in liquids, 30 seconds or less in air, and from 45 seconds to several minutes (depending on density of solid) for surfaces. Most air and wall temperatures reported in this paper were taken with this instrument.

Although the data are not presented here, gross daily and seasonal temperature variation was recorded in five cases using Weksler maximum/minimum thermometers, and 24-hour comparisons between inside and outside temperatures were made using Bacharach Tempscribe recording thermometers, in order to verify our findings. Mean annual surface temperatures (MAST) were obtained from U.S. Department of Commerce (1975a-c) publications. A steel tape or, for the longest distances, a Model 100 Optical Tapemeasure (produced by Ranging Inc., Rochester, N.Y.) were used for cave measurements.

Data from only a few representative caves in the study could be included here, but the omitted observations agree well with those selected for discussion.

FACTORS THAT INFLUENCE CAVE TEMPERATURE

Conduction from Cave Walls -- If one surface of a very large limestone block were exposed to a seasonal cycle of temperature, "it may be predicted that its interior temperature would remain very close to [mean annual surface temperature (MAST)] within a very few feet of its surface." A time lag in temperature adjustment of approximately 7 days for every foot of depth produces this constancy (Cropley 1965). Cropley described as Zone III an area of a cave where isolation from outside conditions is such that "no temperature variations occur except those that are initiated by the conduction of heat from the surface through the cave roof." Although this is the characteristic of the constant temperature cave of popular legend, he found no instance of a "true Zone III location," but concluded that relatively isolated rooms "are sufficiently common that the legend is perpetuated." The main effect of cave wall conduction will be seen to be the tendency to gradually return differing air or water temperatures to mean annual surface temperature-the more isolated from outside influences an area is (whether by distance or physical barriers) the more nearly its temperature will approximate MAST.

Geographic Location -- Vandel (1965) listed geographical location and altitude as important factors affecting cave temperature; their major influence is on the range and mean of the annual surface temperature and on standard barometric pressure. Since the amount of variation from mean annual surface temperature that can be achieved in any given cave is directly proportional to the annual range of surface temperature (see discussion below), caves in tropical regions would be expected to exhibit only the slightest deviations from MAST. To a lesser extent, fluctuations also should be reduced in caves on islands, peninsulas, or even in coastal areas. Within a given area, cave entrances on north versus south slopes, those at different elevations, and those on exposed surfaces versus in deep, protected valleys or sinks will face different means and ranges of surface temperature, which often result in detectable differences in internal temperatures.

Another geographic factor is the nature of the geological structure present; caves of certain configurations may exist primarily in certain areas. Barr (1961:13) documented the existence of strong geographic tendencies in the distribution of caves of "essentially horizontal" versus "steeply or moderately inclined beds." Such structural tendencies would be expected to be reflected in geographic trends in cave temperature and humidity. This in turn may have important zoogeographic implications.

Water Circulation -- In order for internal temperatures to vary above or below mean annual surface temperature, a cave must have a route of communication with the temperature fluctuations of the outside atmosphere. With cave wall conduction exerting only infinitesimal effect extremely short distances from the surface, the two main routes of communication are circulation of air and water. Water is most likely to cause deviations from mean annual surface temperatures when it enters directly from the surface in seasons when surface temperatures deviate farthest from the mean annual temperature (Cropley 1965) or, in rare instances, when it enters from thermal springs (Geiger, 1965). Flooding, as noted by Barr (1968), can produce sudden and pronounced temperature changes and can play a vital role in triggering reproduction of aquatic troglobites (Poulson and Smith 1969; Jegla and Poulson 1970). The "disrupting" influence of outside water will, of course, last only until it has flowed a distance sufficient to allow it to reach thermal equilibrium with the cave walls.

Air Circulation -- Although exceptions do occur, the impact of air circulation in caves is generally far greater than that of water, if for no other reason than the fact that whereas most known caves have some air circulation (those isolated by water sumps being an exception), a much smaller proportion have major water circulation. The four main causes of air circulation affecting cave temperature (see Plummer 1964) will be discussed. It will be seen that the magnitude and type of impact of all air flow types is overwhelmingly determined by the structure (passage configuration) of the cave itself.

Barometric pressure -- Atmospheric (or barometric) pressure frequently has been cited as a primary factor influencing within-cave air movement and temperature fluctuation. Although other factors such as solar-induced atmospheric tides can produce slight pressure changes (Encyclopedia Britannica 1975), the relatively greatest fluctuations in barometric pressure at any given altitude are directly the result of temperature changes (Moore and Nicholas 1964).

At one location pressure changes can, of course, occur that are due to temperature changes (and the resulting winds) at another distant location, as in the case of changes preceding storm fronts. It is only these non-temperature-associated pressure changes that can be discussed meaningfully as barometric pressure influences on cave climate. Changes in the outside air temperature obviously will be accompanied by changes in barometric pressure, since the latter is determined by the weight of air (colder = heavier). In this paper, however, references to barometric pressure effects will refer only to the non- temperature - associated changes; temperature-associated pressure changes will be considered synonymous with temperature fluctuation.

At certain times, as noted by Porter (1974), "All caves should exhibit an airflow into the entrance when the outside atmospheric pressure rises, and should emit air when the pressure falls." Nevertheless, the overall impact of this circulation appears to be relatively minor (Moore and Nicholas 1964; Plummer 1964), especially when compared to that of thermal convection. Its effect certainly is more gradual, transitory, and of less magnitude. Apparently rare cases exist where caves, such as Wind and Jewel Caves in South Dakota, have extremely large volumes and generate significant winds through barometric pressure interactions alone (Conn 1966). Even in these caves, however, internal temperatures probably are affected little, compared to the amount that would occur if thermal convection were directly involved.

Surface wind -- Surface winds carried into or through caves by their own force may be of some importance in certain instances (Plummer 1964; Geiger 1965), but most examples are limited to a cave with a short simple tunnel between its two or more entrances, or to a relatively shallow cave with a large entrance. Plummer (1964) discussed the flow of surface winds through caves with entrances a large distance apart, but points out that in such cases the "motion is not properly ‚caused' by the surface winds." He contends that "both the cave and surface winds result from the same difference in barometric pressure between the locations of the entrances." This effect would be most likely to occur in a cave shaped like a nearly level tunnel.

Resonance -- Schmidt (1959), Eckler (1965), Peters (1965), Moore and Nicholas (1964), Plummer (1964), Porter (1974), Russell (1974) and others have discussed this potential cause of cave "breathing"

