

STRUCTURE AND FUNCTION WITHIN THE TWILIGHT ZONE

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ABSTRACT

The twilight zone of a cave, while showing a microclimate intermediate between the surface environment and the cave aphotic zone, often has its own characteristic fauna. Thus, this zone becomes an ecological entity and can be described in relation to its structure and function. The basic ecophysiological factors of light, temperature, humidity and wind direct or influence the biological activity within this zone. A comparison can be made between the faunas of the surface, cave twilight zone, and cave aphotic zone based on responses to these factors.

Introduction

In addition to studies in other areas of the world, recent investigations into the ecology of Australian cave animals by Harris (1973) on the bent-winged bat guano ecosystem, and Richards (1971b) on the cave ecosystems of the Nullarbor Plain, have focused attention on the importance of surface and cave environmental conditions in governing the distribution and abundance of cave fauna. While Poulson and White (1969) have alluded to the stability of cave climate and the simplicity of cave communities, Harris (1970) emphasizes the complexities of the cave environment.

Because of the reality of these complexities, it is often convenient to divide a cave into zones, to study each one separately, and then to investigate their interrelationships. Instead of using combinations of varying environmental conditions, zonation should be based on a single, biologically significant, measurable, and recurrent environmental factor, and then the fluctuations of other factors should be qualified individually for each cave (Graham 1967). When using light as the deciding parameter, one can conveniently divide the cave into 3 basic zones:—

1. Entrance Zone — While being more similar to a 2-dimensional plane than a 3-dimensional zone, this region is exposed to the immediate light conditions of the surface.
2. Twilight zone — This region of the cave displays a reduced light intensity compared to the surface in a physiologically detectable range — above 10^{-7} lux (Kenagy 1976) — at sometime during a 24-hour period.
3. Aphotic zone — This is the region of constant darkness. The boundary between the twilight and aphotic zones would be determined for any 24-hour period at the maximum extent of the photic tide.

Twilight Zone

The twilight zone exhibits temporal and spatial differences of temperature, humidity and air movements, as well as light. These variations will be intermediate in extent between the great fluctuation on the surface and the relative stability of deep sections of the aphotic zone. In regards to the fauna, Culver and Poulson (1970) have characterized this zone as an ecotone — a transition between two or more diverse communities. The twilight zone complies with the definition of an ecotonal community by containing many of the organisms of each of the overlapping communities, in addition to organisms which are characteristic of, and often restricted to, the ecotone. The number of species is often greater in an ecotone than in the communities on either side, and the twilight ecotone is no exception. The specific faunal elements present in the twilight zone may be of 3 types:—

1. Surface forms — Many surface forms are adequately pre-adapted in utilizing this zone as a continuation of their normal range of ecological tolerances.
2. Aphotic forms — The deep cave's contribution would be troglaphiles and troglobites of the familiar Schiner-Racovitza classification of cavernicoles (see Hamilton-Smith (1971) for discussion on cavernicole classification). Periodically, the environmental conditions of the apho-

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tic zone will extend towards the entrance and, as a result, cave restricted species may be found in the twilight zone.

3. Twilight forms – The majority of the animals found in the twilight zone will be those forms that are distinctly its own. Animals belonging to the cavernicolous classifications of troglone and troglophile will be present, along with other animals which are difficult to categorize under the Schiner-Racovitza scheme.

Hamilton-Smith (1971) acknowledges that the twilight zone is a complex ecological domain and chooses to separate the threshold dwellers from the cavernicolous classification scheme until there is a "satisfactory overall conceptual framework" for their study. I propose in this paper a physiological approach to the study of twilight animals that should contribute to the initial development of such a framework. The physiological nature of the animals commonly found in the twilight zone will be reflective of the microclimatological structure and fluctuation of the zone. Graham (1967) suggests that the microclimate alone is not sufficient to define the biological role of a species of animal, because of the added dimensions of movement and activity. It is my contention that the daily and seasonal extremes of the twilight microclimate will dictate both temporally and spatially the movement and activity of the animals in this zone. As a result, the twilight zone becomes an ecological entity.

The following will be a cursory look at the basic general ecophysiological factors of the twilight zone, and a review of the demonstrated physiological responses of the animals that frequent the zone in comparison with the corresponding responses of surface and aphotic zone dwellers. It is hoped that such an approach to the study of cave animals will find application in the current analysis of Australian cave ecosystem and cave animal evolution.

