ACTIVITY RHYTHM IN THE CAVE CRICKET,

CEUTHOPHILUS CONICAUDUS HUBBELL

by

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INTRODUCTION

This paper describes and analyzes the movements of a population of the cave cricket Ceuthophilus conicaudus Hubbell inhabiting Spider Cave (Carlsbad Caverns National Park) in southern Eddy County, New Mexico. Field data were obtained during July and August 1974 to ascertain both the specific activity exhibited by this population and the environmental conditions of the hypogean and epigean environments that might have directed or influenced the activity. Laboratory data supplemented the description of the activity as to its nature under constant and varying conditions. Hubbell (1936) delineated the range of C. conicaudus as the arid Plains Section of western Texas, Oklahoma, and southern New Mexico; Reddell (1966) and Barr and Reddell (1967) confirmed the collection of this widespread species in the caves of Carlsbad Caverns National Park.

Relative to surface environments caves are more stable with respect to light, relative humidity, and temperature. Troglobites (obligate cavernicoles) and troglophiles (facultative cavernicoles) are subject to little climatic fluctuations. On the other hand, troglloxenes (cavernicoles which return to the surface periodically for food) encounter two basically separate environments; one of constancy in

the cave and one of fluctuation on the surface.

Cave crickets, commonly troglloxenes, have been found and studied throughout the world. Leroy (1967) reviewed research prior to 1967 concerning the biology, morphology, and evolution of cavernicolous Orthoptera. The role of the cave cricket in energy input into cave ecosystems has been suggested by several authors (Park and Reichle, 1964; Mohr and Poulson, 1966; Barr, 1968; Mitchell, 1971). Field studies by Nicholas (1962) on Hadenoeus subterraneus (Scudder) (Ceuthophilinae) of North America, and Richards (1965a, b) on Gymnoplectron and Pallidoplectron (Macro-pathinae) of New Zealand and Australia demonstrated nocturnal activity rhythms for these crickets in response to surface environmental factors. Their results did not include statistical analysis of activity of crickets in relation to climatic conditions (inside and outside the cave). The only laboratory study of cave cricket activity was made by Reichle, Palmer, and Park (1965) on H. subterraneus. This study demonstrated a persistent endogenous activity rhythm while the crickets were maintained under constant conditions. There were, however, no data on the activity of cave crickets under varying light or hunger conditions.

STUDY AREA

Spider Cave (W 104° 15': N 32° 10'), located at the bottom of a canyon of intermittent drainage off Walnut Canyon directly west of the Carlsbad Caverns entrance, is at the edge of the Chihuahuan desert. King (1948) described the geology of the area, including age of the rock in which the cave is excavated, time of uplift, and process of cave formation.

Dates written on formations within the cave suggest there was access to the cave in the early 1930's. Carlsbad Caverns National Park files indicate that a large flood in 1941 completely covered the entrance of Spider Cave with gravel. The entrance was not relocated until 1958. In 1959, Park officials elevated the entrance about five feet from the floor of the canyon to protect it from future floods. At that time an iron grill was placed over the entrance to limit access.

A preliminary survey of Spider Cave was begun in 1958. A more detailed survey is currently being made by the Guadalupe Cave Survey. Based on a preliminary map provided by this Survey along with a personal survey, a detailed map of the front section of the cave is presented in Fig. 1.

At the entrance there is a 3 m vertical drop to a low crawlway proceeding to the northwest for 18 m. The crawlway

Fig. 1. Map of cricket-occupied section of Spider Cave in Eddy Co., New Mexico. Study stations are designated by solid triangles.

SPIDER CAVE

joins with the main walkway passage of the cave through an extended constriction known as the Keyhole. At this point are two passages leading northeast and northwest that are blocked by fill after 21 m and 20 m respectively.