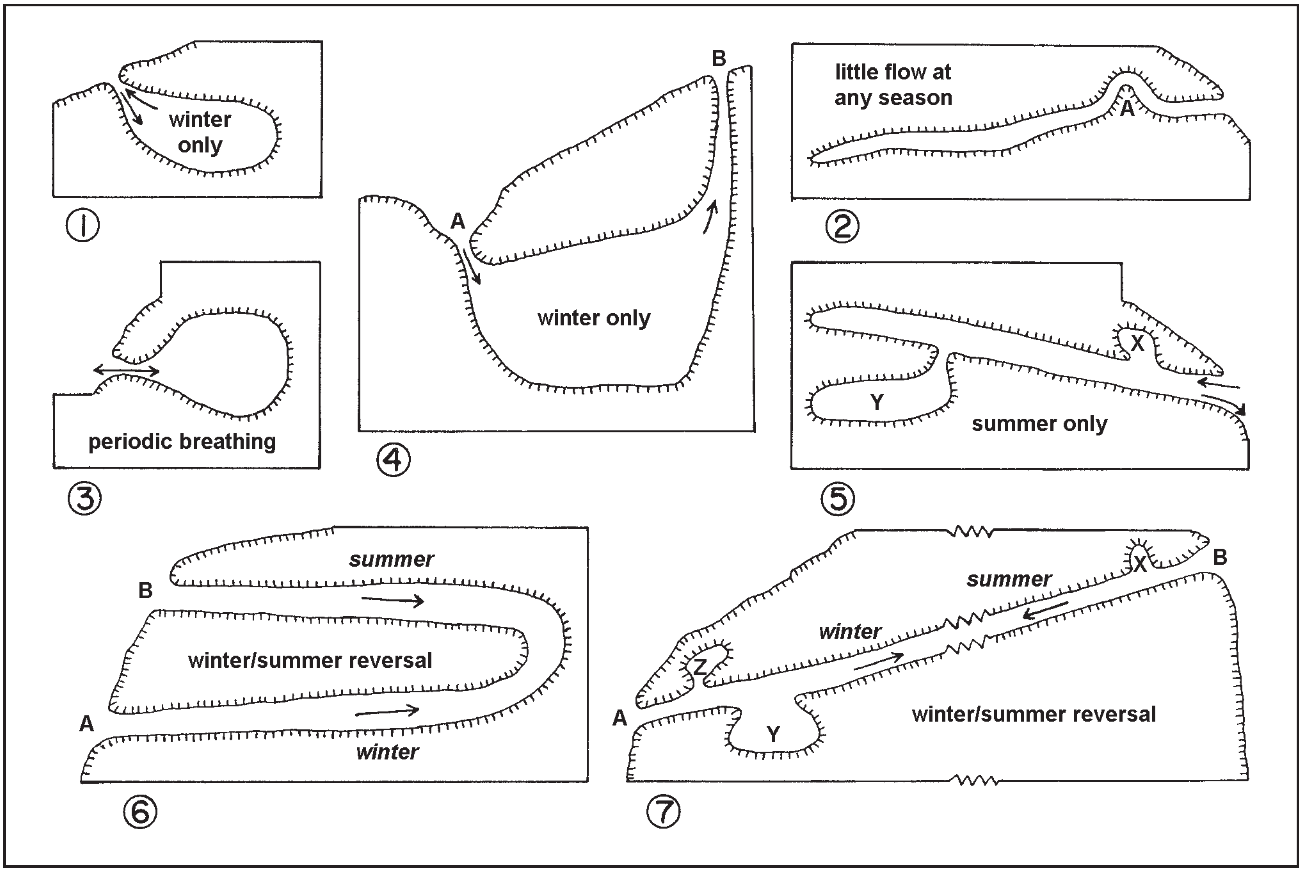

Figure 1. Simplified cave structures. Air flow indicated as occurring in "winter" will generally occur when outside temperature is below mean annual surface temperature (MAST); flow marked "summer" will occur when outside temperature is above MAST. Type 1: Breathes (as indicated by arrows) in winter; stores cold air in summer. Type 2: Undulation at A acts as dam inhibiting air flow; temperature relatively constant beyond dam. Type 3: "Jug" shape often postulated to exhibit resonance; may have pulsing in and out air movement, especially when outside air deviates from MAST. See text for alternate explanation for the oscillation of air. Type 4: Strong air circulation from A to B in winter; stores cold air in summer. Type 5: The reverse of Type 1; warm air enters along ceiling in summer while air cooled by cave walls flows out along floor. No flow in winter. X is a warm air trap, Y stays a relatively constant temperature. Type 6: Strong air flow from A to B in winter; equally strong air flow in opposite direction in summer. Type 7: Same as Type 6, with a warm air trap (X), cold air trap (Y), and an area of relatively constant temperature (Z). Distance between and elevational displacement of the entrances are critical factors in the air flow direction in these two cave types; the flow of air (cooled relative to outside temperatures by the cave walls) down in summer must be strong in order to overcome the tendency for warm outside air to rise into A. Similarly, in winter the "negative pressure" created by air (now warmer than outside air due to the MAST effect of the cave walls) rising out of B must be strong enough to pull cold air up into A.

through a single entrance. The oscillation of air has been attributed to movement of outside air across the entrance, creating resonance similar to that which "produces a sound when a person blows across the mouth of a coke bottle." (Cave 3 of Fig. 1 is of the "jug" shape postulated as suitable for resonance.) Schmidt (see Barr 1968) also suspected that such resonator effects could explain air flow oscillations in passages at the bottom of large "elevator shaft" types of passages; be hypothesized that "vertical air columns of considerable height" in the tall passages could produce effects similar to surface winds.

Although we have not attempted to investigate this phenomenon in any detail, we doubt that the above explanations are of more than rare importance. We have observed both regular and irregular breathing cycles in caves of a variety of structures, and note that oscillations are most likely to occur when outside temperature is fluctuating around or is close to inside temperature. Furthermore, such oscillations often persist in the absence of outside wind. When marked outside temperature changes are occurring, as during a storm (for an example, see Eckler 1965), breathing easily can be explained by thermal convection; Peters

(1965) has discussed differing cave structures and how they might cause patterns of breathing.

Moore and Nicholas (1964) have pointed out that the now famous Breathing Cave in Virginia is itself probably a multiple-entrance cave dominated by air currents caused by thermal convection. They point to internal complexity of structure as the probable source of breathing and discount the idea that the air flow oscillations are caused by outside wind blowing past its entrance. An alternative explanation (using thermal convection as opposed to resonance) will be proposed to explain air flow oscillations in caves of Type 3 (Figure 1) in the section, "Cave Structure and Volume."

Thermal convection -- The impact of thermal convection on air movement in and out of caves (and therefore on cave temperatures) is well known; thermal convection is generally believed to be the most important factor in determining the direction and amount of air exchange with the surface (Halliday 1954; Plummer 1964; Geiger 1965; Peters 1965; Daan and Wichers 1968; Porter 1974; Russell 1974). The principle of thermal convection in caves is that air escapes (rises) through an upper entrance (or through the top of a single entrance) when it is warmer than the outside air. Conversely, air will escape through a lower entrance (or through the bottom of a single entrance) when it is cooler than the outside air. The greater the inside-to-outside temperature gradient, the faster the rate of air movement; flow ceases when the temperatures are the same. (This equilibrium condition theoretically should be reached when the outside temperature equals mean annual surface temperature for the area. Different cave types may deviate so markedly from MAST, however, that this equilibrium point may be shifted at times.) Caves can exhibit such air flow seasonally, on a daily cycle, or in response to passage of weather fronts. Direction and timing (and to a certain extent, rate) of flow will be determined by the structure of the particular cave.

Cave Structure and Volume -- Figure 1 presents several simplified examples of how air circulation works in caves of different structure. Although the number of entrances (including cracks too small for human passage) is an important variable of air circulation, the elevational difference between multiple entrances is of primary importance for thermal convection-induced temperature variation, as noted by Halliday (1954), Plummer (1964), Geiger (1965), Porter (1974) and others. Negative pressure (as described by Peters 1965, and Daan and Wichers 1968) can create powerful chimney effects in caves with entrances at different elevations (Figure 1, Types 4, 6 and 7). Halliday also pointed out that other factors, such as irregular, tortuous passages or narrow entrances, "will act as baffles to air currents." We have noted that vertical undulations are especially effective natural dams against the free flow of convection currents (see Figure 1, Type 2).

The location of a cave's greatest volume relative to its entrance(s) is also of great importance. Distance of a cave's greatest volume from the entrance(s) has been shown to be of importance in determining depth and pattern of air movement in and out of caves where movement is the result of changes in barometric pressure (Conn, 1966). Elevational displacement of cave volume from an entrance(s), however, is perhaps the most important single factor affecting cave temperature (see Figure 1, Types 1, 4, 5, 6 and 7). As noted by Geiger (1965) "if a cave slopes downward from the entrance, cold air flows downward inside it and is no longer affected by warmer and lighter air. Caves of this type are called sack caves and act as cold reservoirs... The opposite thermal effect is obtained when a cave slopes upward from its single entrance." Caves with their greatest volume above the entrance can act as warm air traps; cooled air sinks out as warm air rises in. These considerations also apply to cave chambers or passages that extend above or below passages with air flow, as illustrated in Figure 1, Types 5 and 7.

Small passages, in addition to acting as baffles, also dampen temperature fluctuations through their increased cavewall-surface-to-volume ratio-the tendency of the walls to return air to mean annual surface temperature will have maximum effect. Halliday's (1954) study of ice caves demonstrated not only the importance of having the volume below the lowest entrance but also the necessity of large volume for cold air storage. Halliday, in discussing classical examples of limestone ice caves, repeatedly noted the presence of very large volume. He mentioned room sizes of 100 feet by 30 feet, 200 feet by 50 feet, and 300 feet by 50 feet, and described another as "one immense room of ballroom proportions."