Ecophysiological Factors

1. Light

Within any particular cave, the light intensity of the twilight zone will vary daily and seasonally depending upon the angle of the sun, cloud cover, and the state of vegetation about the cave mouth. In addition to these factors, the amount of light that enters a cave will depend upon the static factors of the cave's orientation, number and dimensions of openings, and internal cave morphology. There is an exponential decay in light intensity as one progresses into the twilight zone from the entrance. The low light intensity and resulting low diurnal variation is attractive to many photonegative animals. By being photonegative, the animals that normally reside in the twilight zone can utilize both the food supply of surface environments during nocturnal foraging and the security of the twilight zone during resting periods.

Light is considered the most important environmental cue used by animals to synchronize their activity periods (Aschoff 1960). With only low intensity diurnal variation experienced by twilight zone dwellers, emphasis is on a highly entrained circadian rhythm that initiates movement under constant darkness or extremely low light conditions. If the animal is sensitive only to high thresholds of light, synchronization can occur only during the day at the entrance during light sampling as demonstrated in bats (Twente 1955). At the entrance to a forest cave, multiple peaks and drops in light intensity may occur during the day due to vegetation cover. Thus, sampling of light in this situation might give a false indication of surface crepuscular conditions. In forest caves, an alternative would be an entrained rhythm sensitive to the lowest thresholds of light only at night, while ignoring extraneous stimuli which are delivered at inappropriate times.

Surface animals have a wide range of reactions to light and can show photopositive and photonegative responses. Photopositive surface animals might venture into a cave during foraging periods during the day, or in search of a secluded resting area at night. A photonegative surface animal could be directed into a cave as a result of its normal response away from light. For those surface animals in which an endogenous circadian rhythm (internally synchronized) has been demonstrated, it is characteristically highly entrained and maintained under constant conditions for periods slightly different than 24 hours.

For an aphotic zone dwelling animal that is geographically likely to venture onto the surface, a photonegative response is selectively advantageous. But along with the morphological regression of eyes, some aphotic animals have either lost their physiological response to light altogether, or at least their reactions are much less pronounced than twilight zone relatives. Likewise, the endogenous circadian rhythm of some aphotic dwellers has undergone regressive evolutionary changes and aper-

iodic activity is evident (Barr 1968). Even in those aphotic animals that would occasionally venture into the twilight region of the cave, the advantage of a well entrained circadian rhythm would be of no selective advantage due to the rhythm's characteristic deviation from 24-hour periods. Thus, for those aphotic animals in which a rhythm is demonstrated, it is likely to be only weakly entrained and not persist under constant conditions.

2. Temperature

Temperature within the twilight zone often varies directly with the surface temperature. But, as seen in Fig. 1, temperature fluctuations in the twilight zone become extremely reduced as compared to the surface variations. In caves with multiple entrances, extreme temperature variations are evident in the aphotic zone due to stream and air currents. Vertical thermal gradients are often established in the twilight area of caves with the formation of hot and cold air traps dependent upon the number of openings, tunnel morphology, and tunnel inclination. In the remote calm areas of a cave, the temperature will be stable at the approximate annual mean temperature for the surface locality. But even in these calm areas, Harris (1973) has demonstrated that biological factors may induce cave temperatures to fluctuate. He showed that cave air temperatures will fluctuate more than 10°C over a year in the nursery caves of the bent-winged bat due to their occupancy and departures.

Twilight animals reflect the same basic preferences and tolerances with respect to temperature as surface forms. There are two basic alternatives for adaptation to extreme temperatures – morphological and behavioural. Morphological adaptation would involve the development of mechanisms that would allow the animal to tolerate broad ranges of temperatures. A behavioural adaptation would emphasize detection of temperature extremes and co-ordination of activity with respect to the narrow favourable limits of temperature. Even though the daily and seasonal temperature fluctuations in the twilight zone are greatly reduced compared to the surface, twilight animals are potentially susceptible to lethal extremes because of their feeding tie with the surface. Thus, morphological and/or behavioural adaptations would have a selective advantage.

Mechanisms for perceiving environmental variability and for surviving in extreme conditions, as illustrated by narrow preferences and high tolerances to temperature, would be of little selective advantage for those animals that are geographically isolated in a stable environment. It is not surprising that certain aphotic zone dwellers (e.g., cavernicolous marine relics) have lost these responses in the interest of energy conservation (Elliott and Mitchell 1973). Other aphotic animals that have the potential for moving to the surface have retained their acute detection responses as mechanisms restricting them to their subterranean environment (Bull and Mitchell 1972, Mitchell 1968).