The main walk passage continues from the Keyhole to the west, then southwest. This passage measures approximately 30 m long; width is 2.5-3.0 m with most of the passage about 3 m wide. The ceiling is about 2.5 m high throughout the passage and marked with many domes in the form of a series of "bone-yard" formations. The floor of the main walkway is covered with flood-washed silt and gravel with the addition of large breakdown slabs. The walk passage is congested at its southwest end by flowstone. This is a very wet area of the cave with a small pool at the base of the flowstone. A crawlway at the side of the flowstone proceeds to a labrynth of crawl and walk passages connected to the more extensive inner part of the cave.

METHODS AND MATERIALS

Field Study

Stations were established within Spider Cave at the entrance, along the crawl tunnel, and along the walk tunnel at varying intervals (Figs. 1 & 2). Station A was on the surface at the entrance to the cave. A thick metal grill perforated by approximately thirty 1/2-inch dia. holes covered the entrance. This station was in an exposed area at the bottom of the canyon. Station B was located in the initial crawlway about 2 m from the inner lip of the entrance drop. Station C was situated at the entrance side of the Keyhole at the northernmost end of the crawl tunnel. Station D was in the walk tunnel 2.5 m from the "inner" Keyhole. Station E was established in the main walk tunnel 12 m from the Keyhole.

Air temperature and relative humidity were continuously recorded with two Belfort hygro-thermographs (sensitivity: 1%, $<1^{\circ}\text{C}$) at Stations A and D, and periodically taken using a mercury thermometer and a motorized psychrometer at Stations B and E. Tunnel air temperature and rate of air movement were taken at hourly intervals at Station C with an Anemotherm air meter (sensitivity: 1°C , 1 FPM). Direction of air flow was determined hourly at the entrance with small pieces of tissue paper. Barometric pressure

- Fig. 2. Field stations established in Spider Cave:
- I. Station A, view of metal grill covering entrance.
 - II. Entrance shaft, view looking up.
 - III. Station B, view looking from crawl tunnel towards entrance.
 - IV. Station C, view looking from crawl tunnel towards Keyhole.
 - V. Station D, view looking from walk tunnel into "inner" Keyhole.
 - VI. Station E, view looking down walk tunnel.

I

II

III

IV

V

VI

was continuously recorded at Stations A and D with two Taylor barographs (sensitivity: 1 in Hg). Measurements of illumination were taken periodically throughout the crawl tunnel and continuously at the surface during dusk and dawn with a General Electric light meter (sensitivity: 1 fc). Surface observations of weather conditions such as precipitation, surface wind, cloud cover, and moon phases were recorded nightly.

Preliminary observations indicated that C. conicaudus left the cave through a small notch in the rock (7.5 cm x 2 cm) immediately under one side of the entrance grill. It was at this point (Station A) that an electronic counter (Smith and Campbell, in prep.) was positioned to monitor the number of crickets leaving and returning to the cave.

The detector part of the apparatus consisted of two small 2.2 volt bulbs placed side by side just under the lip of the grill at the notch in the rock. The bulbs directed two red filtered light beams across the 5 cm opening onto two photocells. The light emitters and photocell were adjustable on four bolts anchored to rock. Interruption of both light beams caused a drop in the photocell current which, with amplification, activated two mechanical counters. It was necessary for both beams to be interrupted for a corresponding count; thus, adjustment of the distance between beams could provide size discrimination. Beams placed 2 cm apart could only be interrupted by an animal over 2 cm long, whereas smaller animals

would not be counted. Directionality of movement was obtained with a circuit flip-flop, which directed the electrical impulse to the appropriate counter depending on which light beam was interrupted first. Even though the counter accurately estimated the number of crickets leaving the cave, it did not represent accurately the number re-entering (most of the crickets enter the cave through the base of the entrance during the morning hours). The counters were checked hourly throughout the night, and the number of crickets leaving recorded.

Multiple factor analysis and regression techniques were used to determine the relative importance of a number of epigeal and hypogean climatic parameters on the dependent variable, number of crickets leaving nightly, for a 10-day period from 3 July to 13 July. Eight climatic variables considered were: (1) surface temperature, (2) surface humidity, (3) tunnel temperature taken at Station C, (4) surface barometric pressure, (5) cave barometric pressure taken at Station D, (6) number of hours each night that wind was leaving the cave, (7) velocity of wind into the cave, and (8) velocity of wind out of the cave.