Thermal convection and the distribution of a cave's volume in relation to its entrance also could provide an alternate explanation of breathing (air flow oscillations) in caves of Type 3, Figure 1. With its volume approximately equally distributed above and

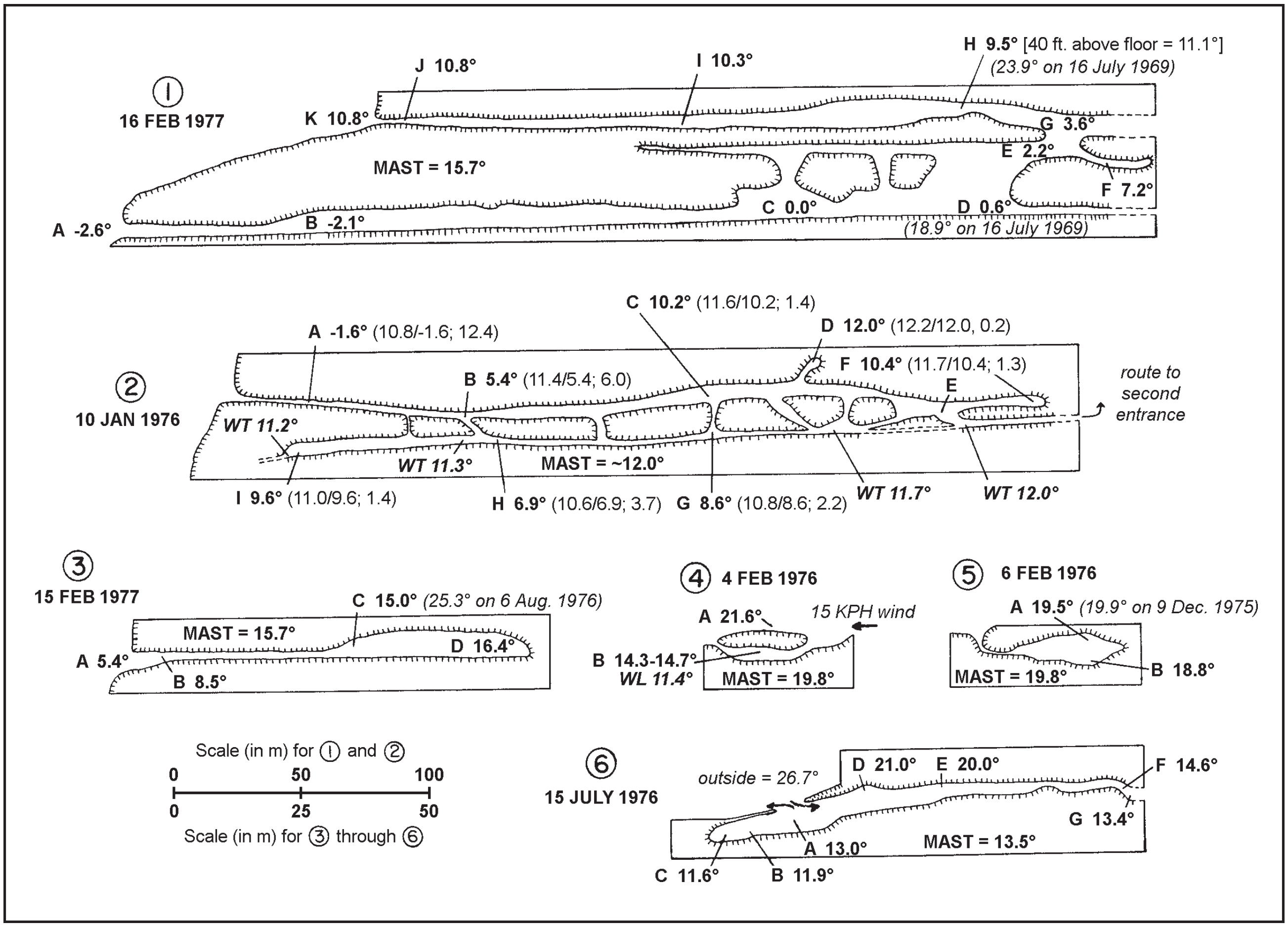

Figure 2. Six southeastern eaves and temperatures (in °C) at some sites for the date indicated near the cave number. Temperatures on additional dates may be given in parentheses. MAST = mean annual surface temperature, WL = wall temperature, WT = water temperature. For cave 2 the range of temperatures from January through August is given in parentheses (maximum/minimum; number of degrees in the range). Streams flow from right to left through the lower levels of caves 1 and 2.

below the entrance, such a cave could be expected to have warm summer air entering along the entrance ceiling, with cooled air spilling out along the bottom of the entrance. The reverse flow pattern would occur in winter. If the entrance were sufficiently constricted, however, breathing could be predicted to occur. There no longer would be room for air to move simultaneously in opposite directions; density differentials should lead to a pulsing action. At some point, further increases in entrance passage length and constriction should almost completely inhibit exchange of inside and outside air in caves of this type.

INTERACTION OF CAVE STRUCTURE AND AIR FLOW

The following examples of specific caves (see Figures 2 and 3) were taken from our studies in the southeastern United States and will illustrate the extent and nature of cave structure/air flow interactions. Cave names and locations are withheld because most of the caves discussed contain populations of endangered bats or other cavernicolous faunas. This information will be provided, on request, to those documenting bona fide need.

Seasonally Reversing Air Flow -- Cave number 1 of Figure 2 is an excellent example of Type 6/7, Figure 1. Due to its relatively simple shape, large passage diameter, and 43-meter elevational difference between entrances, air flow is direct and rapid. We have observed a strong (unmeasured, although probably sometimes exceeding 15 KPH) flow of air exiting the lower entrance and entering the upper on hot summer days, with the reverse being true on cold days in winter. Temperatures at the entrances in February (Figure 2) show the effect of the cold air entering the low entrance, and warmed air exiting the upper one. Local residents and the cave's former owner report complete or nearly complete cessation of air flow, either in or out of either entrance, when the surface temperature is approximately 60°F (15.6°C). Air flow cessation would be expected in this general temperature range due to its proximity to mean annual surface temperature (15.7°).

As a consequence of its strong, seasonally reversing air flow, this cave shows the greatest annual range of temperature of any of the hundreds of caves observed in this study. Note the extremes of deviation from MAST at locations H and D in July and February (outside temperatures approximately 34°C and -3°C respectively). Certainly a temperature of 0.6°C 350 m inside an Alabama cave requires exceptionally strong circulation of outside air. This reading, and the high summer temperature at H, are all the more surprising since the cave passages slope in the "wrong" way: down from K between J and I, and up from A to D. Both readings are attributable to the dramatic impact of the negative pressure created by air exiting such a large cave-in summer cool air pours out of the bottom entrance in such a quantity that warm air is "sucked" in the upper entrance and down the slope. In winter the reverse occurs, when warm (relative to outside) air escaping through the upper entrance creates a partial vacuum which "sucks" cold air into the lower entrance and deep into the cave. Lower outside temperatures in January undoubtedly produced below-freezing temperatures as far in as site D.