2. Humidity

As opposed to temperature, relative humidity within the twilight zone does not often vary directly with the surface fluctuation. For a small cave without a true aphotic zone (Fig. 1) the general fluctuation of humidity can follow the surface variation, but multiple peaks in humidity may occur throughout the day as a result of surface wind deflections through humid cracks. Fig 2 shows that the humidity fluctuation in the twilight zone of a larger cave can lose all synchronization with the surface due to cave airflow reversals. Prediction of surface humidities by twilight animals is complicated by occasional wind direction changes, and as a result, activity rhythms are not normally synchronized with humidity levels.

While surface forms show the same flexibility in dealing with humidity variation as with temperature, twilight zone dwellers characteristically show a very narrow preference range around the saturation point, and show low tolerance to subsaturated air, as reflected by high water loss, in dry air flow. Water loss is determined by temperature and humidity (i.e., saturation deficit) in combination with airflow. Those cryptic animals that lack the morphological adaptations to preclude water loss are attracted to areas of water infiltration, condensation, and high atmospheric moisture which are commonly found in caves.

Humidity preference and detection strategies of aphotic dwellers will reflect the generalizations made concerning temperature responses. The variation in humidity-discriminating abilities of aphotic animals centers on what range the particular species has the potential to experience and the selective advantage of its perception.