A factor analysis was made on the climatic variables to reveal interacting patterns of climatic variation. Values for the climatic variables for each of the ten days were obtained by calculating the mean of the readings for

the hours that crickets left the cave. Factor scores were derived from the factor analysis.

A step-wise multiple regression program was performed using the factor scores of the climatic data as the dependent variables and the number of crickets appearing each night as the independent variable. In this manner, the contribution of different climatic variables to the variation of cricket number could be assessed.

Cricket movement was monitored at Station C by an activity sensing device designed for detecting movement across two 75 cm x 2 cm metal strips of brass shim stock. These were secured to the ceiling of the Keyhole parallel and 1 cm apart. From previous observations it was noticed that C. conicaudus moved through the Keyhole and crawl tunnel on the ceilings and walls. Very little movement took place on the floor.

The recorder consisted of a six-volt battery supply, amplifier circuit, electromagnetic stylus, and a clock driven drum. The resistance caused when a cricket touched both strips simultaneously allowed an electrical impulse to pass through a four-transistor amplifier and initiate movement of the electromagnetically operated stylus which made a corresponding ink mark on a 24-hour clock driven drum. Cricket sensitivity to the current upon completing the circuit of the two metal strips was investigated in the

lab prior to using it in the field. Voltage was reduced to the point of no visible effects on the crickets.

Individual movements, population levels, and distribution of crickets within the cave were further investigated between 20-23 August by the use of a color-coded marking system. An approximate 3 m² ceiling quadrat was marked off at Station E. Encompassed adult C. conicaudus were marked with an orange paint dot on the pronotum and/or hind femurs. A 2.4 m² ceiling quadrat at Station D was also delimited, and these crickets marked with blue paint. Crickets in a single ceiling dome at Station B were marked with green paint. A few specific crickets in all the quadrats were painted so as to be individually identifiable. The paint used in all cases was a "glow-color" enamel with the addition of a small amount of Tween 80, a surface activator. Painted laboratory crickets retained the mark for weeks.

Morning (0600) and evening (1800) censuses involved searching the crawl tunnel and main walk tunnel. The total number of mature C. conicaudus was noted on each census, with special attention given to the color and exact location of all marked crickets. These censuses showed daily population fluctuations and movements of specific groups of crickets.

Laboratory Study

Crickets used in this study were collected in Spider Cave during the months of July, August and September 1974. Upon capture they were placed immediately in light-proof polystyrene foam containers and transported to the laboratory where subsequently they were maintained in an environmental chamber of constant darkness at a constant temperature (21°C). Red-filtered light was used during the capture and transference of the crickets from the light-proof containers to the environmental chamber.

Activity of both males and females was recorded under constant darkness, constant bright (approx. 50 fc) light, and alternating twelve hour periods of light and darkness. The two hunger conditions of food present and food absent were also tested during constant darkness.

The activity chambers used were basically as described by Wiley and Mitchell (in lit.). Movement against a suspended paddle completed an electrical circuit. This movement was registered on an Esterline Angus recorder. The recorder serviced all 10 activity chambers simultaneously.

The substrate used in the containers consisted of a mixture of silt and sand from Spider Cave. Porous rocks were provided in each container as a retreat for the crickets. Increased relative humidity and a constant

water source for the crickets were maintained in the activity chambers by a piece of moist sponge affixed to the lid of the containers. For those trials with food present, the crickets were fed commercially prepared dry dog food placed randomly in the containers. It was replaced at approximately 2 week intervals to avoid fungal contamination.

Activity of individual crickets was expressed as the number of two minute intervals in which any movement was indicated on the continuously fed chart. Individual crickets were placed in eight of the ten activity chambers, with the two empty chambers serving as controls. A total of three trials were run. Reserve crickets replaced the previous eight crickets after each trial. Prior to their respective trials, the reserve crickets were kept in constant darkness with food available. The first trial under constant darkness lasted 18 days, with food available the first nine days and food removed the last nine days. The second trial was run under constant bright light and the third trial under alternating periods of 12 hours in bright light and 12 hours in darkness; each lasted nine days.