Cave number 2 of Figure 2 is a nearly horizontal, two-level tube which, according to Barr (1961), ends at point F. Mean annual surface temperature is probably 12°C or slightly below; temperature recording stations within 70 km on opposite sides from the cave have MASTs of 12.4 and 13.4°C, but the cave is at a higher elevation than either station. This cave is a good example of how knowledge of cave temperature variation can lead to prediction of undiscovered sections. Our observations of a seasonally reversing air flow (into the known entrance in winter and out of it in summer) strongly point toward the existence of a second, previously unsuspected entrance. Furthermore, the direction of flow requires that the second entrance be higher in elevation than the one known, making this cave an example of Type 7, Figure 1. The tell-tale air flow is quite strong in the stream passage beyond point E, indicating that this passage leads toward the undiscovered entrance. Further evidence of a second entrance can be seen in the relative fluctuations of air and wall temperature in the cave, to be discussed later. Given postulation of this second entrance, the pattern of temperatures observed within the cave are what would be expected. Location A shows the lowest January reading and the greatest January to August fluctuation, with B, H, and G following in decreasing order. This follows the flow pattern of cool dense air from the entrance, and the entire lower cave level is a cold air trap. It is not as cold as might be expected; cold air settles into this low area, but it is warmed by the stream which pools there before disappearing in a sump. Note the cooling effect of the lower cave on the stream, which enters the known cave (near E) at 12.0°C and progressively cools to 11.2°C at L C is little affected by air from either entrance; it is too high relative to the known entrance to be cooled in winter, and too distant from the other to be greatly warmed in summer. Warm summer air being drawn into the upper entrance evidently has been cooled approximately to MAST by the time it reaches the known cave. D is an example of a relatively constant-temperature room such as Z, cave type 7, Figure 1. Distance from the warm air (upper) entrance, plus small volume, prevent it from being a warm air trap. Temperatures at F are slightly lower than the presumed MAST, indicating that it is probably nearer to the known cooling entrance than to the undiscovered upper one; its overall temperature stability, however, is indicative of its isolation from both entrances.

The above two caves illustrate the impact of seasonally reversing air flow in multi-entrance, multilevel caves. Cave number 6 of Figure 2 illustrates a more subtle example of seasonally reversing air flow. Its moderately large, sloping entrance, simple structure, and the distribution of volume both above and below entrance level allow year-round air flow through the single entrance. When outside temperature rises above internal cave temperature, cool air spills out the bottom of the entrance. The "negative pressure" so created enhances movement of warm air through the upper part of the entrance into the upper sections of the cave. The size of the entrance is sufficient to allow the two opposing streams of air to pass simultaneously, and they are easily detected by an observer. In winter the relatively warmer cave air will rise through the entrance, being replaced by denser, colder air from outside (air flow arrows would reverse directions). In this type of cave, relative velocities of flow, summer versus winter, depend on the amount of volume above versus below the entrance.

It is important to note that the two ends of the cave will have their major circulation at different times. The lower end will have greatest air flow in winter, and be a cold air trap in summer; the upper end will have greatest air flow in summer and act as a warm air trap in winter. Periods of temperature stability (deviating from MAST in opposite directions within the same cave) will be much longer and more predictable in this cave than in caves 1 or 2 of Figure 2. The range of temperatures between points C (below MAST) and D (well above MAST), and their relationship to MAST and the outside temperature illustrate the difference between the two "trap" areas. The narrow, undulating passage creates a relatively stable MAST regime beyond F. On the day of observation there was no detectable air flow at B and C despite the rapid movement of air above. The outward moving flow of air along the ground outside (1.5 m below the point registering 26.7°) was 18.4°C.

Nonreversing Air Flow -- Cave number 3 of Figure 2 illustrates the impact of having all of the cave volume above entrance level. Its air flow pattern is like that of Type 5, Figure 1, although its elevational rise is only slight. The room containing C and D is a warm air trap, as demonstrated by an August temperature considerably in excess of MAST. Despite strong winds which buffet the entrance from across a large reservoir, the large entrance size (2 m high by 11 m wide), the cave length of only 76 m, a direct, relatively unobstructed path from the entrance to the innermost volume, and its relatively small total volume, this cave does not become cold in winter; the warm air is trapped and very little flow occurs. Even at the end of a record cold winter in 1977, location D remained slightly above the local MAST. If there were a strong upward slope between points B and D and/or if the volume from C to D were greater in an upward direction, this cave's winter temperature would be even higher. Nevertheless, its annual average is well above that expected based on MAST.

Some of the most remarkable thermal gradients known to occur in caves are found in those which have "sack" structures similar to that illustrated in type 4 (Figure 1). A cave located in eastern Tennessee (see Figure 3), where the MAST is approximately 14°C illustrates this. Entrance A, just above the rim of a large sinkhole, slopes upward into the main chamber; entrance C, located 11 m below the rim in the bottom of the same sink, slopes down into the cave. Entrance B, slightly below C, opens directly into the main chamber. In summer, cooled air from the upper portion of the chamber spills out into the sink, which acts as a large dam. Consequently, on 18 July 1976, when the outside temperature at the rim of the sink (site 1) was 23.6°C, the temperature near the bottom of the sink (site 2), outside entrance C, was 14.0°C (approximately MAST). A thermal range of 6.7 (site 3) to 23.5°C (site 4) existed in the main chamber (35 m tall, 54 m long and 12 to 20 m wide). A mild negative pressure created by the escape of cold air probably aids in drawing warm summer air in through A and B; the temperature at the very top of the room may have been even warmer than that recorded at site 4. Though slight air flow is possible in summer, the cave's only strong air flow is limited to periods of cold winter weather. Multiple entrances and its greater overall volume above the highest entrance and below the lowest one, allows this cave to function as a more efficient cold and warm air trap than cave 6, Figure 2.

Data from a second cave of very similar structure illustrate an annual temperature cycle in such a cave (Figure 4). Again, there is an elevational increase (roughly 35 m) from the bottom of the cave's main, large room to the cave's upper entrance. In this cave the main entrance room is 46 m long, 18 m wide and 15 m high, with several major passages extending out to the sides and downward. A single large canyon passage approximately 25 m tall and 1.5-2 m wide connects the lower cave to an upper room that is approximately 27 m long, 18 m wide and 4 m high. The upper room exits to the surface at a level about 1 m below its upper end through an entrance less than 1 m in diameter. The larger lower room is entered through either of two entrances near the upper end of its ceiling, both of

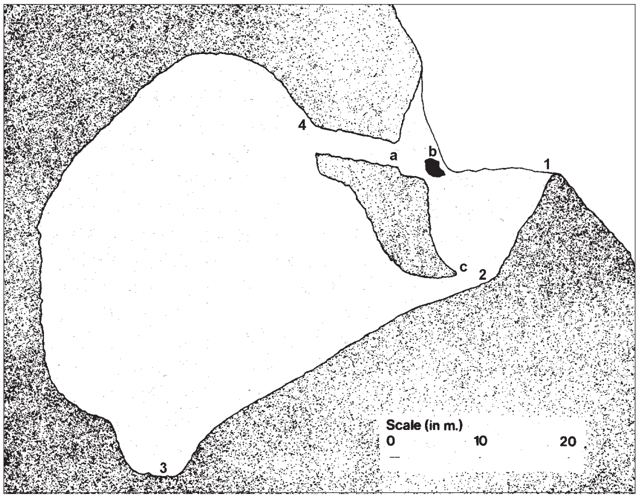

Figure 3. Cross section of an eastern Tennessee cave which acts as both a cold and warm air trap. Air circulation is greatest in winter.

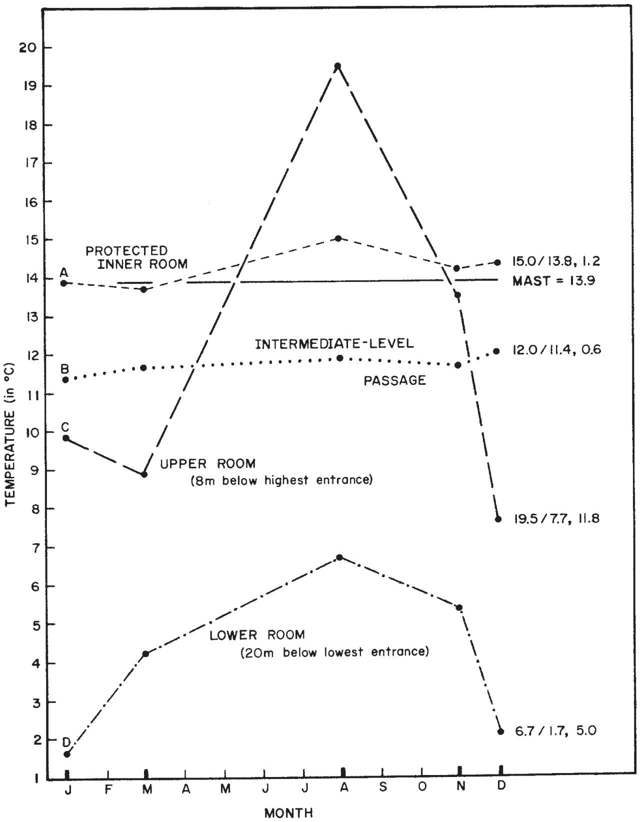

Figure 4. Air temperatures (maximum/minimum, number of degrees in the range) at four sites in a northeastern Tennessee cave on 18 November 1975, and 13 January, 9 March, 1 August and 20 December 1976. The cave is similar to Type 4, Fig. 1, with the addition of a warm air trap near entrance B. MAST = mean annual surface temperature.

which average about 1 m wide by 2 m high. Though this cave is more complex than the last, it serves as another good example of the fourth type shown in Figure 1.