CAMPBELL – TWILIGHT ZONE

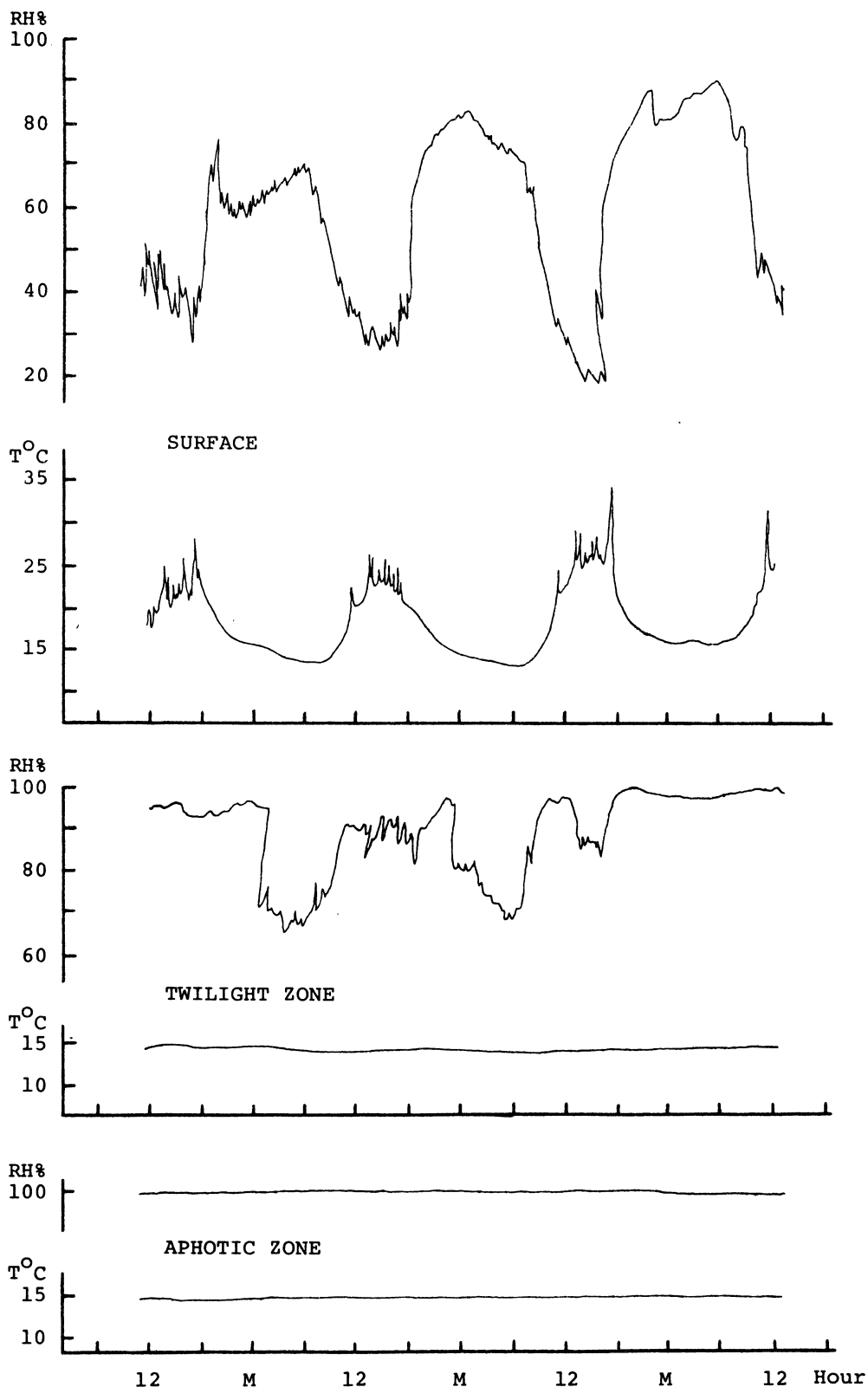


Fig. 1. Relative humidity and temperature fluctuations of the surface and twilight zone of Pipeline Cave, Tibbooburra, NSW, from 30 March to 2 April 1976. The first thermohygrograph was placed in front of entrance overhang; the second placed 7 m into cave. An aphotic zone was absent in this cave.