RESULTS

Field Study

The number of crickets leaving the cave each hour of the 10-day period between 3-13 July is represented in the histograms of Fig. 3. The periodic nature of the emergence is evident, with movement out of the cave beginning each night at about 2000 (MST), a period of nocturnal activity, and a long period of diurnal inactivity. There were significant differences ($P < .01$) between the total number of crickets leaving the cave during the hours of the day. An average of the 10 nights showed that 91% of the crickets left the cave between 2000 and midnight, with absolutely no emergence during the daylight hours between 0600 and 1800.

A typical night (9-10 July) saw the emergence of 781 crickets, with the first appearing at 1955. Between 2000 and 2100, a total of 140 crickets had emerged; the majority appearing in the latter half of the hour. The greatest number of crickets, 389, emerged between 2100 and 2200. Emergence during this time was characterized by spurts of 5-10 crickets. The hour between 2200 and 2300 indicated a moderate emigration of 164 crickets, whereas the hour from 2300 to midnight showed a low of 62. During the next four hours, only 25 crickets left the cave.

Fig. 3. Nocturnal emergence of C. conicaudus at entrance to Spider Cave, 3-13 July 1974. Data are based on electronic counts recorded at hourly intervals. Total emergence for each night is indicated by (N).

At 0400 the first cricket re-entered the cave through the electronic counter. For almost an hour prior to that time, there was cricket activity around and near the entrance. From 0400 to 0600, 11 crickets were counted entering the cave. Approximately three times that number were observed to enter the cave via the air holes in the grill, and an even greater number entered the cave at the base of the entrance wall.

Periodic hourly observations indicated that the electronic counter not only gave an accurate indication of the relative movement out of the cave, but also a reliable representation of the number of crickets emerging each hour. Multiple electronic counts due to cricket congestions at the counter were, more often than not, compensated by crickets leaving through the air holes in the grill.

The number of crickets leaving the cave (Fig. 3) was found to be significantly different between nights ($P < .05$). There was a range from the high of 1195 crickets leaving the cave 7-8 July to a low of 110 leaving 3-4 July.

Climatic conditions of the surface and cave environments were investigated with regard to their influence on this nightly fluctuation of the total number of crickets leaving the cave. The hourly recordings of surface, tunnel

and inner cave temperature and humidity, surface and cave barometric pressure, and wind velocity and direction are given in Appendixes A-C. To give an adequate indication of weather conditions during the emergence of the crickets, averaged hourly (2000 to midnight) values for the various climatological factors for each of 10 nights were used in the analysis.

The eight environmental variables used in a factor matrix gave correlation values as seen in Table 1. The rotated factor matrix (Table 2) yielded three distinct environmental factors. Factor I is an axis combining the wind variables (average velocity in and out of the cave, and direction of wind) with tunnel temperature and surface barometric pressure. Factor II is a factor reflecting surface temperature and surface relative humidity. There is an inverse relationship seen in their correlation matrix with humidity decreasing as temperature increases. Factor III is a cave barometric pressure factor.

In the multiple regression analysis (Table 3), using factor scores for the three climatic factors, a total of 63% of the variation of the number of crickets emerging nightly during the 10 days was explained. Of this percentage, the surface temperature and humidity (Factor II) accounted for 45%, and Factor I accounted for 14%. The remaining component (Factor III) accounted for only 4%.

TABLE 1

CORRELATION MATRIX OF EIGHT ENVIRONMENTAL VARIABLES OF SPIDER CAVE

	Surface Temp. 1	Surface Humid. 2	Tunnel Temp. 3	Surface Press. 4	Cave Press. 5	Wind Into 6	Wind Out of 7	# Hours Into 8
1	1.000							
2	-0.755	1.000						
3	0.738	-0.360	1.000					
4	0.293	0.027	0.739	1.000				
5	-0.119	0.094	0.235	0.719	1.000			
6	0.371	0.015	0.827	0.710	-0.198	1.000		
7	-0.645	0.316	-0.941	-0.804	-0.363	-0.852	1.000	
8	0.784	-0.572	0.885	0.685	0.310	0.717	-0.921	1.000