The record of air temperature from location A (Figure 4) in this cave is from a deep, inner room, protected from air flow by a very narrow irregular passage and several vertical turns that act as ideal dams (as in Figure 1, example 2) against flow of either warm or cool air. As expected, air temperature there closely approximates MAST and shows an annual fluctuation of only 1.1°C. Even this small fluctuation is thought to have been caused by the occasional use of the room as a roosting place for several thousand bats. Location B was in a major side passage roughly half way between upper and lower levels of the cave. Here air temperature varied by only 0.6°C, despite relatively free circulation of air, but constantly was below MAST. Site C was located in the uppermost room 18 m from the upper entrance. At this location small amounts of cold air "leaked" in, lowering temperatures in winter, while slight summer loss of cool air from the lower entrances created sufficient negative pressure to draw warm outside air down into the room, resulting in a nearly 12°C annual fluctuation. The temperature record for site D, located near the bottom of the main, lower room, 40 m from the lower entrances, shows an annual fluctuation of 5°C with the annual high temperature still 7.3°C below that expected based on MAST. Its large volume below the lowest entrance makes this main room an exceptionally efficient cold trap.

As in the previous example, the lower entrances were surrounded by a deep sinkhole which reduced loss of cold air. Summer air movement was slow enough that it was detected only at the small upper entrance. During cold winter weather a strong flow of cold air enters the lower entrances, while relatively warm air exits through the single upper entrance.

Air Flow Prevention -- As previously discussed, lack of elevational differences between multiple entrances, small entrance size (particularly in single-entrance caves), and natural dams can reduce or nearly eliminate air circulation. When these characteristics are present, singly or in combination, the result generally will be caves or sections of caves with the relatively constant temperatures of popular legend.

Cave 5 (Figure 2) provides a very simple example of the impact of a small entrance. The entrance passage into this cave includes a 5 meter-long horizontal section that is only ¼ m in height and 1.5 m wide. With an enlarged entrance, this cave would be of type 1 (Figure 1) and would fall well below MAST in winter, yet due to its restrictive entrance size and shape, its average air temperature on 6 February 1976 was less than a degree below MAST. The 18.8°C temperature near the lowest point in the cave may have reflected the impact of cold surface water flowing into the sinkhole entrance during winter rains. A prominent factor in reducing air exchange with the outside in this cave is the cross-sectional shape of the entry passage. If the passage were simply turned 90°, placing its greatest width in a vertical plane, this cave's annual temperature fluctuation likely would increase considerably. Warm and cool air could then exit and enter simultaneously.

Surface Wind -- Cave 4 (Figure 2) of this study illustrates the relative ineffectiveness of surface wind, even on a tunnel-like cave only 17 m long with two entrances (4.9 m wide by 1.4 m high and 3.5 m wide by

0.8 m high). Although a 15 KPH surface wind was blowing in the same direction as the cave passage, the air temperature in this cave at 1700 on 6 February 1976 was more than 71 below the outside temperature and approximately 5°C below MAST. Despite this cave's small size, simple shape, relatively large entrances, and its directional orientation, the surface wind had only moderate impact; slight directional air flow along the cave ceiling in the expected direction was noted, and the 3° difference between air and wall temperature demonstrated that a relatively rapid rise in air temperature had occurred during the day. This cave and cave 3 (Figure 2) demonstrate that surface winds probably have little effect on any but the smallest and simplest caves.

EFFECT OF WATER ON CAVE TEMPERATURE

A central Tennessee cave with a single vertical entrance (6 m deep and 4 m in diameter; located in the bottom of a shaded, 8-m-deep sinkhole) provides an excellent example of the potential impact of surface water on cave temperature. A 100-m section of passage below the entrance averages 11 m wide and 3 m tall and would be expected to have an average air temperature below the mean annual surface temperature of 14°C. Even if air circulation were poor, a cave below such a single sinkhole entrance should not exceed MAST. However, on 30 July 1976 we found that the air temperature 90 m inside the described large passage was 21.1°C, some 7°C above MAST. This could be accounted for only by the presence of a large stream flowing through the main passage below the cave entrance. Though the stream clearly fluctuates in size, at the time of our visit it averaged 7 m wide, 0.25 m deep, and was flowing rapidly.

At its point of entry, the water temperature was 21.3°C (0.2°C warmer than the air 2 m above), but 90 m downstream it already had lost 0.1°C to the surrounding cave. Cave air at that point (nearly directly below the entrance) was 20.3°C. Approximately 100 m farther downstream the air temperature was 19.4°C. At this point an upper level passage, averaging about 2 m in diameter, slopes very slightly upward and continues for at least 100 m, and probably much farther. Air temperatures near the ceiling 25 and 75 m into this side passage were 17.2 and 15.3°C, respectively. At 95 m, just past the first downward dip in the passage, the air temperature near the floor was 14.3°C, approximating the expected temperature based on MAST. Clearly, the high temperature of this cave's stream had measurable impact on the cave's air temperature, even at a considerable distance beyond the main stream passage. Due to the structure of the cave's single entrance, it is very unlikely that warm air entered from outside.

While working in caves of northwest Florida in winter, we repeatedly observed not only the impact of cold surface water, but also that of deep pools of subterranean water. Two caves less than 5 km apart illustrate these temperature differences. On 3 February 1976 the first cave was approximately half-full of surface water from winter rains, and the water temperature was 11.4°C. Air temperature 1.5 m above the water ranged from 11.3 to 12.4°C. The second cave, visited 5 February 1976, sloped sharply downward from its 2-m entrance and bad an easily detected flow of cold air along its floor, with warm air exiting along the ceiling. Despite these characteristics (which favored entrapment and storage of cold air) its air temperature 28 m inside and 1.5 m above a pool of water roughly 30 m long, 12 m wide and more than 12 m deep ranged from 16.6 to 17.8°C. The water was of subterranean origin, and its temperature was 19.9°C, only 0.1°C above the MAST reported by a nearby weather station.

RELATIONSHIP BETWEEN AIR AND WALL TEMPERATURE

Wherever air in a cave is isolated from the external atmosphere it should come into thermal equilibrium with surrounding cave walls. As already noted, the locations of such protected places are highly predictable, as are the locations of probable large differentials between air and wall temperatures. The magnitude of difference in air and wall temperature provides a test of one's assumptions regarding constancy of temperature for any given location: areas of assumed constant temperature should show consistent equilibrium of air and wall temperatures. (It should be remembered, however, that even areas of great fluctuation may frequently exhibit air/wall temperature equilibrium, for example, during sustained periods of minimal air flow.)