CAMPBELL – TWILIGHT ZONE

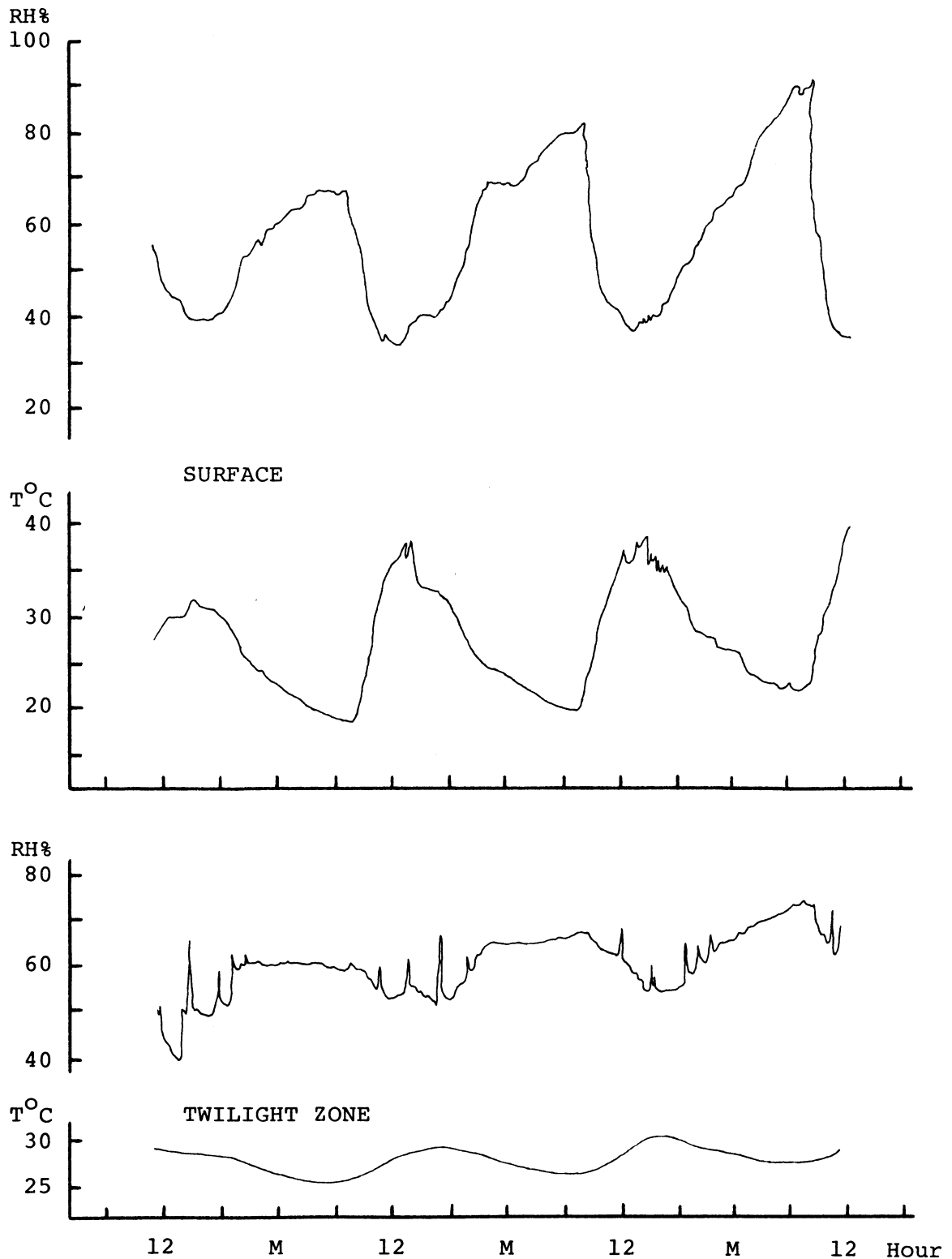


Fig. 2. Relative humidity and temperature fluctuations of the surface, twilight and aphotic zones of Barnett's Cave, Kempsey, NSW from 22 November to 25 November 1976. The first thermohygrograph was placed on the surface 1 m from entrance; the second was placed 3 m into cave; the third placed 15 m into the cave.

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TABLE 1: SUMMARY OF DEMONSTRATED ECOPHYSIOLOGICAL RESPONSES

(References are intended to be representative not exhaustive)

ENVIRONMENTAL FACTORS	ECOPHYSIOLOGICAL RESPONSES		
	Surface	Twilight	Aphotic
LIGHT Preference	photopositive (Gelderloos, 1976) photonegative (Kenagy, 1976)	photonegative (Twente, 1955)	photonegative (Ginet, 1960) photoneutral (Breder, 1944 in Vandel, 1964)
CIRCADIAN RHYTHM Entrainment	highly entrained (Thines & Ermengem, 1965)	highly entrained (Voute, Sluiter & Grimm, 1974)	weakly entrained (Lamprecht & Weber, 1975) not entrained (Ginet, 1960)
TEMPERATURE Tolerance	high (Cloudsley- Thompson, 1962) low (Spotila, 1972)		high (Ginet, 1960) low (Ginet & Mathieu, 1968)
TEMPERATURE Preference	broad (Gardefors, 1966) narrow (Toye, 1966)	broad (Thibaud, 1970*)	broad (Elliott & Mitchell, 1973) narrow (Mitchell, 1968)
HUMIDITY Preference	broad (Gunn & Cosway, 1938) narrow (Spotila, 1972)	narrow (Spotila, 1972)	broad (Bull & Mitchell, 1972) narrow (Derouet, 1960)
WATER LOSS Rate	high (Herreid, 1969) low (Loveridge, 1968)	high (Packer, 1963)**	high (Derouet, 1960)

* edaphic form

** burrowing form

Conclusions

This simplified review of the environmental structure of the twilight zone shows the complexities with which the twilight animals must contend. Cave environmental studies by Roussett (1967), Andrieux (1970 a,b,c) and Barr and Kuehne (1971) give excellent descriptions of the conditions of diverse cave systems. The physiological responses by twilight animals, while being no less complex, reflect their adaptations to the cave environment. Table 1 summarizes the range of a few ecophysiological responses exhibited by surface, twilight zone, and aphotic zone animals. The references included in the table serve as examples of studies that have demonstrated these responses. Surface and aphotic zone animals exhibit a wide range of physiological responses; the former as a result of their susceptibility to gross environmental extremes, and the latter as a result of the evolutionary adaptations to different selection pressures. Twilight animals appear to be more homogeneous in their responses. Perhaps this is only a reflection of the paucity of physiological studies on ecotonal animals. I am certain that physiological studies on cavernicolous animals will be an important tool for modern biospeleologists. The following are a few of the immediate areas in which physiological studies may contribute:

1. How similar are twilight animals to "pre-adapted" animals of epigeal environments (see Barr 1968)?
2. Are morphological characters regressed before physiological characters under the same selection pressures (see Wiley 1973)?
3. Are Australian second-level troglaphiles (Hamilton-Smith 1971) physiologically troglobitic?
4. To what position(s) in the cavernicolous classification scheme should species of the Family Rhaphidophoridae be relegated (see Hamilton-Smith 1971, 1972 and Richards, 1971a)?

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