TABLE 2
 ROTATED FACTOR MATRIX OF EIGHT ENVIRONMENTAL
 VARIABLES OF SPIDER CAVE

Variable	Factors		
	I	II	III
Surface temperature	0.395	-0.905	-0.080
Surface humidity	0.013	0.872	-0.008
Tunnel temperature	0.853	-0.451	0.128
Surface pressure	0.736	-0.032	0.600
Cave pressure	0.168	0.120	1.078
Wind velocity into	0.975	0.002	0.026
Wind velocity out	-0.876	0.367	-0.248
# hours wind into	0.711	-0.595	0.258

TABLE 3

SUMMARY OF STEP-WISE MULTIPLE REGRESSION OF ENVIRONMENTAL
FACTOR SCORES ONTO NUMBER OF CRICKETS
EMERGING NIGHTLY AT SPIDER CAVE

Step	Variable entered	Multiple R	Multiple RSQ	Increase in RSQ
1	Factor II	0.674	0.454	0.454
2	Factor I	0.770	0.593	0.138
3	Factor III	0.796	0.634	0.041

Figs. 4-11 suggest the associations found in the multiple regression analysis by graphically comparing the nightly averages of the climatic values with the total number of crickets appearing each night.

A fourth component not included in the factor matrix or regression analysis was moonlight. The restricted lower range of the light meter did not permit quantitative measurements of moonlight intensity. Observations of moon phase and cloud cover, however, do give a fairly accurate picture of relative moonlight intensity. Moonlight and cloud cover for each of the nights were plotted and compared with nightly variation of cricket appearance (Fig. 12). This fourth factor may account for some, if not all, of the unexplained variance seen in the multiple regression analysis.

Analysis of environmental conditions at the time of the appearance of the first cricket each night suggested the factor that might trigger emergence. At the time of the first emergence there is a high deviation of climatic values between the different nights for surface temperature, surface humidity, tunnel temperature, wind velocity and direction, cave barometric pressure, and surface barometric pressure (Fig. 13). Conversely, light intensity variation between the nights is quite low, leading one to suspect a key role played by this factor in initiating cricket

Fig. 4. Nightly average surface temperature of Spider Cave, 3-13 July 1974. Dotted line indicates nightly cricket number fluctuation. The scale for temperature has been inverted.

Fig. 5. Nightly average surface relative humidity of Spider Cave, 3-13 July 1974. Dotted line indicates nightly cricket number fluctuation.

Fig. 6. Nightly average tunnel temperature (taken at Station C) of Spider Cave, 3-13 July 1974. Dotted line indicates nightly cricket number fluctuation. The scale for temperature has been inverted.

Fig. 7. Nightly total number of hours wind leaves Spider Cave, 3-13 July 1974. Dotted line indicates nightly cricket number fluctuation.

Fig. 8. Nightly average wind velocity into Spider Cave, 3-13 July 1974. Dotted line indicates nightly cricket number fluctuation.

Fig. 9. Nightly average wind velocity out of Spider Cave, 3-13 July 1974. Dotted line indicates nightly cricket number fluctuation.

Fig. 10. Nightly average surface barometric pressure of Spider Cave, 3-13 July 1974. Dotted line indicates nightly cricket number fluctuation.

Fig. 11. Nightly average cave barometric pressure (taken at Station D) of Spider Cave, 3-13 July 1974. Dotted line indicates nightly cricket number fluctuation.

Fig. 12. (A) Total nightly cricket emergence compared to (B) relative moonlight intensity as determined by cloud cover and moon phase. The solid black bars represent moon phase and the stippled bars cloud cover.

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Fig. 13. Environmental factors at the time of the first cricket emerging from Spider Cave, for 3-13 July 1974. Ordinates reflect approximate total factor variation during field study.

- A. Surface temperature
- B. Tunnel temperature (Station C)
- C. Wind velocity (Station C)
- D. Light intensity at surface
- E. Surface relative humidity
- F. Cave barometric pressure (Station D)
- G. Surface barometric pressure

appearance to the outside. At approximately the same time each night as the light intensity quickly diminished (2000), the first crickets emerged from the cave.