Air/wall temperature differences should be greatest near cave entrances where air enters. Near such "sucking" entrances, air temperature should average above wall temperature in summer, while it should average below wall temperature in winter. However, these expected differences will decrease with distance of air flow through a cave, so that even

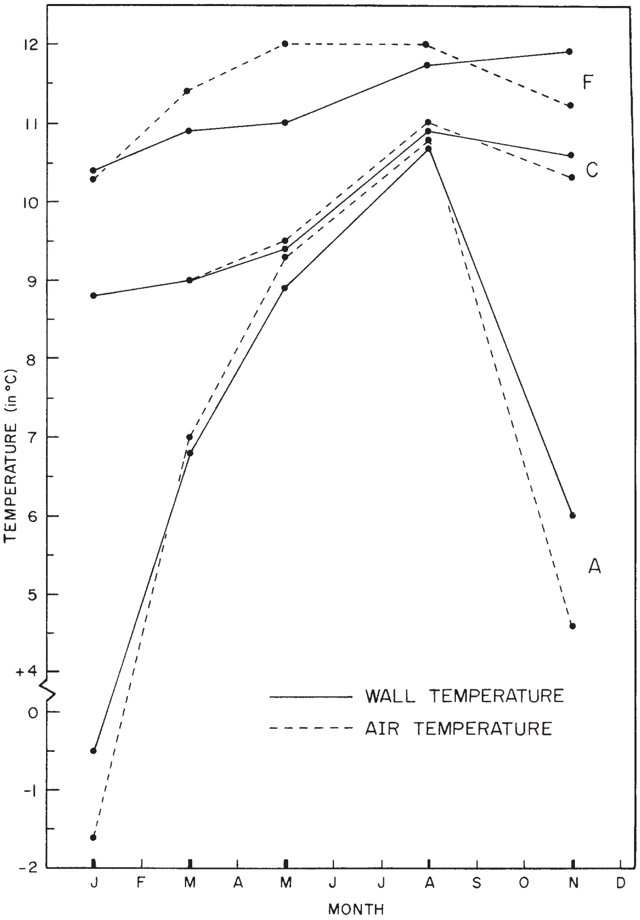

Figure 5. Air and wall temperatures through a seasonal cycle at 3 sites in cave number 2, Fig. 2. Dates of the measurements are 15 November 1975, and 10 January, 6 March, 16 May and 18 August 1976.

rapidly moving air exiting through distant entrances may have reached equilibrium with surrounding walls. Accordingly, analysis of air/wall temperature differences (Figure 5) in cave 2 of Figure 2 provided additional evidence in favor of the existence of a second, unknown entrance, as noted previously. Near the known entrance (site A), which "sucked" air in winter, the greatest differences between air and wall temperatures occurred in November and January (air temperature below wall temperature). Differences were very small in March, May, and August (with air slightly higher than wall in temperature, and both still below MAST), when the entrance was "blowing." The reverse was true at site F near the end of the known cave, on the way to the undiscovered entrance; the greatest difference occurred in May (air higher than wail temperature), and the least in January. Clearly, "warm" air was passing this location during the spring on its way from the undiscovered to the known entrance. The relative slowness of wall temperature response to air temperature fluctuations is pointed out by the August-November and January-March readings at sites A and F where air temperature drops below wall temperature with the beginning of cold weather, and rises above wall temperature in spring. Finally, site C, which is relatively isolated from either entrance and from air flow (as noted previously), exhibits the expected minimal air/wall temperature difference.

When comparing differences in air and wall temperatures it is important to remember that, regardless of season, both the amount and direction of air flow will be determined by the amount and direction of differences between inside and outside temperature. These differences may fluctuate widely, not only as a result of the passage of storm fronts, but also on a daily basis, due to night-day changes. Although we visited the respective locations of temperature measurement in cave 2 at approximately the same time of day each visit (to maximize comparability of readings among visits), we recorded several day-to-day and within-day fluctuations between air and wall temperatures at location A in order to illustrate the potential extent of such fluctuations.

On 28 December 1976 the air temperature in front of the known entrance was +8.6°C at 1145 hr and -2.8°C at 2250. At 1200 the air temperature at location A was fluctuating from 5.8 to 6.1°C, and the wall temperature was 3.9°C. (Unfortunately no temperatures were recorded at location A at 2250.) Clearly, outside temperatures during the previous night had fallen well below freezing, and the cave walls, cooled by that incoming night air, were now being warmed but were still cooling incoming air to below the higher daytime temperature.

The reverse situation is well illustrated by data from the following exceptionally cold day. At 1250 on 29 December 1976 the outside temperature was -6.1°C, and at 1935 the temperature had fallen to -8.2°C. Inside the cave at 1300 the air temperature at location A was fluctuating from -3.3 to -2.9°C, and the wall temperature was 0.8°C. At 1925 the air temperature at this site had continued to fall, varying from -4.7 to -4.5°C, and the wall temperature was -1.4°C. On this day continually falling outside temperature prevented the situation recorded on the previous day when inflowing air was warming the cave walls. On the second day incoming air ranged 2.1 to 3.3°C lower than wall temperature, as opposed to 1.9 to 2.2°C above wall temperature on the previous day. The first day's data are undoubtedly more representative of average daily cycles.

These data probably can explain the contradiction between our findings and those of several previous authors who claimed that wall temperatures in caves are normally about 1°C lower than that of adjacent air masses (Twente 1955; Nieuwenhoven 1956; Hall 1962; McNab 1974). These researchers limited their investigations to winter studies of hibernating bats. Bats normally hibernate in caves whose structures act as cold air traps, and such caves tend to take in more and colder outside air at night than during the warmer days. By mid- or late morning, when researchers generally arrive at their caves, air flow often has slowed considerably and may have stopped altogether. Nevertheless, the last air drawn in was probably considerably warmer than the coldest night air, leading to the observation that air temperatures are generally higher than those of adjacent walls.

RELATIONSHIP BETWEEN AIR MOVEMENT, TEMPERATURE, AND HUMIDITY

A thorough study of cave humidity and the subtle interrelationships between humidity and the many factors that may bear upon it is far beyond the scope of our research. We did, however, make sporadic comparisons among humidity, temperature, and air movement in 10 of the caves investigated. Substrate type, ground moisture, and the presence of streams or standing water all contribute to basic cave humidity levels. Superimposed upon these basic factors, rates of air flow, nearness to a "sucking" entrance and the humidity and temperature of air entering from outside compared to existing cave conditions were found to be of importance in determining daily and seasonal patterns of humidity.

Regardless of season or temperature of the inflowing air, relative humidity was lowest near the entrance where outside air entered. A gradient of increasing relative humidity existed between the places of entry and exit of the flow. Further, in caves with seasonally reversing air flow, passages that have low relative humidity at one season may have high relative humidity at another. These patterns are illustrated by our recordings from cave 2 (Figure 2). On 10 January 1976 when air movement was past locations A, B, H, G, and E, in that order, sample relative humidities were as follows: B – 49 percent; halfway between H and G – 82 percent; halfway between G and E – 86 percent; halfway between E and D (upper cave: air flow nearly nonexistent) – 98 percent. The movement of outside air through the cave clearly affected relative humidity levels along its route. On 16 May, when the direction of air flow had reversed (passing from E to D, C, B, and A), the relative humidity halfway between E and D had dropped as expected (to 88 percent). No other measurements were taken on that visit.

Strong air flow has been considered by some to be closely associated with low humidity throughout a cave (Vandel 1965; Barr 1968). Although it is true that air flow often can be a desiccating influence, particularly near "sucking" entrances in winter, ground moisture or areas of water can increase relative humidity of even strongly flowing air to near saturation as it passes through the cave. For example, despite the fact that troglobitic trechine beetles are limited to areas where the relative humidity is 98 percent or above (Barr 1959), a number of individuals of three species have been observed feeding in a "wind tunnel" in a Kentucky cave where the air flow exceeded 40 m per minute (Barr 1968). Barr seemed puzzled by this apparent contradiction, but we suspect that the contradiction was only apparent-as we have pointed out, rapidly moving air in caves is not necessarily dry. One of us (Tuttle) once made a similar observation of trechine beetles in a "wind tunnel" in a Kentucky cave; the relative humidity was 98 percent, despite the strong air flow.

In reference to the relationship between the total volume of air flow through a cave system and the cave's humidity, it also is important to note that air flow rates will vary greatly in different sections of the cave even along the main route of flow. For example, in a single passage, diameter and shape may vary dramatically, so that a given volume of air flow through the area would be rapid and potentially very influential on humidity in a narrow section while remaining virtually undetectable in a very large area. Within the parameters discussed in this section, however, our limited data indicate that overall patterns and timing of relative humidity changes are largely correlated with, and dependent upon, predictable daily and seasonal patterns of air flow.

Finally, although it is usually relative humidity which is reported in the literature, it is important for cave biologists to keep in mind the distinction between this measurement and absolute humidity (mass of water vapor present in a unit volume of atmosphere). In some instances the two measurements follow the same relationship from site to site. This is the case for the cave 2 example above-absolute humidities (in the same site order, in g/m^3) on 10 January were 2.6, 7.5, 8.0 and

9.9. The 16 May absolute humidity had dropped to 8.8. In other cases, high 'relative humidities at low temperatures actually may be more potentially desiccating than lower relative humidities at higher temperatures, due to the lesser amount of water vapor present in the air in the former case. For example, in the cave discussed in Figure 4 the relative humidity at location C on 10 January 1976 was 99 percent. On 1 August 1976 it was only 92 percent. Although the August relative humidity was lower, absolute humidity was nearly two times higher 15.5 g/m^3 in August versus 8.4 g/m^3 in January. In a similar cave (Figure 3) the relative humidity on 18 July 1976 was only 70 percent in the path of incoming air (site 4), while it was 100 percent at the floor of the same room (site 3) and 99 percent just inside entrance C (where air exited very slowly). These relative humidities follow the pattern discussed in the paragraph above but, due to the great temperature gradient in the room, absolute humidities (14.1, 7.6 and 8.8g/m^3 respectively) are totally reversed in relationship among sites. Temperature of the air, due to its effect on absolute humidity, must be included in the list of factors considered in evaluating the impact of a cave's humidity regime on its faunas.

BIOLOGICAL IMPLICATIONS

Humidity is a very important environmental parameter for many terrestrial cavernicolous animals (Barr 1959, 1961, 1967; Vandel 1965). Cold dry air entering a cave in winter, as it warms inside, certainly can be a desiccating influence to organisms in that area. In particular, respiratory water loss for an animal with a body temperature warmer than the air will be more severe the greater the temperature difference. It is important to note, however, that besides the large-scale factors influencing humidity (discussed in the previous section), a number of other considerations influence the effect of given levels of air flow and humidity on organisms. The size of the boundary layer associated with a particular organism's coupling with its environment is proportional to the size of the organism and the roughness of the substrate on which the animal rests, as well as to the wind speed (see Juberthie 1969, for a cave study of microclimate). Substrate moisture in many situations, then, may be of more importance to small arthropods than air moisture. In other words, in addition to the fact that flowing air in a cave is not always dry, different organisms in a particular area of cave in fact may be exposed to very different environments-low air humidity (relative or absolute) may have little effect on a small terrestrial arthropod on a rough, moist floor compared with its effect on a bat.

Air flow, despite its potential for lowering humidity, should not be assumed to be entirely bad for most or even any cave organisms. It may be of considerable importance as a directional cue for some cave animals. Trechine beetles are reported to be highly sensitive to air flow (see Barr 1968), and two species of cave crickets (*Ceuthophilus conicaudus* and *Hadenoecus subterraneus*) are believed to use air currents in their orientation to and from cave entrances (Reichle et al. 1965; Campbell 1976; Levy 1976). Additionally, air flow and associated patterns of temperature and humidity are as predictable in many caves as are many other cues that are used by surface animals. Many cavernicolous animals are thought to be extremely sensitive to even slight changes in air flow, temperature, and humidity (Barr 1959, 1961, 1964, 1967; Vandel 1965), and the role of air flow as a seasonal or daily cue may be of major importance in some caves.

Beyond the cue effects of air movement and temperature, temperature directly affects a variety of trogloxenes (animals that live in caves but cannot complete their life cycles without leaving caves). Bats will be discussed in detail later. Our casual observations indicate that cold caves which harbor hibernating bats often additionally serve as hibernating sites for a variety of otherwise surface arthropods (e.g. culicine mosquitoes and the noctuid moth *Scoliopteryx libatrix*) that were not often found in warmer caves. On the other hand, these same cold caves rarely contained amphibians, such as *Eurycea lucifuga* and *Plethodon glutinosus* (even when relative humidity remained high), which often were abundant in other caves nearby. Even if the major effects of air movement and temperature were limited to determining the within and among cave distributions of such troloxenes as bats and cave crickets, they ultimately could exert strong indirect effects on troglobitic (animals that are so highly specialized that they cannot live outside of caves) and troglophilic (animals that often live their entire lives underground but also can live in moist places under rocks or logs on the surface) cave animals that depend on these animals as primary sources of energy.

Dependable food sources in a cave environment are of vital consequence to its fauna; whether they be guano from bats and crickets, entrance litter, or detritus from floods, supplies vary seasonally (Barr 1967). Strong selective pressure must exist for the development of responses to such available cues as changes in water temperature, pH and oxygenation (for aquatic animals), air flow, temperature and humidity (for terrestrial animals), and flooding. In fact, initial studies indicate that many troglobites, both terrestrial and aquatic, use seasonal flooding to time peaks of reproduction (see Barr 1968; Poulson and Smith 1969; Juberthie 1975, among others).

Clearly, the potential impact of the above environmental factors in determining species survival and distribution is great and the problems complex. We make no pretense of understanding more than the potential importance of these variables. It is important, however, to note the extent to which the environment of the cave depends on its exchange of air and water with the outside. Hopefully, our discussion of cave structure and the causes and predictability of daily and seasonal patterns of air flow, temperature, and humidity will act as a stimulus for much further investigation of these potentially important environmental parameters.

Temperature Constraints on Cave Bats -- For most bats, and especially for cave dwelling species, the selection of appropriate roosting temperatures is of critical importance (Harmata 1973). Twente (1955) noted that it was vital for bats to choose roosts with temperatures appropriate to the desired metabolic processes: warm for digestion and growth in the summer, and cool for torpor in the fall and winter, with the exact optimum temperatures varying somewhat among species. McManus (1974) found that hibernating Myotis lucifugus in a New Jersey mine “demonstrated a clear preference for temperatures near 20°C,” the temperature at which Hock (1951) found the species’ oxygen consumption to be lowest. Harmata (1969) demonstrated that Rhinolophus hipposideros could select “the proper temperature of hibernation” with accuracy as near as 0.8°C.

Whatever the mechanism of selection, microspatial distribution preferences and movements along temperature gradients also have been demonstrated in summer roosts of many species, with clustering playing a role in behavioral temperature regulation then as well as in winter (Licht and Leitner 1967; Harmata 1969, 1973; Tuttle 1975; Trune and Slobodchikoff 1976, among others). A number of authors have noted the high metabolic cost of the wrong ambient temperature for bats (Hock 1951; Herreid 1963; Stones 1965; Davis 1970; McManus 1974).

For cave dwelling species, caves with roosts of appropriate temperatures are limited in number. At extremely high latitudes caves may be too cold for use at any time. At somewhat lower latitudes, where MAST ranges 2 to 12°C, caves often provide appropriate hibernating quarters but are normally too cold to permit summer use. In areas of intermediate latitudes (MAST 12 to 20°C), most caves are too warm in winter and too cold in summer, and few are used by bats in any season. At lower latitudes nearer the equator, increasingly warm caves are ideal for maternity use but unsuitable for hibernation (Dwyer 1971).

Throughout most of the cavernous areas of the United States, caves are of the intermediate type with regard to temperature. Consequently, although bats may be able to utilize them in spring or fall when their temperatures may be acceptable (Harmata 1973), most U.S. caves are unsuitable for bat use for summer nurseries or winter hibernacula. Thus, those species that use caves are often severely roost limited. (The problem is compounded for species which use caves in summer, since the cave must have not only appropriate temperatures available but also must be close enough to proper feeding habitat.) Distribution of caves of appropriate temperature, then, likely plays an important role in the determination of many distributional boundaries (McNab 1974; Humphrey 1975).

For example, although numerous caves and mines exist in Utah, Twente (1960) concluded that virtually all were of inappropriate structure to provide temperature ranges essential to bat hibernation. He did not find a single suitable cave or mine among more than 500 examined. Additionally, the endangered gray bat (*Myotis grisescens*), a species which uses caves year-round, appears to be limited in its north-south distribution primarily by the absence of warm caves for rearing young in the north and by a lack of cold hibernating sites in southern caves (Tuttle 1975, 1976). Few caves anywhere within its range provide roosts of appropriate temperature, and even in Alabama, where gray bats probably were once most abundant, this species is not known to have ever occupied more than 2.4 percent of the area’s 1635 known caves in summer or 0.1 percent in winter (Tuttle 1979). This is despite the fact that this species is behaviorally able to reduce thermoregulatory costs during summer by clustering together in large numbers in ceiling domes or in restricted passages where heat can be trapped (Tuttle 1975), thereby utilizing otherwise marginal caves.