Investigations into the movement of individuals within the cave were facilitated by the use of the metal-strip activity recorder (6-9 July) and a marking census (20-23 August). Fig. 14 illustrates those hours that any movement through Station C occurred as indicated by the activity recorder. Each day two nocturnal periods of movement, 2200-0200 and 0500-0900 were evident, with a corresponding lack of movement during the "daylight" hours, 0900-2100. Directionality of cricket movement could not be detected with this recorder.

The marking census technique gave an indication of more generalized movements throughout the cave (Table 4). Morning censuses showed a continuous distribution of new elements of the population along the crawl tunnel. Evening censuses indicated an aggregation at Station B with sparse distribution along the crawl tunnel. Station D appeared to be a transition area having a constantly large aggregation of crickets with elements of the population moving to this station from the entrance area and the main walk tunnel. Station E maintained a localized population of crickets that exchanged individuals only rarely.

Fig. 14. Hourly movement through Station C (Keyhole) in Spider Cave, 6-9 July 1974, as indicated by the metal-strip activity recorder.

TABLE 4

DISTRIBUTION OF MARKED *C. conicaudus* IN SPIDER CAVE, 20-23 AUG. 1974.
DESCRIPTION OF CENSUSES IN TEXT.

Distance from Entrance (meters)	Total Marked Aug 20 PM	Number of Marked Insects Recovered August			
		21 AM	21 PM	22 AM	22 PM 23 AM
0-5 Station B	27 Green (G)	3 (G)	1 (G)	1 (O)	1 (B)
5-10		3 (B)	8 (B)	4 (B)	
		6 (B)	13 (B)	13 (B)	4 (B)
10-15				1 (O)	
15-20 Station C		13 (B)		1 (B)	3 (B)
		15 (B)	1 (B)	10 (B)	1 (B)
			1 (O)	1 (O)	3 (B)
20-25 Station D	337 Blue (B)	182 (B)	40 (B)	17 (B)	8 (B)
		5 (O)	2 (O)	3 (O)	1 (O)
25-30		3 (B)	1 (B)	6 (B)	2 (B)
				1 (O)	
30-35		7 (B)	3 (O)	5 (B)	3 (O)
		5 (O)			
35-40 Station E	117 Orange (O)	38 (O)	39 (O)	17 (O)	14 (O)
		6 (B)	8 (B)	3 (B)	1 (B)
40-		4 (O)	1 (O)	1 (B)	

Individually marked crickets and periodic observations indicated a three-day movement from Station E to Station B. Movement to the Keyhole from Station E was gradual, with almost a full day pause at Station D. Movement through the Keyhole occurred during the second night, with the crickets occupying a section near the entrance of the cave (Station B) by morning. As the third night approached, the crickets had moved to a place just below the grill and emerged that night. This generalized pattern of movement of marked individuals was occasionally modified with a longer stay (two nights) at the entrance drop.

Laboratory Study

Mean hourly values for nine days of activity of eight (4♂, 4♀) C. conicaudus in constant darkness with and without food available are shown in Fig. 15. There was a highly significant ($P < .01$) difference in activity between those crickets having food available throughout the runs and those without food. An 95% increase in total activity was noted for those crickets without food. When food was available, periods of increased activity during the middle of the night were indicated, with 85% of all the activity between 1800 and 0600. In the hunger state more activity occurred throughout all hours of the day, but was still concentrated (73%) between 1800 and 0600.

Fig. 15. Hourly activity of eight crickets under constant darkness with and without food available. The solid black histogram represents the condition with food and the stippled without food. Activity is expressed as the number of two-minute periods in which activity occurred.

There were no significant differences in the activities of the two sexes.