Since most U.S. caves are in the intermediate, unusable range of temperature, cave bats generally are forced to select the very few caves that have structures permitting them to deviate well above MAST (for summer use) or below (for winter use). Structures of caves chosen for winter hibernation are easily predictable. Except at high latitudes or elevations, they almost invariably fall into categories 1, 4, 6 or 7 (Figure 1). Of these, Type 4 is by far the best. Without a cold air trap, Type 6 does not provide adequate stability. A midwinter period of outside warmth could prove highly detrimental to bats (many of which cannot go out to feed) hibernating in a simple cave of this type. A small, simple cave of Type 1 could prove equally unsatisfactory in an unusually cold winter. Accordingly, among the eight largest bat hibernating caves known in the Southeast, five are of Type 4 and three are Type 7. All of these occupied caves are large and have structural complexity adequate to provide temperatures ranging from near freezing to 12 to 15°C.

Summer maternity roosts usually are restricted to heat traps, especially in caves of Type 6 (if a trap exists) and 5 and 7 (where the rooms marked "X" probably would be best). *Myotis grisescens*, despite its ability to heat summer roosts by aggregating in large colonies, still prefers caves of these types; one of the largest maternity colonies ever known existed in Cave 3 (Figure 2), a Type 5 cave. Although few observations of summer cave colonies of *Corynorhinus* (*Plecotus*) *rafinesquii* have been made, the several maternity colonies observed by us in southeastern caves each numbered fewer than 200 individuals. Such small colonies lack the ability to heat roosts of marginally low temperature, and as might have been expected, each was located in a heat trap of the kind illustrated by Xs in Types 5 and 7 (Figure 1). Temperatures in these roosts were all between 21° and 25°C, although MAST ranged only 14° to 16°C. Other examples could be presented, but it is sufficient to point out that bats must either abandon caves during the maternity period, seek exceptionally efficient heat traps near cave entrances, or heat their cave roosts by clustering together in very large numbers on domed ceilings (a strategy for which any benefit must be balanced against the cost of increased intraspecific competition for food). Successful growth and survival of young gray bats depend on the success of one of the last two strategies (Tuttle 1975).

Finally, the ideal bat cave is generally one which offers a large thermal range. Ability to move among temperature zones within a cave can allow bats to control embryonic development (thereby synchronizing parturition time Racey 1969; Dwyer and Harris 1972), to achieve deeper torpor when stressed by inclement weather during summer or when fat acquisition becomes important in late summer, or to adjust to temperature fluctuations throughout a season or between years. Obviously, structural and elevational complexity and increased cave size generally will contribute to this desired thermal range. Tall canyon passages often provide especially suitable temperature gradients for winter hibernation.

It is rare for any one cave to provide sufficient thermal complexity for year-round occupation; seasonal migration between caves is usually necessary for bats which use caves year-round (see Tuttle 1976). Two caves discussed in this paper, however, are important to bats both in winter and summer. The cave (discussed in the section on Nonreversing Air Flow) from which the readings in Figure 4 were taken houses one of the largest winter populations of Myotis grisescens known, as well as a sizeable summer bachelor colony of the species. The hibernation roosts are in areas of the cave which are protected from freezing but are well ventilated by cool winter air; the summer roosts are in warm areas much higher in the cave.

The second such cave, Cave 1 of Figure 2, contains the largest summer colony of *Myotis grisescens* known. The main roost, located in the dome-like area around H, is warmed by the summer air sucked in from entrance K by the strong air circulation discussed previously, and by the body heat of the colony of 128,000 bats (formerly more than 250,000). In winter, the appendix-like area (F), due to its configuration and location, traps and stores air of low temperature, providing a hibernation roost of relatively constant temperature for a number of bat species, including *M. grisescens* and *M. sodalis.*

MANAGEMENT IMPLICATIONS

Choosing Caves for Protection **--** Clearly, knowledge of cave structure and its relation to temperature and humidity is of potentially great importance in predicting species distributions within and among caves, and in determining the relative merits of any given cave for protection. Data on such factors as number, size, shape and location of entrances, internal passage size, contour and slope, distribution and amount of volume relative to cave entrances, and source and amount of water flow (if any), can be used to predict and/or verify the probable seasonal temperature and humidity regime of a cave.

Given the limitations of resources, time and manpower, it often is important to establish criteria for recognition of caves of special or unique merit. Obviously no single structural type can be singled out for exclusive protection, since each cave type presents a potentially different setting for the evolution of different faunas and survival strategies. In fact, a wide variety of cave types should be protected. For example, caves that are good for bat hibernation may not be good for some terrestrial cavernicoles, and vice versa. Frequently the object of cave protection is centered around one or two endangered species. In such situations it is vital to ascertain not only the species' temperature, humidity, and other microhabitat requirements, but also its food requirements and sources when relevant, in order to guarantee that all important parameters are adequate.

For bats, when food supply availability and other external variables are equal, caves of greatest structural and therefore thermal complexity generally are best. Nevertheless, in the case of maternity colonies, where warmth is of primary concern, even simple caves (for example cave 3, Figure 2) may be of great importance. Also, in the case of endangered bats, their present usage of a cave often is not a reliable indicator of its suitability for use. The best caves often have been heavily disturbed and now contain very few bats. On the other band, other nearby caves, of very marginally suitable temperature but less disturbed, may contain more bats. In many cases the most important cave, in terms of the species' long-term survival, is the one that presently has few bats.

A good example is illustrated in Figure 3. As a result of this cave's popularity with local cavers, it has not housed major bat populations for perhaps as long as 50 or more years. Although no bats were present at the time of our visit, scattered recent droppings indicated that some bats continue to visit the cold area at night in the summer and probably in the fall. If the cave were protected, it could potentially become an important bat hibernating site, as it undoubtedly once was prior to disturbance. In addition to its cold trap characteristics, which make it suitable for hibernation, there is evidence (in the form of feces) in the warmest area which indicates that some bats continue to attempt to use the area as a summer roost. Similarities with known roosts suggest that the species involved may be *Corynorhinus* (*Plecotus*) *rafinesquii*. In this case as in many others, then, the cave's structure and resulting environment can tell more about its importance to bat populations than does its present degree of usage. This is almost certain to be true for caves valuable to other animals as well.

Means of Protecting Caves -- Knowledge of factors affecting cave environments also is of great importance in determining the proper means of cave protection. In a number of instances, improper gating of caves has reduced or destroyed the bat populations intended for protection, either through reducing free access by the bats or reducing the air flow necessary for maintenance of appropriate temperature and humidity (Mohr 1972; Tuttle 1977). Creation of additional entrances also can have disastrous results. Specific recommendations for cave protection through gating or fencing are provided by Tuttle (1977). In brief, structures which in any way alter air flow should be avoided. Any structure which blocks an entrance can affect not only air flow, but also the supply of food (in the form of entrance debris) for those cavernicoles requiring within-cave sources. In general, it is sound policy to simply avoid tampering directly with an entrance unless absolutely necessary.

It is of interest to note that alterations in temperature and humidity can have negative effects not only on cave life, but also on cave formations by altering development. Furthermore, protection or destruction of one species may influence the survival of a whole group of other species; for example, protection of a summer bat colony protects the whole guano ecosystem which may be present. Another vital factor for the public and individuals responsible for caves to be aware of is that even actions outside of caves can have great impact inside; in particular, smoke from fires built in or near an entrance can be drawn into a cave, as McCavit (1975) noted. At the very least, unnecessary disturbance is the result; at the worst, whole populations of bats and perhaps other animals may be killed.

Hopefully, this discussion of the factors influencing cave environments and our examples will prove useful to those who deal with caves in a scientific, managerial, or recreational capacity. It is apparent that, at times, lack of understanding of the many complexities involved has impeded the progress of both research and protection of faunas. Improved understanding of these factors, combined with increased knowledge of cavernicolous species habitat requirements, should provide guidelines for utilization and/or protection of valuable cave resources.

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