Fig. 16 shows the results of the activity of eight crickets under normal (LD 12:12) and constant light conditions. Food was continually available to all individuals throughout both trials. A period of pronounced activity around midnight was evident under the LD 12:12 cycle as similarly noted under the constant darkness conditions. However, in the normal LD 12:12 cycle, there was a more dramatic reduction in activity as the light was turned on. There was virtually no activity (4%) during the 0700 to 1900 lighted cycle as compared to 15% for the same period under constant darkness. Light appeared to be a definite retardant. With the onset of darkness in the LD 12:12 cycle, there was a corresponding dramatic increase in activity. During the nine-day run under constant light, there was a drastic reduction in activity. That which did occur was of a completely random nature without concentration in any particular time periods. Crickets remained concealed under or within their rock retreats throughout much of this trial.

Fig. 16. Hourly activity of eight crickets under normal (A) and constant (B) light conditions with food available. Top bar represents the light cycle for the normal light condition (LD 12:12). Activity is expressed as the number of two-minute periods in which activity occurred.

DISCUSSION

This study demonstrated a persistent endogenous rhythm in C. conicaudus. Laboratory experiments showed the rhythm to be retained under constant conditions, while field studies have demonstrated the influence of various environmental factors on the expression of the rhythm. Internal oscillators are assumed to control the rhythm, while external elements (light intensity, surface relative humidity and surface temperature) are important as synchronizers or entraining agents.

Minimal fluctuations of environmental conditions occurred in the inner areas of the cave (along the walkway). It is in this area that one would expect the least correlation between movement and environmental factors. In fact, the intrinsic condition of hunger appears to have been the stimulator of activity in this area of environmental constancy. The laboratory study demonstrated that those crickets maintained under constant environmental conditions in a hunger state experienced greater and earlier activity than those crickets having food available. Reichel et al. (1964) postulated that hunger also is a phasing mechanism for Hadenoeus subterraneus and determines the particular night that any one individual will leave the cave.

Evidence of a rhythmic movement of C. conicaudus within the cave was revealed by the metal-strip activity recorder at the Keyhole. This recorder showed C. conicaudus to move through the cave only during evening, night, and early morning hours. A cyclic environmental factor also was evident at the Keyhole. Direction of air movement fluctuated with air moving into the cave during the evening and alternating in and out several times during the night, while during daylight hours air only exits the cave. Air velocity and direction is evidently controlled by the interaction of cave and surface barometric pressure. The sudden reversal of air into the cave through the Keyhole at the inception of the crickets' endogenously stimulated movement could have served to orient cricket migration. Reichle et al. (1965) had postulated that direction of air currents may account for the orientation of H. subterraneus in White Cave, Mammoth Cave System. An orientation device would be of a high selective value in a labyrinth cave with an obscure opening into the entrance tunnel as seen in Spider Cave.

Cricket movement along the crawlway did not culminate in immediate emergence from the cave. There was a 12 hour delay at the entrance drop until the following night. This two day migration from the inner cave to the entrance is in contrast to single night movements described in

previous investigations (Nicholas, 1962; Richards, 1965a, b). While at the entrance drop, the crickets were susceptible to a wider range of climatological fluctuations. In the early evening hours, when the crickets again showed a tendency to move, they occupied an area directly below the grill where surface ambient environmental conditions could be directly detected before departing from the cave.

Emergence of C. conicaudus corresponded closely with the time of sunset. It appeared that light was a retardant to activity with no crickets leaving the cave before light intensity had approached 0 foot-candles. Under the LD 12:12 laboratory condition cricket activity was sharply delineated by the turning on and off of the lights. Constant light drastically reduced activity, and all indication of periodocity was lost. One would expect a species shielded from light intensity fluctuations in nature, as in the case of this cricket, to exhibit little endogenous entrainment in constant light conditions. Richards (1965b) suggested that movement of Pallidoplectron turneri was initiated by rapidly changing light intensity at dusk and dawn. In C. conicaudus emergence is clearly initiated by decreasing light intensity with increasing intensity impeding activity.

Variation in total number of crickets emerging each night suggests a possible relationship of the animal with

a number of environmental factors. It was evident that certain surface and cave climatic variables were highly correlated. A factor analysis resolved these correlations, and factor scores provided a new set of variables (combinations of correlated climatic variables) that could be analyzed as to their influence on nightly emergence activity. Of the statistically analyzed variables, surface temperature and humidity were most important in explaining cricket level variation between nights. Surface temperature and humidity are closely related with humidity proportionally decreasing as the temperature rises. Peak cricket emergence occurred on those nights with the highest relative humidity and a corresponding low temperature. On those nights with low relative humidity, cricket movement to the outside was reduced.

Hesse, Allee and Schmidt (1951) stressed the role of humidity in controlling the distribution of animals. The presence of a waxy or greasy layer, which provides a high degree of resistance to water loss to the epicuticle of some insects, has been demonstrated in a few orthopterans. Cave crickets as a group are normally associated with dark damp micro-habitats, perhaps because they lack such a waterproofing layer. If so, low temperature and high humidity would seem prerequisites for maximum emergence.

It is clear that more data are needed to resolve the varying degrees of tolerance to humidity and temperature found between surface and cavernicolous insects.

A complex consisting of cave wind variables and tunnel temperature explained little (14%) of the cricket emergence variation. The variation that was explained probably centers on the relatively high correlation between the number of hours that wind was entering the cave and cricket appearance. As was suggested for the inner cave area of the Keyhole, evening reversal of wind into the cave might have stimulated movement towards the direction of the entrance.

During the field study rhythmic daily variations in surface barometric pressure were demonstrated with a sharp drop in pressure at approximately 0700 and a gradual increase beginning at 1800. Superimposed upon this daily pressure cycle were the changes brought about as a result of the approach and withdrawal of weather fronts (thunderstorms) on several occasions during the study. Surface atmospheric pressure was shown to have played no direct part in influencing nocturnal cricket levels. Wellington (1946) has suggested that either increases or decreases in atmospheric pressure affect some insects by influencing development, ecdysis, feeding, oviposition, and locomotor activity. Insects sensitive to barometric pressure are

often characterized as possessing tympanal organs (as in the case of migratory locusts). Since crickets of the Family Rhaphidophoridae lack tympanal organs, it is not surprising that barometric pressure has no direct effect.

The interaction of cloud cover and moon phases in affecting moonlight intensity had a definite relationship to cricket activity. Peaks in cricket activity during the study period corresponded to the nights with little moonlight. Cave crickets, as observed in the laboratory and in the field, are quite strongly negatively phototactic. This avoidance behavior, as similarly seen in other nocturnal animals, is likely a mechanism to evade predation. During moonlit nights of the field study period, much scorpion activity was present at the entrance to Spider Cave. Decreased activity was of an advantage to the crickets on those particular nights. As opposed to a direct influence, the correlation of moonlight intensity and cricket activity may be due to other factors which are associated with periods of cloudiness (i.e., reduced surface temperature and high relative humidity). However, the results found in the laboratory with a very reduced cricket activity under constant light tend to support a more direct influence of light (moonlight) intensity on the cricket activity levels each night.

Having left the entrance of the cave, the crickets dispersed into the sparse vegetation of the canyon floor. It is believed that this nocturnal activity is for feeding purposes. Subsequent analysis of stomach content revealed a conglomerate of both animal and plant material. Foraging activities for C. conicaudus normally continued into the early morning hours, at which time much activity was noticeable around the entrance with individuals entering at the base. Observations from within the entrance shaft indicated that the crickets filter through cracks of the rock wall into the cave.

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APPENDIX

- A. Temperature recorded at Spider Cave, 3-13 July 1974.
- B. Relative Humidity recorded at Spider Cave, 3-13 July 1974.
- C. Barometric pressure and wind velocity recorded at Spider Cave, 3-13 July 1974.

APPENDIX A. Temperature recorded at three stations of Spider Cave, 3-13 July 1974.

APPENDIX A. Continued

APPENDIX B. Relative humidity recorded at three stations of Spider Cave, 3-13 July 1974.

APPENDIX B. Continued

APPENDIX C. Barometric pressure recorded at two stations and wind velocity recorded at one station of Spider Cave, 3-13 July 1974.

APPENDIX C. Continued